Mycosphaerellaceae revisited

Sandra I. R. Videira

Propositions

1. Fungal species and genera cannot be accurately identified without DNA sequence data to support their morphological characteristics.
   (this thesis)

2. Matrix assisted laser desorption ionization time of flight mass spectrometry (MALDI-TOF MS) is a valuable tool for identification of fungal species, provided they are cultured under standardized conditions.
   (this thesis)

3. The inability to identify cryptic species will prevent effective outcomes in different scientific fields.

4. The quality of biodiversity databases needs to be improved for their optimal use in biological research.

5. Citizen science, the generation of data about nature by citizens, is invaluable for wider sampling and thus plays a major role in the uncovering of hidden biodiversity.

6. Scientific research dependent on precarious workers is not sustainable and will give science a bad image as it is no longer attractive for young talents.

Propositions belonging to the thesis, entitled:

***Mycosphaerellaceae* revisited**

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Mycosphaerellaceae revisited

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CHAPTER 1

Introduction

General Introduction

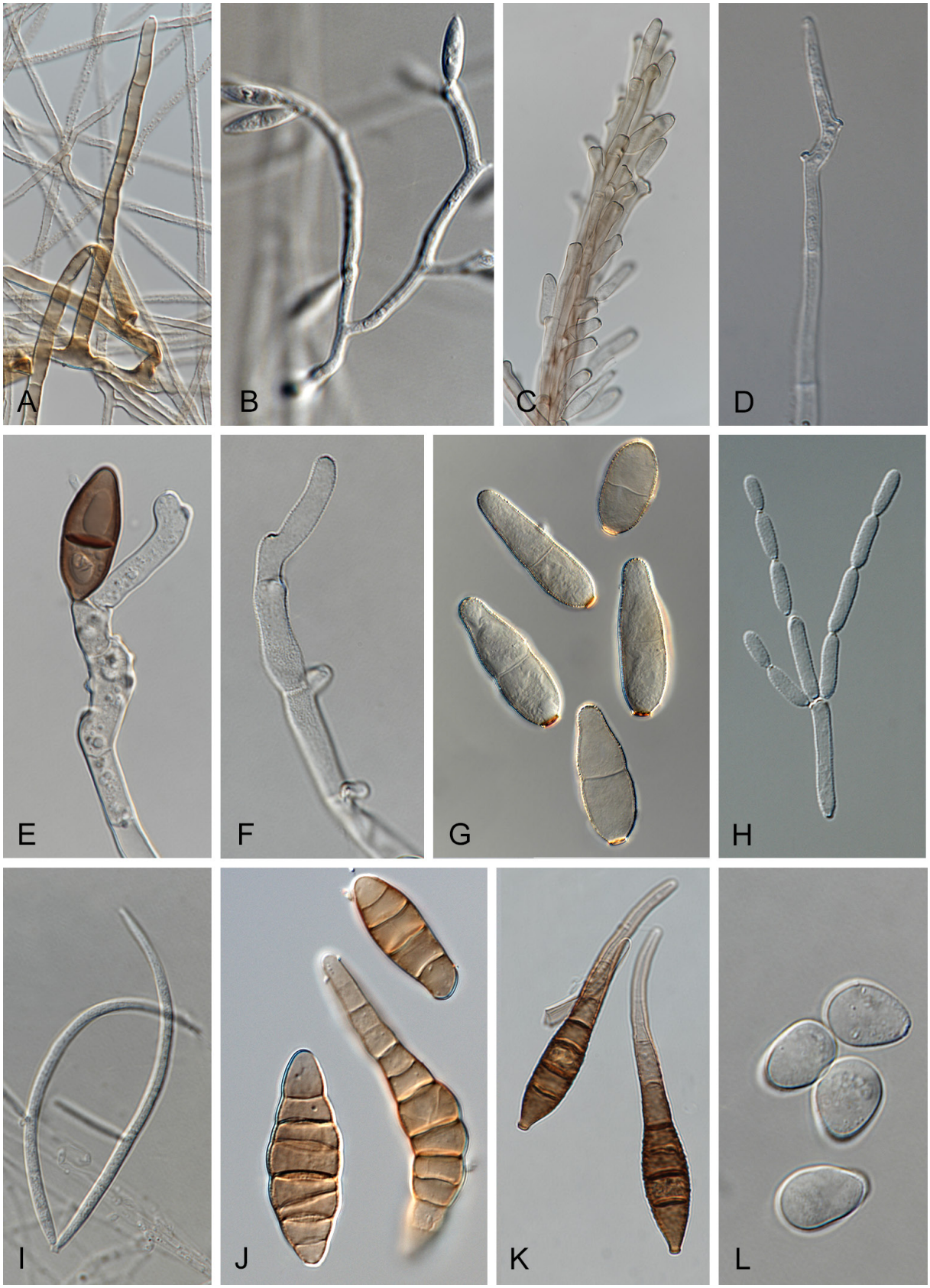
The *Mycosphaerellaceae* (*Capnodiales, Dothideomycetes*) is a genus-rich family that includes thousands of species with diverse lifestyles. Several species are plant pathogens that cause severe damage to crops we depend on for food, feed and fuel, while others are saprobes or mycophilic. Most are considered to be host-specific but a few plurivorous species are known. Multiple species often co-occur in the same lesion which often hinders their identification. Some species are only known by their sexual or asexual morphs, and links between both morphs have been experimentally proven in very few cases. Species identification of fungi is usually based on the morphology of the reproductive structures and the host it was observed on. However, with the introduction of molecular tools, especially DNA sequencing and phylogenetic analysis, a more comprehensive approach has become available for identifying or describing new species. These tools also emphasized the view that dual nomenclature in fungi was superfluous, and the International Code of Nomenclature of algae, fungi and plants (ICN) has since changed accordingly to reflect this fact (Hawksworth *et al*. 2011, Wingfield *et al*. 2012). Previous studies based on DNA sequencing supported the hypothesis that *Mycosphaerella* s. str., based on *Mycosphaerella punctiformis* (= *Ramularia endophylla*), should be limited to species with *Ramularia* asexual morphs, and that the remaining mycosphaerella-like species should be allocated to other genera (Verkley *et al*. 2004, Crous *et al*. 2009e). *Ramularia* is a species-rich genus that includes hyphomycetous species with hyaline conidiophores and conidia with thickened, darkened, and refractive conidial hila and conidiogenous loci. Recent molecular studies indicated that morphological characters were not always phylogenetically informative, and that the generic concept of several asexual genera within the *Mycosphaerellaceae* warranted revision (Verkley *et al.* 2004, Kirschner 2009).

Taxonomic history

Mycosphaerella

Mycosphaerella s. lat. (Johanson 1884b) is one of the largest genera of *Ascomycetes* and includes numerous economically important crop pathogens. Species in *Mycosphaerella* are characterised by the formation of spherical pseudothecial ascomata that are immersed or superficial in host tissue, with ostiolar periphyses, no interascal tissue at maturity, forming ascospores that are mostly hyaline and predominantly 1-septate. Based on these simple and highly conserved morphological characters more than 3 000 taxa were included in this generic complex since its

Fig. 1. Morphological characteristics of asexual morphs of genera belonging to *Mycosphaerellaceae.* A. Simple conidiophore, pigmented (*Zasmidium schini*). B. Branched conidiophore, hyaline (*Cercosporella catenulate*). C. Synnematous conidiophores, pigmented (*Mycovellosiella cajani*). D. Geniculate-sinuous conidiophore, hyaline (*Ramularia bosniaca*). E. Intercalary and terminal conidiogenous cells with multiple conidiogenous loci, hyaline (*Pseudocercosporidium venezuelanum*). F. Intercalary and terminal conidiogenous cells with a single apical conidiogenous locus, hyaline (*Pleurovularia polliniae*). G. Single conidia, pigmented (*Graminopassalora graminis*). H. Catenate conidia, hyaline (*Ramularia glechomatis*). I. Single conidia, acicular, with microconidia, hyaline (*Ramulispora sorghi*). J. Single conidia, straight and curved, dictyoseptate, pigmented (*Pantospora guazumae*). K. Conidia with apical elongated beak, septate, slightly verruculose, pigmented (*Pseudocercospora cratevicola*). L. Single conidia, obovoid, aseptate, smooth, hyaline (*Pleurovularia polinae*).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introduction (Aptroot 2006, Crous 2009c, Koike *et al*. 2011). In contrast, the morphology of the asexual genera associated with *Mycosphaerella* is quite diverse and includes both coelomycete and hyphomycete forms (Crous *et al*. 2009e). The separation of these genera relied on the variation of morphological characters such as the presence or absence of pigmentation in the conidiogenous structures, arrangement and branching of conidiophores, the conidiogenous cell placement, proliferation and scar type (conidiogenous loci), and conidial formation, shape and septation (Fig. 1). Among those, the scar type and mode of conidiogenesis were considered to be particularly important. However, many difficulties were encountered surrounding the definition of these genera based on intermediate characters, and species that exhibited more than one mode of conidiogenesis (Crous & Braun 2003).

Early phylogenies based on DNA sequencing of the ITS locus indicated that *Mycosphaerella* was monophyletic. However, with the introduction of more taxa to the dataset and additional genetic loci, subsequent research showed that it was in fact polyphyletic (Crous *et al*. 2009d, e). Further research then resulting in members of *Mycosphaerella* being allocated to different families such as *Schizothyriaceae* (Batzer *et al*. 2008), *Cladosporiaceae* (Schubert *et al*. 2007, Dugan *et al*. 2008, Bensch *et al*. 2010, 2012), *Dissoconiaceae*, *Mycosphaerellaceae* and *Teratosphaeriaceae* (Crous *et al*. 2009c, Li *et al*. 2012). From these results it became evident that the mycosphaerella-like morphology had evolved multiple times and a new circumscription of *Mycosphaerella* was urgently required.

The type species *Mycosphaerella punctiformis* was epitypified from freshly collected material and its asexual morph described as *Ramularia endophylla* (Verkley *et al*. 2004). Phylogenetic analyses based on DNA sequence data of the SSU and ITS regions grouped *Mycosphaerella punctiformis* within the genus *Ramularia* in a monophyletic group with high bootstrap support (Verkley *et al*. 2004, Crous *et al*. 2007a). *Mycosphaerella* s. str. was therefore restricted to species with *Ramularia* asexual morphs, and the remaining mycosphaerella-like species were shown to belong to other genera (Crous *et al*. 2009e).

The use of dual nomenclature in fungi has been a controversy for many years among mycologists. Having two or more names for the same species hinders research by creating confusion. The widespread use of phylogenetic analyses, based on DNA sequence comparisons, has not only emphasized the existing problems but provided the means to a solution (Taylor 2012). At the eighteenth International Botanical Congress in Melbourne, a revised ICN was put forth that ended the dual nomenclature system (Hawksworth *et al*. 2011, Wingfield *et al*. 2012). In pleomorphic fungi, priority should be given to the oldest name, regardless of its sexuality. However, for widely used names, particularly where the asexual morph names replace sexual morph names, additional considerations are needed as specified in ICN Art. 57.2. The name *Ramularia* (Unger 1833) is older than *Mycosphaerella* (Johanson 1884b) and, while *Mycosphaerella* s. lat. represents numerous genera distributed over different families, *Mycosphaerella* s. str. has *Ramularia* asexual morphs. Choosing *Ramularia* over *Mycosphaerella* requires less name changes since most established connections already have species names in *Ramularia*. Therefore, the name *Ramularia* has been selected for this genus and included in a list of protected names (Chapter 2, Wijayawardene *et al*. 2014).

Ramularia

Ramularia (Unger 1833) is a species-rich genus in the order *Capnodiales* that includes more than 1000 species with very diverse lifestyles. Most species are phytopathogenic and cause leaf spots, necrosis or chlorosis that lead to early defoliation. Disease symptoms usually develop

under conditions of high relative humidity and low temperatures (e.g. *Ramularia beticola*). *Ramularia* species can also be endophytic (e.g. *Ramularia endophylla*), saprobic or even mycophilic (e.g. *Ramularia uredinicola*). Endophytic species usually grow symptomless within the leaves and mature in overwintering leaves on the soil, releasing ascospores that can re-infect young leaves in spring. There are only a few mycophilic species described in the genus and they are usually associated with rusts (e.g. *Coleosporium* and *Melampsora*).

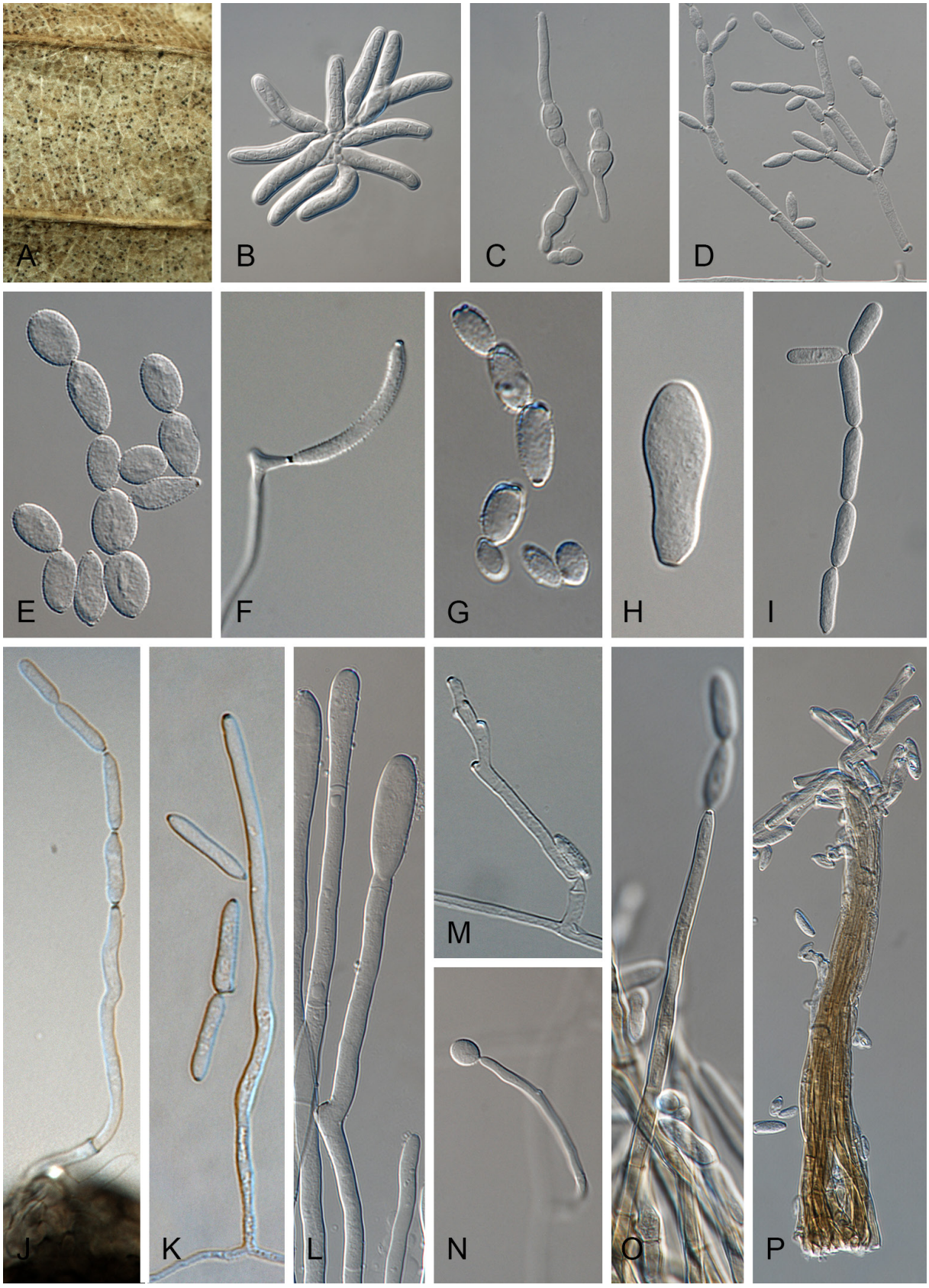
Ramularia has been monographed by Braun (1995, 1998), who defined *Ramularia* species as hyphomycetes with hyaline conidiophores and conidia with distinct, thickened, darkened and refractive conidial scars and hila (Fig. 2). The identification of species of *Ramularia* and allied genera has thus far mainly relied on host taxonomy and morphological characters such as the shape, size and septation of conidia and the type of conidiogenous loci and conidial hila. A particular emphasis has been placed on the type of conidiogenous loci (scar) and hila. *Ramularia* and allied genera were divided in two main groups: genera with conspicuous conidial scars (i.e. more or less darkened, thickened and refractive) and genera with inconspicuous conidial scars (i.e. not darkened, not thickened and not refractive). Genera with conspicuous conidial scars included *Cercosporella*, *Neoovularia*, *Phacellium*, *Pseudodidymaria*, *Ramularia*, and *Ramulariopsis*, while genera with inconspicuous conidial scars included *Neoramularia* and *Pseudocercosporella*. These characters are variable and the conidiogenous loci and conidial hila are difficult to distinguish using light microscopy (Kirshner 2009). In addition, recent molecular studies indicate that these characters were not always phylogenetically informative, and that the generic concept of some genera warranted revision (Verkley *et al.* 2004, Kirschner 2009).

Ramularia species have mycosphaerella-like sexual morphs but the number of experimentally proven links is small and some species may be true asexual holomorphs (Sivanesan 1984, Braun 1995, Verkley *et al*. 2004, Crous *et al*. 2009e, Koike *et al*. 2011). Currently *Ramularia* species are accepted as being host-specific, although some exceptions are likely to emerge (Braun 1998).

Cercosporoid fungi

The term Cercosporoid is applied to a non-taxonomic group of fungi that encompasses hyphomycetous cercospora-like fungi as presented in the monograph by Chupp (1954) which followed a very broad generic concept of *Cercospora* but maintained *Passalora* as a separate genus. Cercosporoid fungi are mostly defined as dematiaceous hyphomycetes with conidiophores formed singly, in groups (fascicles), synnemata or even sporodochia, having integrated, terminal or intercalary conidiogenous cells. Conidiogenesis is holoblastic and generates amerosporous to scolecosporous conidia, which are solitary or in chains (Braun *et al.* 2013). In a broader sense, it also encompasses ramularioid fungi that are the hyaline counterparts of cercosporoid fungi, forming conidia singly or in chains. Species in this group are mostly asexual and the ones with a known sexual morph present a mycosphaerella-like morphology, which is characterised by pseudothecial ascomata, with ostiolar periphyses but without interascal tissue, hyaline or slightly pigmented ascospores that are predominantly 1-septate (Barr 1987, Crous *et al.* 2009c).

The hyphomycetes are characterised by producing solitary conidiophores, fascicles or sporodochia while the coelomycetes are recognised by producing acervuli or pycnidial conidiomata. The coelomycete genera linked to mycosphaerella-like morphs were largely treated by Sutton (1980) and, to a lesser degree, by Nag Raj (1993). The hyphomycete cercosporoid genera were primarily addressed by Chupp (1954), who took a wide approach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and described many cercosporoid fungi in the genus *Cercospora*. Pollack (1987) followed and built up on Chupp's concept. Deighton (1967, 1974, 1976a, 1979) recognised several genera within Chupp's broad *Cercospora* concept and introduced new names for them. Crous & Braun (2003) narrowed down the true cercosporoid fungi to *Cercospora*, *Pseudocercospora*, *Stenella* and *Passalora*. The hyaline counterparts of *Cercospora*, including *Ramularia* and allied genera, were treated by Braun (1995, 1998). The separation of these genera relied on the presence or absence of pigmentation in the conidiogenous structures, arrangement and branching of conidiophores, the conidiogenous cell placement, proliferation and scar type (conidiogenous loci), and conidial formation, shape and septation. However, some species present more than one mode of conidiogenesis and intermediate characters that do not clearly fit the definition of these genera (Crous & Braun 2003).

With the introduction of phylogenetic analyses based on DNA sequences, the genera *Cercospora* (Groenewald *et al.* 2013) and *Pseudocercospora* (Crous *et al.* 2013a, Nakashima *et al.* 2016) have been more narrowly defined and their names are now applied to morphologically distinct monophyletic clades based on the respective generic type species. The genus *Stenella* was allocated to the *Teratosphaeriaceae* based on the phylogenetic placement of the type species, *Stenella araguata*, while the stenella-like species remaining in *Mycosphaerellaceae* were included in the genus *Zasmidium* (Arzanlou *et al.* 2007, Braun *et al.* 2010a, 2013). Although several phylogenetic studies have included species of *Zasmidium* (Huang *et al*. 2015) and *Passalora* (Crous *et al*. 2009c), a comprehensive phylogenetic analysis of both genera including their respective type species has yet to be performed. Based on the existing studies, the position of several species in different phylogenetic analyses suggest these genera may be paraphyletic, showing that some morphological characters have evolved more than once within the family. Additional accepted cercosporoid genera also have an uncertain status since no suitable type, or ex-type culture, is available (e.g. *Distocercospora*, *Phaeoramularia* and *Mycovellosiella*). These fungi represent a very large heterogeneous group for which the existing monographs are in urgent need of revision (e.g. Braun *et al.* 2013, 2014, 2015a).

Species concepts and species recognition criteria

The confusion between the concept of a species and the criteria that delimit a particular species has led to the impression that there is no general agreement amongst biologists about what a species is (Queiroz 2007; Hey 2006). The concept of a species is a description of the entity that constitutes a species while the species recognition criteria are the practical standards used to recognise if individuals should be considered members of the same species. In other words, "the species criteria correspond to the different events that occurred during lineage separation

Fig. 2. Morphological characteristics in *Ramularia* spp. A. Leaf symptoms of sexual morph proliferation (*R. vizellae*) B. Asci and ascospores (*R. vizellae*). C. Germinating ascospores (*R. vizellae*). D. Catenate, cylindrical-fusiform, hyaline, smooth conidia (*R. unterseheri*). E. Catenate, ellipsoid, hyaline, smooth conidia (*R. aplospora*) F. Catenate, cylindrical, curved, hyaline, smooth conidia (*R. diervillae*). G. Catenate, ellipsoid, hyaline, smooth conidia (*R. interstitiales*). H. Solitary, obovoid, smooth, hyaline conidia (*R. maliicola*). I. Catenate, cylindrical, straight, smooth, hyaline conidia (*Ramularia agastaches*). J. Conidiophore curved, emerging from stromata (*R. geraniicola*). K. Conidiophore curved, emerging from mycelium (*R. inaequalis*). L–N. Conidiophore geniculate-sinuous, smooth, hyaline (L. *R. maliicola*, M. *R. abscondita*, N. *R. pusilla*). O. Conidiophore straight, pigmented, slightly verruculose (*R. weigelae*). P. Conidiophore synnematous, pigmented (*R. alangiicola*).

and divergence, rather than to fundamental differences in what represents a species" (Cai *et al*. 2011). Based on these definitions, most biologists agree on an Evolutionary Species Concept that is based on the criterion that monophyletic lineages have evolved independently from one another (Queiroz 1998). In fact, most of the species concepts are bound to the species criteria they emphasize (Queiroz 2007; Hey 2006; Taylor *et al*. 2000). The Biological Species Concept (BSC) emphasizes the criterion of reproductive isolation, the Morphological Species Concept (MSC) emphasizes the criterion of morphological divergence, the Ecological Species Concept (ESC) emphasizes the criterion of adaptation to a particular ecological niche, and the Phylogenetic Species Concept (PSC) emphasizes the criterion of nucleotide divergence between monophyletic lineages (Giraud *et al*. 2008, Taylor *et al*. 2000). A single species criterion cannot be universally applied since speciation occurs at a different pace depending on the organism, the events that promoted species diversity do not occur in a chronological order for all organisms and the characteristics of certain organisms may hinder the application of some criteria (Giraud *et al*. 2008).

The phylogenetic species criterion mostly relies on the phylogenetic analysis of DNA sequences of selected genes or genomes. A single gene analysis may be misleading since it is dependent on the genes having an evolutionary history that reflects that of the entire fungus (Aguileta *et al*. 2008). Consequently, the use of concordance of multiple gene genealogies has been frequently used in mycology to determine species boundaries. This is known as the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) principle and is an adaptation of the Phylogenetic Species Concept (Taylor *et al.* 2000). The GCPSR criterion has proved immensely useful in fungi because they often have simple morphologies and it is difficult to demonstrate *in vitro* crosses (Reynolds 1993, Taylor *et al*. 2000, Prihastuti *et al*. 2009, Glienke *et al*. 2011). Based on GCPSR, some of the previously applied morphological characters that were used to define taxa were found to be non-phylogenetically informative and need to be re-evaluated. An increasing number of cryptic species are being discovered amongst plant pathogenic fungi using the GCPSR principle. Two or more species are considered to be "cryptic" if they are classified as a single species because they are at least superficially morphologically indistinguishable (Bickford *et al*. 2007). Although the GCPSR has allowed the recognition of many species it is not a panacea for species delimitation and its combination with other types of data has become increasingly used. This trend led to the proposal of the Consolidated Species Concept that weighs a combination of the criteria used on the PSC, MSC and ESC in order to determine which taxa represent separate species (Quaedvlieg *et al*. 2014).

Despite all the efforts in implementing species recognition criteria based on DNA sequence data, much work remains to be done in order to have a more natural classification system in place. One of the major problems hindering progress is that many species are only known from their morphological descriptions and often they have not been deposited in public culture collections. In addition, only a fraction of the known species has had fragments of their DNA sequenced and used in phylogenetic studies. The implementation of DNA barcoding together with well-curated databases should improve rapid molecular identification in fungi (Begerow *et al*. 2010). The ITS was introduced as the official barcode for fungi due to its ease of amplification and its ability to distinguish species across the kingdom (Schoch *et al.* 2012). However, phylogenies based on ITS sequences have often failed to separate closely related species, and several studies have highlighted the need to use additional phylogenetic markers to achieve accurate species identification (e.g. Bensch *et al.* 2012, Damm *et al.* 2012a, b, Quaedvlieg *et al.* 2012, Phillips *et al.* 2013, Wikee *et al.* 2013, Bakhshi *et al.* 2014). In general, protein-coding genes have higher species resolution power due to their variable intron sequences. In addition, partial sequences

from the mating-type ideomorphs (MAT1-1 and MAT1-2), specifically the alpha box (MAT1-1-1) and the high mobility group (MAT1-2-1), have also been found valuable due to their high inter- and low intraspecific variability (Du *et al.* 2005, Paoletti *et al.* 2005).

Economic importance

Plant pathogens

Agricultural production must be improved in order to meet the future demand for food, feed and biofuel. An increase in yield can be attained by breeding, improving agricultural practices and reducing the losses caused by weeds, animal pests and pathogens (Oerke & Dehne 2004). The *Mycosphaerellaceae* includes several important plant pathogens that cause diseases such as the Sigatoka disease on banana (Arzanlou *et al.* 2007, Churchill 2010, Chang *et al.* 2016), angular leaf spot of bean (Crous *et al.* 2006a), tomato leaf mould (de Wit 2016) and Cercospora leaf spot of olive (Ávila *et al.* 2005) to name but a few. The Sigatoka disease complex, caused by the fungi *Pseudocercospora musae* (yellow sigatoka), *Pseudocercospora eumusae* (eumusae leaf spot), and *Pseudocercospora fijiensis* (black sigatoka), is currently one of the most devastating diseases on banana worldwide. *Pseudocercospora fijiensis* is able to infect a wider range of cultivars, including those with resistance to *P. musae*, and can lead to losses of up to 76 %. *Pseudocercospora eumusae* is able to infect banana and plantain cultivars that are resistant to both *P. musae* and *P. fijiensis*, causing yield losses of up to 40 % (Chang *et al*. 2016). The tomato leaf mould disease, which is caused by the pathogen *Fulvia fulva*, affects mostly the leaves but occasionally also stems, blossoms, petioles and fruit (Butler & Jones 1949, de Wit 1977, 1992, Jones *et al.* 1997). *Fulvia fulva* was once a devastating pathogen of tomato that required treatment with agrochemicals, but extensive research led to identification of resistance genes that have been introduced in commercial tomato cultivars by breeders, providing effective disease control (Thomma *et al.* 2005; de Wit, 2016).

In addition, six species of *Mycosphaerellaceae* are currently quarantine listed and under EU regulations to promote crop safety and prevent disease spread (Quaedvlieg *et al.* 2012). These include *Pseudocercospora angolensis* causing fruit and leaf spot disease on citrus (Kirk 1986, Pretorius *et al.* 2003), *Pseudocercospora pini-densiflorae* causing brown needle blight of pine (Deighton 1987, Crous *et al.* 1990), *Sphaerulina musiva* causing canker of poplar (Peace 1962, Waterman 1954, Quaedvlieg *et al.* 2013), *Mycosphaerella laricis-leptolepidis* causing needle cast of Japanese larch (Peace 1962), *Septoria malagutii* causing angular leaf spot of potato (Cline & Rossman 2006) and *Lecanosticta acicula* causing brown spot needle blight on *Pinus* spp. (Quaedvlieg *et al.* 2012).

Most species of *Ramularia* are phytopathogenic and associated with leaf spots, necrosis or chlorosis. Foliar diseases occur mostly under conditions of high relative humidity and low temperatures. The most important pathogens in this genus are *R. collo-cygni* and *R. beticola* that cause severe economic losses to barley and sugar beet crops, respectively. *Ramularia collo-cygni* is responsible for yield losses of 15–25 % in winter barley in northern European countries and New Zealand (Cromey *et al.* 2004). Yield losses in sugar beet due to plant pathogens and pests are estimated in general to be 26 % with, and more than 80 % without using fungicides (Oerke & Dehne 2004). Currently *Ramularia* species are accepted as being host-specific. As host-specific plant pathogens, some species have shown potential as biocontrol agents of invasive species (e.g. *Ramularia crupinae*, *Ramularia destructiva*), but no commercial application was formulated or tested thus far.

Post-harvest pathogens

Pathogen infections are responsible for the spoilage of fruits and vegetables during their postharvest handling, storage and distribution. Postharvest pathogens can lay to waste up to 33 % of the total production of fruit and vegetables worldwide (FAO 2011, OECD 2014, Dukare 2018). Fungal infections caused by species of *Alternaria*, *Aspergillus*, *Botrytis*, *Fusarium*, *Geotrichum*, *Gloeosporium*, *Monilinia*, *Mucor, Penicillium* and *Rhizopus* are of major concern (Barkai-Golan 2001). In addition to spoilage, some species belonging to the genera *Alternaria*, *Aspergillus*, *Fusarium*, and *Penicillium* pose an additional health hazard since they are able to produce mycotoxins. The control of postharvest fungal infections is usually handled by the use of fungicides applied in the field or after harvest (Vitoratos *et al*. 2013).

Thus far, no species belonging to *Mycosphaerellaceae* have been of concern as a postharvest pathogen, until a recent report identified the pathogen *Ramularia eucalypti* as the causal agent of lenticel rot observed in fruits of apple (*Malus malus* cv. Ambrosia) and pear (*Pyrus communis* cv. Conference) in the Piedmont Province in Italy (Gianetti *et al*. 2012, Giordani *et al*. 2012). Investigations into the epidemiology showed that apple trees in the orchards had leaf spots caused by *R. eucalypti*, and symptomless fruits harvested from infected plants exhibited disease symptoms during the subsequent four months of cold storage (Gianetti *et al*. 2012). *Ramularia eucalypti* is a recently described species that was isolated from mature *Corymbia grandifolia* leaves collected in Italy that exhibited severe leaf spotting symptoms (Crous *et al*. 2007c). Since its description, the species has been reported from a range of different hosts and countries. However, small morphological differences and some heterogenicity on their ITS sequences were observed that lead to the suspicion of this being a species complex. The apple tree orchards in Piedmont are an important crop that in 2011 produced 140 000 tons of fruit. In 2013, in the Trentino Alto-Adige province in Italy, apples from *Malus domestica* cv. Golden Delicious developed the lenticel rot in cold storage and the disease affected 50–60 % of the crop. Due to the importance of this crop and the severe damage caused by this fungus it is important to correctly identify the responsible pathogen and to learn more about its life cycle.

Clinical importance

Filamentous fungal infections that are usually considered of low clinical relevance have increased in the past few years, especially among immunocompromised patients (Cassagne *et al*. 2011, Lu *et al*. 2013). Mycoses caused by hyaline, septate fungal hyphae fall under the medical term hyalohyphomycosis and some of the pathogens involved have been demonstrated to be resistant to certain antifungals (Tortorano *et al*. 2014). Therefore, a fast and accurate diagnosis is critical for patient management in order to determine appropriate treatment.

No species of *Mycosphaerellaceae* is currently known to be a human pathogen. However, in the Netherlands, *Ramularia eucalypti* has been isolated not only from different plant hosts but has also been obtained from clinical samples in different hospitals. Small morphological differences and some heterogenicity on their ITS sequences were observed that lead to the suspicion of this being a species complex. Although this is the first time a *Ramularia* species is associated with human infection, it is not the first time a plant pathogenic fungus has been reported to be able to infect human hosts (Mostert *et al*. 2006, van Baarlen *et al*. 2007, Phillips *et al*. 2013).

In a clinical setting, it is important to accurately and quickly identify the responsible pathogenic agent of a disease. Traditionally, the identification of microbial species is based

on microscopy and biochemical methods that are time consuming and require high levels of expertise. The methods based on DNA sequencing, although still laborious, are faster and produce more reliable results. The most recently developed clinical diagnostic method applied to microorganisms is known as Matrix-Assisted Laser Desorption Ionisation Time of Flight Mass Spectrometry (MALDI-TOF MS). This technique analyses the unique protein fragment peak pattern of a microorganism and compares it with a database of reference main mass spectra (MSPs), therefore providing an identification of that microorganism. The peaks present in the MSP represent mostly ribosomal proteins but structural proteins, cold-shock proteins and others may also be detected. MALDI-TOF MS is a simple, fast and accurate procedure that has been validated in numerous laboratories for the identification of yeasts (Goyer *et al*. 2012, Kolecka *et al*. 2013) and bacteria (Seng *et al*. 2009) from clinical samples. Recently, an effort has been made towards the validation of standardised procedures for routine mould identification (Cassagne *et al*. 2011, Lau *et al*. 2013) and dermatophytes (L'Ollivier *et al*. 2013) from clinical samples. All reports showed that MALDI-TOF MS had a good discriminative power for species separation, effectively decreased the time of identification and improved its accuracy. Furthermore, MALDI-TOF MS has also been used in studies where it was used as a complementary tool for taxonomical discriminatory purposes: Degenkolb *et al*. (2008) used MALDI-TOF MS in a polyphasic approach to support the description of *Trichoderma brevicompactum* as a novel species, while Brun *et al*. (2013) tested this technique to distinguish closely related species of *Alternaria*.

Outline of thesis

Previous studies on *Ramularia* and allied genera focused mainly on species associated with specific hosts and consisted of very small sample sizes. With the phylogenies and classifications presented herein, a more robust and understandable taxonomy and nomenclature in *Ramularia* and allied genera is presented, which will serve as a starting point for research conducted by plant pathologists, breeders and medical mycologists. In addition, a review of the *Mycosphaerellaceae* based on morphological and phylogenetic analysis is presented in order to address some of the controversial generic circumscriptions presented in literature.

Chapter 1 provides an introduction to the genus *Ramularia* and the family *Mycosphaerellaceae*, with an overview of the taxonomic history based on both the morphological and molecular approaches. It further explores the economic importance of some species within the family.

Chapter 2 focuses on the species complex *Ramularia eucalypti*. Several isolates of *R. eucalypti* were determined to be somewhat heterogeneous in their morphology and on sequence data of the ITS region. In this study we aimed to resolve this species-complex by applying a polyphasic approach involving morphology, multi-gene phylogeny and matrix assisted laser desorption ionization time of flight mass spectrometry (MALDI-TOF MS). A multi-gene phylogenetic analysis was performed based on a concatenated alignment containing six partial genes (ITS, *actA, tef1-α, gapdh, his3, rpb2*) showed significant support for separation of seven species within *R. eucalypti* s. lat. The Principal Component Analysis (PCA) dendogram based on the Main Mass Spectra (MSPs) of several *R. eucalypti* s. lat. strains supported three species. Nevertheless, the clinically relevant strains were successfully identified by MALDI-TOF MS.

Chapter 3 describes the reappraisal of the *Ramularia endophylla* (= *Mycosphaerella punctiformis*) species complex. A polyphasic approach involving morphology and multi-gene phylogeny was applied. Eleven partial genes (LSU, ITS, *actA, tef1-α, gapdh, his3, rpb2, cmdA, tub2,* MAT1-1-1, MAT1-2-1) were targeted for amplification and sequencing for several isolates representing *R. endophylla* s. lat. and *Ramularia* species that were previously linked to a *Mycosphaerella* sexual morph in literature. Based on a combined five-locus dataset (ITS, *actA, gapdh, his3, rpb2*), both the Bayesian and the maximum parsimony phylogenetic trees showed significant support for three species within the complex. The supported species are nearly indistinguishable based on morphological characteristics alone. A bibliographic review of the proposed links between *Ramularia* spp. and their purported *Mycosphaerella* sexual morphs is also presented.

Chapter 4 treats the genus *Ramularia* and its closest allied genera. *Ramularia* species have a simple morphology with hyaline conidiophores and conidia with distinct, thickened, darkened, refractive conidiogenous loci and conidial hila. In order to improve the delimitation of *Ramularia* from allied genera and the circumscription of species within the genus *Ramularia*, a polyphasic approach based on multilocus DNA sequences, morphological and cultural data were used in this study. Isolates belonging to *Ramularia* and allied genera were targeted for the amplification and sequencing of 11 partial genes (LSU, ITS, *actA*, *chs-1*, *cmdA*, *gapdh*, *his3*, *mcm7*, *rpb2*, *tub2*, *tef1*-α). The phylogenetic analysis of *Ramularia* and allied genera based on the concatenated alignment of two genes (LSU, *rpb2*) showed that *Ramularia* and *Ramulariopsis* were monophyletic while *Cercosporella* and *Pseudocercosporella* were polyphyletic. Species not congeneric with the ex-type strains of the respective genera were assigned to existing genera or to newly introduced genera. The phylogenetic analysis of *Ramularia* species based on the concatenated alignment of five genes (ITS, *actA*, *gapdh*, *rpb2*, *tef1*-α) allowed the circumscription of several species complexes and the description of several new species.

Chapter 5 focuses on a current circumscription of the *Mycosphaerellaceae* based on phylogenetic data. Several species within the *Mycosphaerellaceae* have a strong impact on agriculture, horticulture and forestry. Previous studies have focused on the circumscription of a few genera but some remain understudied. In the present study several phylogenetic analyses were performed based on concatenated alignments of two (LSU, *rpb2*) or three (LSU, *rpb2*, ITS) genes and using Bayesian, Maximum-Likelihood and Parsimony methods. The resulting trees showed that many well-known genera are paraphyletic and that several synapomorphic characters have evolved more than once within the family. As a consequence, several old generic names including *Cercosporidium*, *Fulvia*, *Mycovellosiella*, *Phaeoramularia* and *Raghnildiana* are resurrected, and 32 additional genera are described as new. Based on phylogenetic data 120 genera are now accepted within the family, but many currently accepted genera still remain unresolved pending fresh collections and DNA data.

Chapter 6 discusses the data presented in this thesis. The implications of the performed studies are placed in a broader context, with a focus on the relation between morphology and the new species classification based on molecular tools.

CHAPTER 2

Elucidating the *Ramularia eucalypti* species complex

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Abstract The genus *Ramularia* includes numerous phytopathogenic species, several of which are economically important. *Ramularia eucalypti* is currently the only species of this genus known to infect *Eucalyptus* by causing severe leaf-spotting symptoms on this host. However, several isolates identified as *R. eucalypti* based on morphology and on nrDNA sequence data of the ITS region have recently been isolated from other plant hosts, from environmental samples and also from human clinical specimens. Identification of closely related species based on morphology is often difficult and the ITS region has previously been shown to be unreliable for species level identification in several genera. In this study we aimed to resolve this species-complex by applying a polyphasic approach involving morphology, multi-gene phylogeny and matrix assisted laser desorption ionization time of flight mass spectrometry (MALDI-TOF MS). Six partial genes (ITS, *actA*, *tef1*-α, *his3*, *gapdh* and *rpb2*) were amplified and sequenced for a total of 44 isolates representing *R. eucalypti* s.lat. and closely related species. A multi-gene Bayesian phylogenetic analysis and parsimony analysis were performed, and both the resulting trees showed significant support for separation of seven species in *R. eucalypti* s.lat., including two previously described (*R. eucalypti* and *R. miae*), four novel species here described (*R. haroldporteri*, *R. glennii*, *R. mali* and *R. plurivora*) and one undescribed *Ramularia* species (sterile). Additionally, *Mycosphaerella nyssicola* is newly combined in *Ramularia* as *R. nyssicola*. Main mass spectra (MSPs) of several *R. eucalypti* s.lat. strains were generated using MALDI-TOF MS and were compared through a Principal Component Analysis (PCA) dendogram. The PCA dendrogram supported three clades containing *R. plurivora*, *R. glenni* / *R. mali* and *R. eucalypti* /*R. miae*. Although the dendrogram separation of species differed from the phylogenetic analysis, the clinically relevant strains were successfully identified by MALDI-TOF MS.

INTRODUCTION

Ramularia (Unger 1833) is a species-rich genus in the order *Capnodiales* that includes more than 1 000 legitimate species names (www.MycoBank.org, acc. Apr. 2014). The genus has been monographed by Braun (1995, 1998), who defined *Ramularia* species as hyphomycetes with hyaline conidiophores and conidia with distinct, thickened, darkened and refractive conidial scars and hila. The sexual morph of *Ramularia* species belongs to *Mycosphaerella* (*Mycosphaerellaceae*) but the number of experimentally proven links is small and some species may be true asexual holomorphs (Sivanesan 1984, Braun 1995, Verkley *et al*. 2004, Crous *et al*. 2009e, Koike *et al*. 2011). Currently *Ramularia* species are accepted as being host-specific, though some exceptions are likely to emerge (Braun 1998). Most species are phytopathogenic and associated with leaf spots, necrosis or chlorosis, but some species can be saprobic or even hyperparasitic. Foliar diseases occur mostly under conditions of high air humidity and low temperatures and result indirectly in crop loss due to defoliation. The most harmful pathogens in this genus are *R. collo-cygni*, *R. beticola* and *R. grevilleana* that cause severe economic losses in barley, sugarbeet and strawberry crops, respectively. *Ramularia eucalypti* is a recently described species that was isolated from mature *Corymbia grandifolia* leaves collected in Italy that exhibited severe leaf spotting symptoms (Crous *et al*. 2007c). It is currently the only species of the genus known to infect *Eucalyptus* and *Corymbia*, since *R. pitereka* and aggregate species have been reassigned to *Quambalaria* (*Quambalariaceae*) (Beer *et al*. 2006). Over the past few years several isolates have been collected and identified as *R. eucalypti* based on morphology and on sequence data of the ITS region of the nrDNA operon which has recently been adopted as the universal DNA barcode for fungi (Schoch *et al*. 2012). However, in several genera of phytopathogenic fungi, ITS phylogenies have often failed to separate closely related species, and a better resolution could only be achieved by using protein-coding loci (Lombard *et al*. 2010, Cabral *et al*. 2012, Crous *et al*. 2013a, Groenewald *et al*. 2013, Quaedvlieg *et al*. 2013, Woudenberg *et al*. 2013). In Italy, *R. eucalypti* has been reported as an emerging problem on pome fruit in cold storage where it causes lenticel rot in healthy fruits of apple (*Malus domestica* cv. Ambrosia) and pear (*Pyrus communis* cv. Conference) (Giordani *et al*. 2012). Investigations into the epidemiology showed that apple trees in the orchards had leaf spots caused by *R. eucalypti*, and symptomless fruits harvested from infected plants exhibited disease symptoms during the subsequent four months of cold storage (Gianetti *et al*. 2012). In the Netherlands, *R. eucalypti* has been isolated not only from different plant hosts but has also been obtained from clinical specimens in different hospitals. This is the first time a *Ramularia* species is associated with human infection and little is known of its epidemiology. However, this is not the first time a plant pathogenic fungus has been reported to be able to infect human hosts (Mostert *et al*. 2006, van Baarlen *et al*. 2007, Phillips *et al*. 2013). The number of infections caused by filamentous fungi previously considered of low clinical relevance has increased in the past few years, especially among immunocompromised patients (Cassagne *et al*. 2011, Lu *et al*. 2013). Mycoses caused by hyaline, septate fungal hyphae fall under the medical term hyalohyphomycosis and some of the pathogens involved have been demonstrated to be resistant to certain antifungals (Tortorano *et al*. 2014). Therefore, a fast and accurate diagnosis is critical for patient management in order to determine appropriate treatment. The identification of microbial species is usually based on microscopy and biochemical methods that are time consuming and require high expertise. The DNA sequencing approach gives more reliable and faster results but still remains laborious. Recently, a technique known as Matrix-Assisted Laser Desorption Ionisation Time of Flight

Mass Spectrometry (MALDI-TOF MS) has been revolutionising the clinical diagnostics field. This technique allows the identification of microorganisms by analysing their unique protein peak pattern and comparing it with a database of reference main mass spectra (MSPs). The peaks present in the MSP represent mostly ribosomal proteins but structural proteins, cold-shock proteins and others may also be detected. MALDITOF MS is a simple, fast and accurate procedure that has been validated in numerous laboratories for the identification of yeasts (Goyer *et al*. 2012, Kolecka *et al*. 2013) and bacteria (Seng *et al*. 2009) from clinical samples. Recently, an effort has been made towards the validation of standardised procedures for routine mould identification (Cassagne *et al*. 2011, Lau *et al*. 2013) and dermatophytes (L'Ollivier *et al*. 2013) from clinical samples and all reports showed that MALDI-TOF MS had a good discrimination power for species separation, effectively decreased the time of identification and improved its accuracy. Furthermore, MALDI-TOF MS has also been used in studies where it was used as a complementary tool for taxonomical discriminatory purposes: Degenkolb *et al*. (2008) used MALDITOF MS in a polyphasic approach to support the description of *Trichoderma brevicompactum* as a novel species and Brun *et al*. (2013) tested this technique to discriminate closely related species of *Alternaria*.

In this study we aimed to: i. resolve the *R. eucalypti* species-complex by applying a polyphasic approach involving morphology, multi-gene phylogeny and MALDI-TOF mass spectrometry; and ii. build an in-house library of MSPs of *R. eucalypti* s.lat. strains in order to evaluate the taxonomic resolution power of this technique for the identification of the set of clinical isolates within this species complex.

MATERIALS AND METHODS

Fungal strains

The 44 isolates used in this study are maintained in the culture collection of the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, The Netherlands, and the working collection of Pedro Crous (CPC), housed at CBS (Table 1).

DNA extraction, amplification and sequencing

The fungal strains (Table 1) were grown on Malt Extract Agar (MEA), for 7 d at room temperature (20 °C). The mycelium was harvested with a sterile scalpel and the genomic DNA was isolated using the UltraCleanTM Microbial DNA Isolation Kit (MoBio Laboratories, Inc., Solana Beach, CA, USA) following the manufacturers' protocols. Ten partial nuclear genes were initially targeted for PCR amplification and sequencing, namely, 28S nrRNA gene (LSU), internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS) of the nrDNA operon, actin (*actA*), translation elongation factor 1-α (*tef1*-α), histone H3 (*his3*), glyceraldehyde-3-phosphate dehydrogenase (*gapdh*), RNA polymerase II second largest subunit (*rpb2*), calmodulin (*cmdA*), β-tubulin (*tub2*) and chitin synthase I (*chs-1*). The primers employed are listed in Table 2. The PCR amplifications were performed on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA). The PCR mixtures consisted of 1 µL genomic DNA, 1× GoTaq® Flexi buffer (Promega, Madison, WI, USA), 2 µM MgCl2, 40 µM of each dNTP, 0.2 µM of each primer and 0.5 Unit GoTaq® Flexi DNA polymerase (Promega) in a total volume of 12.5 µL. The PCR mixtures for *his3*, *gapdh*, *rpb2*, *cmdA*, *tub2* and *chs-1* contained 2 µL genomic DNA. The PCR conditions were: initial denaturation

(94 °C, 3 min); 35 cycles amplification (94 °C, 30 s; annealing (Table 2), 30 s; 72 °C, 45 s) and final extension (72 °C, 5 min). For *gapdh* and *his3*, 40 amplification cycles were used. To obtain the partial *rpb2*, a touchdown PCR protocol was used: initial denaturation (94 °C, 3 min), five amplification cycles (94 °C, 45 s; 60 °C, 45 s; 72 °C, 2 min), five amplification cycles (94 °C, 45 s; 58 °C, 45 s; 72 °C, 2 min), 30 amplification cycles (94 °C, 45 s; 54 °C, 45 s; 72 °C,2 min) and a final extension (72 °C, 8 min). The resulting fragments were sequenced in both directions using the PCR primers and a BigDye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems Life Technologies, Carlsbad, CA, USA). DNA sequencing amplicons were purified through Sephadex G-50 Superfine columns (Sigma- Aldrich, St. Louis, MO) in MultiScreen HV plates (Millipore, Billerica, MA). Purified sequence reactions were analysed on an Applied Biosystems 3730xl DNA Analyzer (Life Technologies, Carlsbad, CA, USA). The DNA sequences generated were analysed and consensus sequences were computed using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium).

Phylogenetic analyses

Ramularia nyssicola (CBS 127665) has recently been revised and separated from *R. endophylla* (= *Mycosphaerella punctiformis*) (Minnis *et al*. 2011). *Ramularia nyssicola* is basal in the genus *Ramularia* (Videira, unpubl. data) and was therefore considered as an adequate outgroup for the *R. eucalypti* species complex. The generated sequences for each gene were aligned with MAFFT v. 6.864b (http://mafft.cbrc.jp/alignment/ server/index.html) according to the gene characteristics. The alignments were manually checked and improved where necessary using MEGA v. 5 (Tamura *et al*. 2011) and were concatenated with Mesquite v. 2.75 (Maddison & Maddison 2011). In order to check the stability of each species clade a neighbour-joining analysis using the HKY85 substitution model was applied to each gene partition individually using PAUP v. 4.0b10 (Swofford 2003) (data not shown). Alignment gaps were treated as missing data and all characters were unordered and of equal weight. When ties were encountered they were randomly broken. The robustness of the obtained trees was evaluated by 1 000 bootstrap replications (Hillis & Bull 1993). Parsimony and Bayesian analyses were used to estimate phylogenetic relationships for the aligned combined dataset. Parsimony analyses were conducted with PAUP v. 4.0b10 (Swofford 2003). Alignment gaps were treated as fifth base and all characters were unordered and of equal weight. The robustness of the obtained trees was evaluated by 1 000 bootstrap replications (Hillis & Bull 1993).

MrModeltest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model settings for each data partition in order to perform a model-optimised Bayesian phylogenetic reconstruction using MrBayes v. 3.2.0 (Ronquist & Huelsenbeck 2003). The heating chain was set to 0.15 and the Markov Chain Monte Carlo (MCMC) analysis of four chains was started in parallel from a random tree topology and lasted until the average standard deviation of split frequencies reached a value of 0.01. Burn-in was set to 25 % after which the likelihood values were stationary. Trees were saved each 100 generations and the resulting phylogenetic tree was printed with Geneious v. 5.5.4 (Drummond *et al*. 2011). All new sequences generated in this study were deposited in NCBIs GenBank nucleotide database (www.ncbi.nlm.nih.gov) and the accession numbers of the sequences used for the phylogenetic analyses are detailed in Table 1. The alignment and phylogenetic tree were deposited in TreeBASE (www.TreeBASE.org).

Table 1. Collection details and GenBank accession numbers of isolates included in this study.

Species	Accession number(s)[1,2]	Host/isolation source	Country	Collector	GenBank Accession numbers[3]					
					ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*
Ramularia agrimoniae	CPC 11653	*Agrimonia pilosa*	South Korea	H.-D. Shin	KJ504784	KJ504448	KJ504699	KJ504567	KJ504655	KJ504611
R. calcea	CBS 101612	*Symphytum* sp.	Germany	G. Arnold	KJ504785	KJ504449	KJ504700	KJ504568	KJ504656	KJ504612
R. collo-cygni	CBS 101181	*Hordeum vulgare*	Germany	E. Sachs	KJ504786	KJ504450	KJ504701	KJ504569	KJ504657	KJ504613
R. decipiens	CBS 114300	*Rumex aquaticus*	Sweden	E. Gunnerbeck	KJ504787	KJ504451	KJ504702	KJ504570	KJ504658	KJ504614
R. eucalypti	CBS 155.82	*Puccinia* sp. on *Carex acutiformis*	Netherlands	W. Gams & O. Constantinescu	KJ504789	KJ504453	KJ504704	KJ504572	KJ504660	KJ504616
	CBS 356.69	*Malus sylvestris*	Netherlands	—	KJ504790	KJ504454	KJ504705	KJ504573	KJ504661	KJ504617
	CBS 101045	*Geranium pusillum*	Netherlands	H.A. van der Aa	KJ504791	KJ504455	KJ504706	KJ504574	KJ504662	KJ504618
	CBS 120726 [T], CPC 13043	*Corymbia grandifolia*	Italy	W. Gams	KJ504792	KJ504456	KJ504707	KJ504575	KJ504663	KJ504619
	CBS 120728, CPC 13304	*Eucalyptus* sp.	Australia	P.W. Crous	KJ504793	KJ504457	KJ504708	KJ504576	KJ504664	KJ504620
	CPC 13044	*Corymbia grandifolia*	Italy	W. Gams	KJ504794	KJ504458	KJ504709	KJ504577	KJ504665	KJ504621
	CPC 13045	*Corymbia grandifolia*	Italy	W. Gams	KJ504795	KJ504459	KJ504710	KJ504578	KJ504666	KJ504622
	CPC 16804	*Pinus wallichiana*	Netherlands	W. Quaedvlieg	KJ504796	KJ504460	KJ504711	KJ504579	KJ504667	KJ504623
	CPC 19187	*Phragmites* sp.	Netherlands	P.W. Crous	KJ504797	KJ504461	KJ504712	KJ504580	KJ504668	KJ504624
	CPC 19188	*Phragmites* sp.	Netherlands	P.W. Crous	KJ504798	KJ504462	KJ504713	KJ504581	KJ504669	KJ504625
R. glechomatis	CBS 108979	*Glechoma hederacea*	Netherlands	G. Verkley	KJ504799	KJ504463	KJ504714	KJ504582	KJ504670	KJ504626
R. glennii	CBS 120727, CPC 13046	*Corymbia grandifolia*	Italy	W. Gams	KJ504767	KJ504431	KJ504682	–	KJ504638	KJ504594
	CBS 122989, CPC 15195	Human skin	Netherlands	—	KJ504768	KJ504432	KJ504683	KJ504551	KJ504639	KJ504595
	CBS 129441 [T]	Human lungs	Netherlands	—	KJ504769	KJ504433	KJ504684	KJ504552	KJ504640	KJ504596
	CPC 13047	*Corymbia grandifolia*	Italy	W. Gams	KJ504770	KJ504434	KJ504685	KJ504553	KJ504641	KJ504597
	CPC 13048	*Corymbia grandifolia*	Italy	W. Gams	KJ504771	KJ504435	KJ504686	KJ504554	KJ504642	KJ504598
	CPC 16560	*Eucalyptus camaldulensis*	Iraq	A. Saadoon	KJ504772	KJ504436	KJ504687	KJ504555	KJ504643	KJ504599

Table 1. Continued).

Species	Accession number(s)[1,2]	Host/isolation source	Country	Collector	GenBank Accession numbers[3]					
					ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*
	CPC 16561	*Eucalyptus camaldulensis*	Iraq	A. Saadoon	KJ504773	KJ504437	KJ504688	KJ504556	KJ504644	KJ504600
	CPC 16565	*Eucalyptus camaldulensis*	Iraq	A. Saadoon	KJ504774	KJ504438	KJ504689	KJ504557	KJ504645	KJ504601
	CPC 18468	Rubber of refrigerator	USA: Athens	A.E. Glenn	KJ504775	KJ504439	KJ504690	KJ504558	KJ504646	KJ504602
	CPC 18469	Rubber of refrigerator	USA: Athens	A.E. Glenn	KJ504776	KJ504440	KJ504691	KJ504559	KJ504647	KJ504603
	CPC 18470	Rubber of refrigerator	USA: Athens	A.E. Glenn	KJ504777	KJ504441	KJ504692	KJ504560	KJ504648	KJ504604
R. haroldporteri	**CBS 137272** [T]; CPC 16296	Unidentified bulb plant	South Africa	P.W. Crous	KJ504766	KJ504430	KJ504681	–	KJ504637	KJ504593
R. major	CPC 12543	*Petasites japonicus*	South Korea	H.-D. Shin	KJ504800	KJ504464	KJ504715	KJ504583	KJ504671	KJ504627
R. mali	**CBS 129581** [T]	Apple in storage	Italy	—	KJ504778	KJ504442	KJ504693	KJ504561	KJ504649	KJ504605
R. miae	**CBS 120121** [T], CPC 12736	*Wachendorfia thyrsiflora*	South Africa	M.K. Crous & P.W. Crous	KJ504801	KJ504465	KJ504716	KJ504584	KJ504672	KJ504628
	CPC 12737	*Wachendorfia thyrsiflora*	South Africa	M.K. Crous & P.W. Crous	KJ504802	KJ504466	KJ504717	KJ504585	KJ504673	KJ504629
	CPC 12738	*Wachendorfia thyrsiflora*	South Africa	M.K. Crous & P.W. Crous	KJ504803	KJ504467	KJ504718	KJ504586	KJ504674	KJ504630
	CPC 19835	*Gazania rigens* var. *uniflora*	South Africa	P.W. Crous	KJ504804	KJ504468	KJ504719	KJ504587	KJ504675	KJ504631
	CPC 19770	*Leonotis leonurus*	South Africa	P.W. Crous	KJ504805	KJ504469	KJ504720	KJ504588	KJ504676	KJ504632
R. nyssicola	**CBS 127665** [ET]	*Nyssa ogeche* x *sylvatica* hybrid	USA: Maryland	R. Olsen	KJ504765	KJ504429	KJ504680	–	KJ504636	KJ504592
R. plurivora	CBS 118693, CPC 12206	Human skin	Netherlands	—	KJ504779	KJ504443	KJ504694	KJ504562	KJ504650	KJ504606
	CBS 118743 [T], CPC 12207	Human bone marrow	Netherlands	—	KJ504780	KJ504444	KJ504695	KJ504563	KJ504651	KJ504607
	CPC 11517	*Coleosporium plectanthri* on *Plectranthus excisus*	South Korea	H.-D. Shin	KJ504781	KJ504445	KJ504696	KJ504564	KJ504652	KJ504608
	CPC 16123	Melon in storage	Netherlands	—	KJ504782	KJ504446	KJ504697	KJ504565	KJ504653	KJ504609
	CPC 16124	Melon in storage	Netherlands	—	KJ504783	KJ504447	KJ504698	KJ504566	KJ504654	KJ504610
R. pratensis	CBS 136.23	—	—	A. Weber	KJ504806	KJ504470	KJ504721	KJ504589	KJ504677	KJ504633

Table 1. Continued).

Species	Accession number(s)[1,2]	Host/isolation source	Country	Collector	GenBank Accession numbers[3]					
					ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*
Ramularia sp.	CBS 114568	*Epilobium hirsutum*	Sweden	E. Gunnerbeck	KJ504788	KJ504452	KJ504703	KJ504571	KJ504659	KJ504615
R. tovarae	CBS 113305	*Persicaria filiformis*	South Korea	H.-D. Shin	KJ504807	KJ504471	KJ504722	KJ504590	KJ504678	KJ504634
R. vizellae	**CBS 130601** [T], CPC 18283	*Vizella interrupta*	South Africa	P.W. Crous	KJ504808	KJ504472	KJ504723	KJ504591	KJ504679	KJ504635

[1] CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, the Netherlands; CPC: Culture collection of P.W. Crous, housed at CBS.

[2] [T]: ex-type strain; [ET]: ex-epitype strain

[3] ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; *actA*: actin ; *tef1-α*: translation elongation factor 1-alpha; *gapdh*: glyceraldehyde-3-phosphate dehydrogenase; RPB2: RNA polymerase II second largest subunit; *his3*: histone H3.

Table 2. Details of primers used and/or developed for this study for the PCR amplification and sequencing of the different genes.

Gene	Primer Name	Sequence 5'→3'	Annealing temperature (°C)	Orientation	Reference
actA	ACT-512F	ATG TGC AAG GCC GGT TTC GC	55	Forward	Carbone & Kohn (1999)
	ACT-783 R	TAC GAG TCC TTC TGG CCC AT	55	Reverse	Carbone & Kohn (1999)
	ACT-2Rd	ARR TCR CGD CCR GCC ATG TC	55	Reverse	Groenewald *et al*. (2013)
tub2	T1	AAC ATG CGT GAG ATT GTA AGT	52	Forward	O'Donnell & Cigelnik (1997)
	β-Sandy-R	GCR CGN GGV ACR TAC TTG TT	52	Reverse	Stukenbrock *et al*. (2012)
	Bt2a	GGT AAC CAA ATC GGT GCT GCT TTC	52	Forward	Glass & Donaldson (1995)
	Bt2b	ACC CTC AGT GTA GTG ACC CTT GGC	52	Reverse	Glass & Donaldson (1995)
cmdA	CAL-228F	GAG TTC AAG GAG GCC TTC TCC C	58	Forward	Carbone & Kohn (1999)
	CAL-737R	CAT CTT TCT GGC CAT CAT GG	58	Reverse	Carbone & Kohn (1999)
	Cal2Rd	TGR TCN GCC TCD CGG ATC ATC TC	58	Reverse	Groenewald *et al*. (2013)
chs-1	CHS-79F	TGG GGC AAG GAT GCT TGG AAG AAG	52	Forward	Carbone & Kohn (1999)
	CHS-354R	TGG AAG AAC CAT CTG TGA GAG TTG	52	Reverse	Carbone & Kohn (1999)
GAPDH	gpd1	CAA CGG CTT CGG TCG CAT TG	55	Forward	Berbee *et al*. (1999)
	gpd2	GCC AAG CAG TTG GTT GTG C	55	Reverse	Berbee *et al*. (1999)

Table 2. (Continued).

Gene	Primer Name	Sequence 5'→3'	Annealing temperature (°C)	Orientation	Reference
his3	CylH3F	AGG TCC ACT GGT GGC AAG	52	Forward	Crous *et al*. (2004d)
	CylH3R	AGC TGG ATG TCC TTG GAC TG	52	Reverse	Crous *et al*. (2004d)
ITS	V9G	TTA CGT CCC TGC CCT TTG TA	52	Forward	Hoog & Gerrits van den Ende (1998)
	ITS4	TCC TCC GCT TAT TGA TAT GC	52	Reverse	White *et al*. (1990)
LSU	LSU1Fd	GRA TCA GGT AGG RAT ACC CG	52	Forward	Crous *et al*. (2009a)
	LR5	TCC TGA GGG AAA CTT CG	52	Reverse	Vilgalys & Hester (1990)
rpb2	RPB2-f5f	GAY GAY MGW GAT CAY TTY GG	60→58→54	Forward	Liu *et al*. (1999)
	RPB2-7cR	CCC ATR GCT TGY TTR CCC AT	60→58→54	Reverse	Liu *et al*. (1999)
	Rpb2-F1	GGTGTCAGTCARGTGYTGAA	60→58→54	Forward	This study
	Rpb2-R1	TCC TCN GGV GTC ATG ATR ATC AT	60→58→54	Reverse	This study
tef1-α	EF-728F	CAT CGA GAA GTT CGA GAA GG	54	Forward	Carbone & Kohn (1999)
	EF-2	GGA RGT ACC AGT SAT CAT GTT	54	Reverse	O'Donnell *et al*. (1998)
	TEF-1R	CTT GAT GAA ATC ACG GTG ACC	54	Reverse	This study

MALDI-TOF MS

Sample preparation

The cultures were prepared according to the method used in the protocol for the construction of the Filamentous fungi v. 1 Library (Bruker Daltonics, Germany) with a few modifications. Falcon tubes (15 mL) containing 7 mL of Saboraud dextrose broth (Difco, REF 238230) were inoculated with the isolates and incubated at 21 °C for 48–72 h on a tube rotator SB2 (Stuart). The tubes were centrifuged (1 min, 3 000 rpm) and 1.5 mL of the sediment was collected into 1.5 mL Eppendorf tubes. These were centrifuged (3 min, 14 000 rpm), the supernatant was removed and 1 mL of sterile Milli-Q water was added to the pellet followed by vortexing. This washing step was performed twice. The supernatant was removed and 1.2 mL of 70 % ethanol was added. The samples were stored up to 5 d at room temperature. The crude protein content was extracted using the Formic Acid/Ethanol sample preparation method (Bruker Daltonics, Germany) with a few modifications. The samples were centrifuged (3 min, 14 000 rpm), the supernatant was removed and the pellets were air-dried in a laminar flow cabinet for 30 min. The pellets were incubated for 10–20 min in 20–40 µL of 70 % formic acid (FA) (Sigma-Aldrich, Zwijndrecht, The Netherlands), followed by 10–20 min in 20–40 µL of 100 % acetonitrile (ACN) (Fluka) and were then centrifuged (2 min, 14 000 rpm). The supernatant, now containing the protein crude extract, was immediately used to generate mass spectra.

In-house library and identification

The in-house library of *Ramularia* comprises 22 reference MSPs, of which 21 were created from strains of *R. eucalypti* s.lat. and one from a strain of *R. vizellae*. The reference MSPs were generated with a MALDI Biotyper 3.0 Microflex LT (Bruker Daltonics, Germany) mass spectrometer. For each strain, 1 µL of protein crude extract was deposited on eight spots of a polished steel target plate (Bruker Daltonics, Germany), air-dried and covered with 1 µL of alpha-cyano-4-hydroxycinnamic acid (HCCA) matrix solution (Kolecka *et al*. 2013). Twenty-four spectra were acquired per isolate using FlexControl v. 2.4 (Bruker Daltonics, Germany). A minimum of 20 high quality spectra were selected with Flex analysis v. 3.3 (Bruker Daltonics, Germany) to create the respective reference MSP entry to be stored in the in-house library. Comparison of the MSPs was performed by Principal Component Analysis (PCA) (Shao *et al*. 2012) resulting on a distance score-oriented dendrogram (Fig. 1). The library was challenged with the identification of a set of four clinical isolates. The identification of each isolate was performed in duplicate using MALDI Biotyper 3.0 RTC application (Bruker Daltonics, Germany) with the standardised parameters recommended by the manufacturer for routine diagnostics in hospitals (Kolecka *et al*. 2013). In the automatic identification runs the clinical isolates were compared with reference MSPs selected simultaneously from the BDAL Bruker database (5627 MSPs), the Bruker Filamentous fungi v. 1 Library (365 MSPs) and the *Ramularia* in-house library (24 MSPs). Identification results were scored as log-values and, according to the manufacturer, classified as follows: secure genus and species identification (> 2.0), secure genus identification (1.7–2.0) and no reliable identification (< 1.7).

Taxonomy

The 33 isolates belonging to *R. eucalypti* s.lat. were inoculated on Synthetic Nutrient-poor Agar (SNA) (Crous *et al*. 2009f) and incubated at 21 °C for 7 d. Morphology of the strain CBS 118743

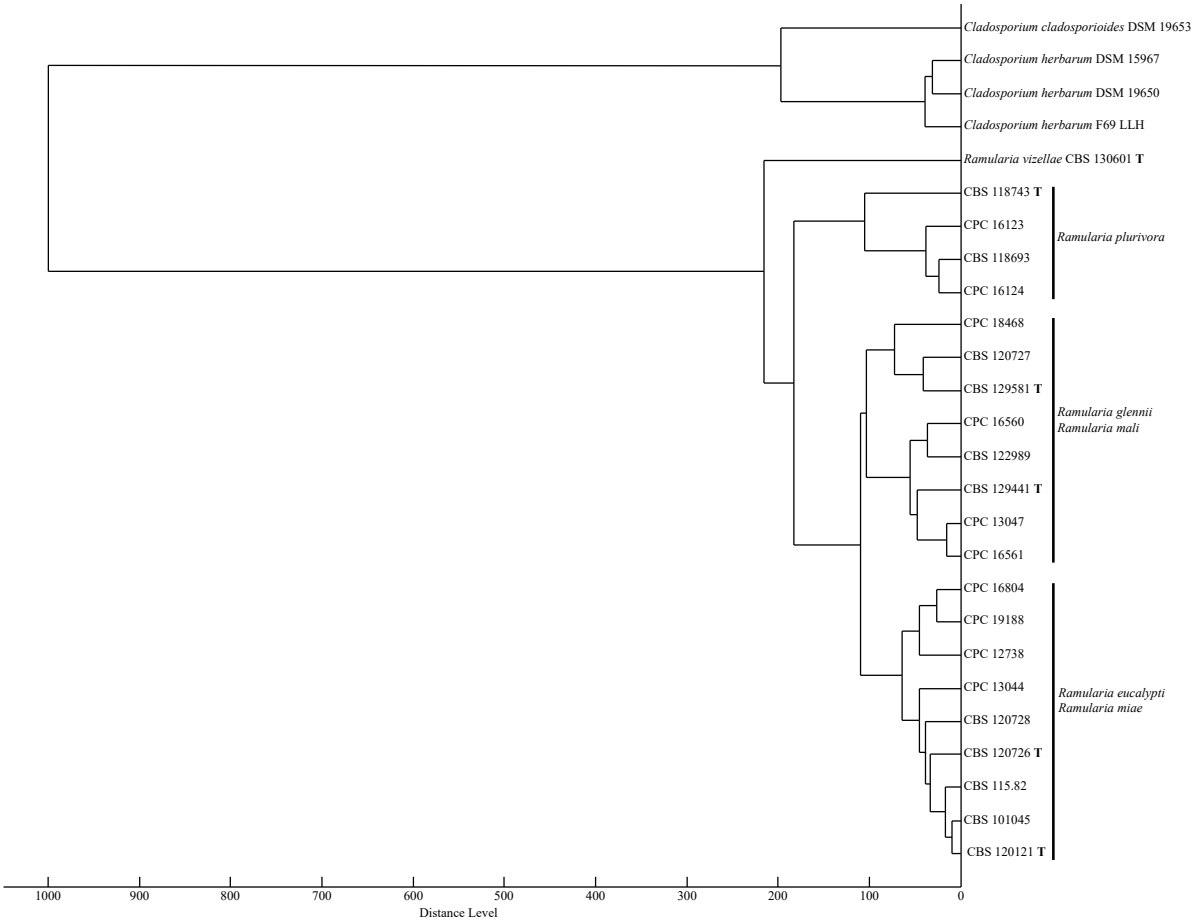

Fig. 1. PCA dendrogram based on the measured MSPs.

was also observed and described at 33 °C, because it showed morphological dimorphism at different temperatures. Observations of the conidiogenous structures were performed using a Nikon Eclipse 80i light microscope with differential interference contrast (DIC) illumination (Figs. 4–9). Slides were prepared using the inclined coverslip method (Kawato & Shinobu 1959, Nugenta *et al*. 2006) and also with transparent adhesive tape (Titan Ultra Clear Tape, Conglom Inc., Toronto, Canada) (Bensch *et al*. 2012). Lactic acid (clear) was used as mounting medium for the measurements and Lactophenol cotton blue was used in some preparations to improve the contrast of the naturally hyaline structures. The terminology of morphological structures followed those used for description of *Ramularia* species by Crous *et al*. (2011c). The recorded measurements represent the minimum value followed by the 95 % confidence interval of 30 individual measurements and the maximum value for both length and width. For colony macromorphology the isolates were inoculated on Potato Dextrose Agar (PDA), Oatmeal Agar (OA) and Malt Extract Agar (MEA) (Crous *et al*. 2009f), and incubated in the dark at 25 °C. After 14 d, the colony diameter was measured and the colony colour was described according to the mycological colour charts of Rayner (1970). Additionally, for each species, representative strains were selected to be included in a growth study. The isolates were inoculated onto MEA plates in triplicate, and placed in a serial incubator, in the dark, at temperatures ranging from 6–36 °C, with 3 °C intervals, and also at 40 °C. Measurements of colony diameters were taken after 14 d (Fig. 2). Nomenclatural data was deposited in MycoBank (Crous *et al*. 2004a).

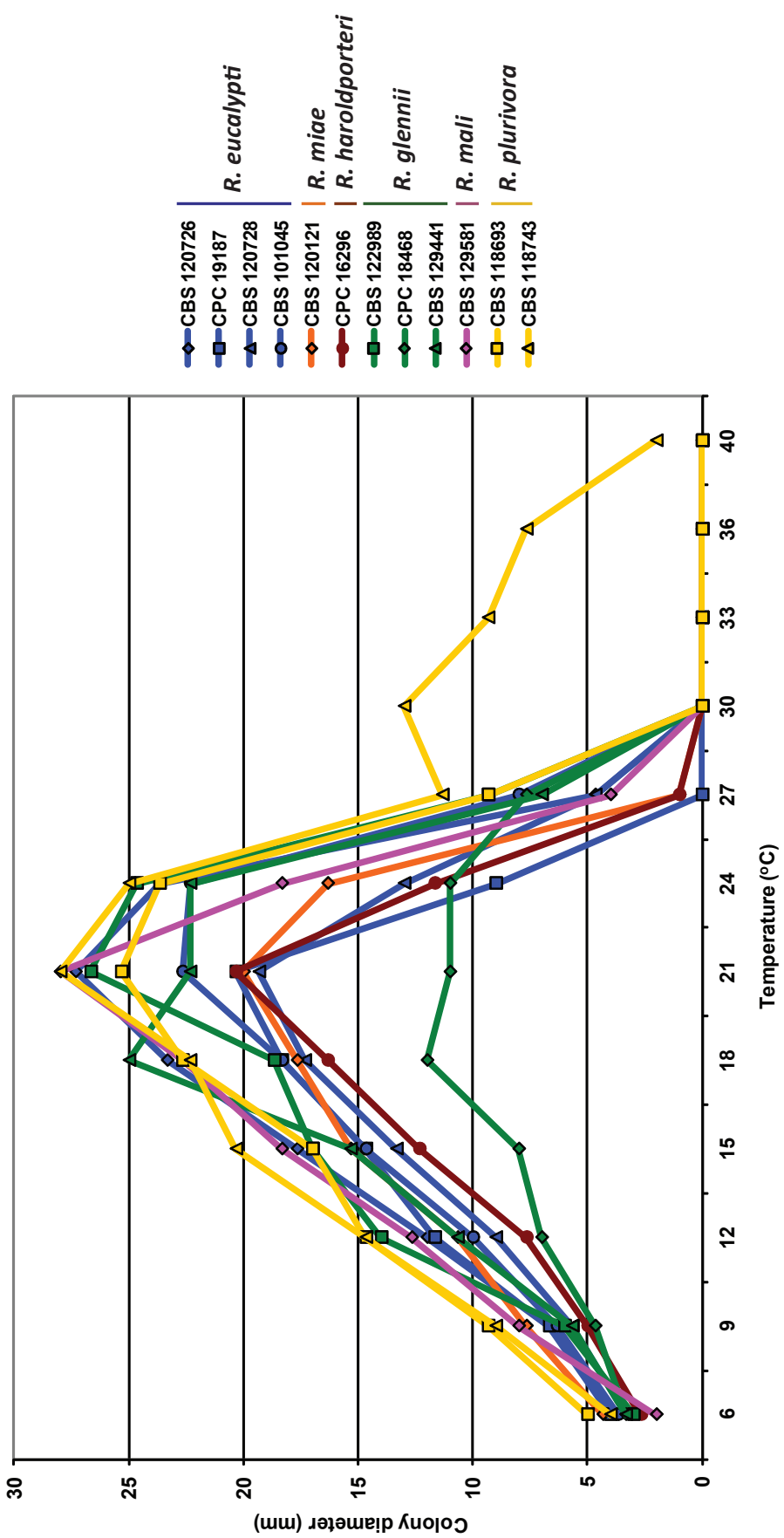

Fig. 2. Growth measurements of colony diameters (mm) of representative isolates from each clade (Fig. 3) taken from 6–36 °C, with 3 °C intervals, and also at 40 °C. Lines with the same colour represent strains from the same clade. Different strains within each clade are represented with different symbols. Colony diameters differed with less than 2 mm between replicates and are therefore not supplied with error bars.

RESULTS

DNA amplification and phylogenetic analysis

New primers for the *gapdh*, *tef1*-α and *rpb2* loci were designed based on a larger dataset of *Ramularia* and other cercosporoid genera (Videira, unpubl. data) that proved to be effective for species within the genus *Ramularia.* These primers were used when no amplification was obtained with the standard primers (Table 2).

In the phylogenetic analysis six of the 10 screened loci were used, namely ITS, *rpb2*, *gapdh*, *actA*, *tef1*-α and *his3*. The LSU sequences obtained were nearly identical to one another and did not provide useful information to resolve the speciescomplex and were therefore not included in the subsequent phylogenetic analyses. The amplification of *cmdA* and *chs-1* was not successful for all the isolates and the inclusion of missing data in the alignment would negatively influence the posterior probability and bootstrap support values. The amplification of *tub2* often generated multiple PCR products and was only successful for a reduced number of isolates. Although these sequences were excluded from the phylogenetic analyses, they have been deposited in GenBank under accession numbers KJ504473–KJ504495 (TUB), KJ504496–KJ504529 (*cmdA*), KJ504530–KJ504550 (CHS) and KJ504724–KJ504764 (LSU). Neighbour-joining analysis using the HKY85 substitution model was applied to each data partition in order to check the stability and robustness of each species clade (data not shown). The ITS locus did not differentiate species well, supporting only *R. eucalypti*, *R. miae*, *R. plurivora* and *Ramularia* sp., while most of the isolates formed a basal polytomy. The tree based on the *actA* gene had a better resolution by additionally segregating strains of *R. glennii* and *R. haroldporteri*. The *his3* phylogeny resolved seven species but with very low bootstrap support values. The individual trees based on the *rpb2*, *gapdh* and *tef1*-α loci all supported seven species with high bootstrap support. These genes also suggested a split of *R. glennii* in two clades but with a low support value and with internal subclades that were not supported either by the geographical origin or by the morphological characteristics of the isolates.

The concatenated alignment contained 33 strains, including the outgroup sequence (*R. nyssicola*). A representative strain was selected from strains representing the same substrate and country and which shared identical sequences for all loci (Table 1). The final alignment contained a total of 2 651 characters divided in 6 partitions containing 665 (*rpb2*), 486 (ITS), 551 (*gapdh*), 358 (*his3*), 177 (*actA*), 389 (*tef1*-α) characters, respectively. From the total alignment, 40 characters were excluded from the phylogenetic analysis: 25 characters were artificially introduced as spacers to separate the genes and 15 characters in the *gapdh* locus (alignment positions 1216–1230, see TreeBASE) represented a longer sequence in the outgroup compared to the ingroup sequences.

The results of the MrModelTest analyses indicated that the ITS partition had fixed (equal) base frequencies, whereas all the other partitions had dirichlet base frequencies. The optimised models for this dataset were K80+I+G for ITS and GTR+I+G for all the other partitions.

The Bayesian analysis generated 1 702 trees from which 424 trees were discarded (25 % burnin). The 50 % majority rule consensus tree (Fig. 3) and posterior probabilities (left numbers) were calculated from the remaining 1 278 trees. The alignment contained a total of 933 unique site patterns: 255 (*rpb2*), 74 (ITS), 210 (*gapdh*), 81 (*his3*), 99 (*actA*), 214 (*tef1*-α).

The parsimony analysis generated the maximum limit of 1 000 equally most parsimonious trees and the bootstrap support values (right numbers) higher than 75 % are displayed (Fig. 3). The gaps in the alignment were treated as fifth base and from the analysed characters 1 670 were

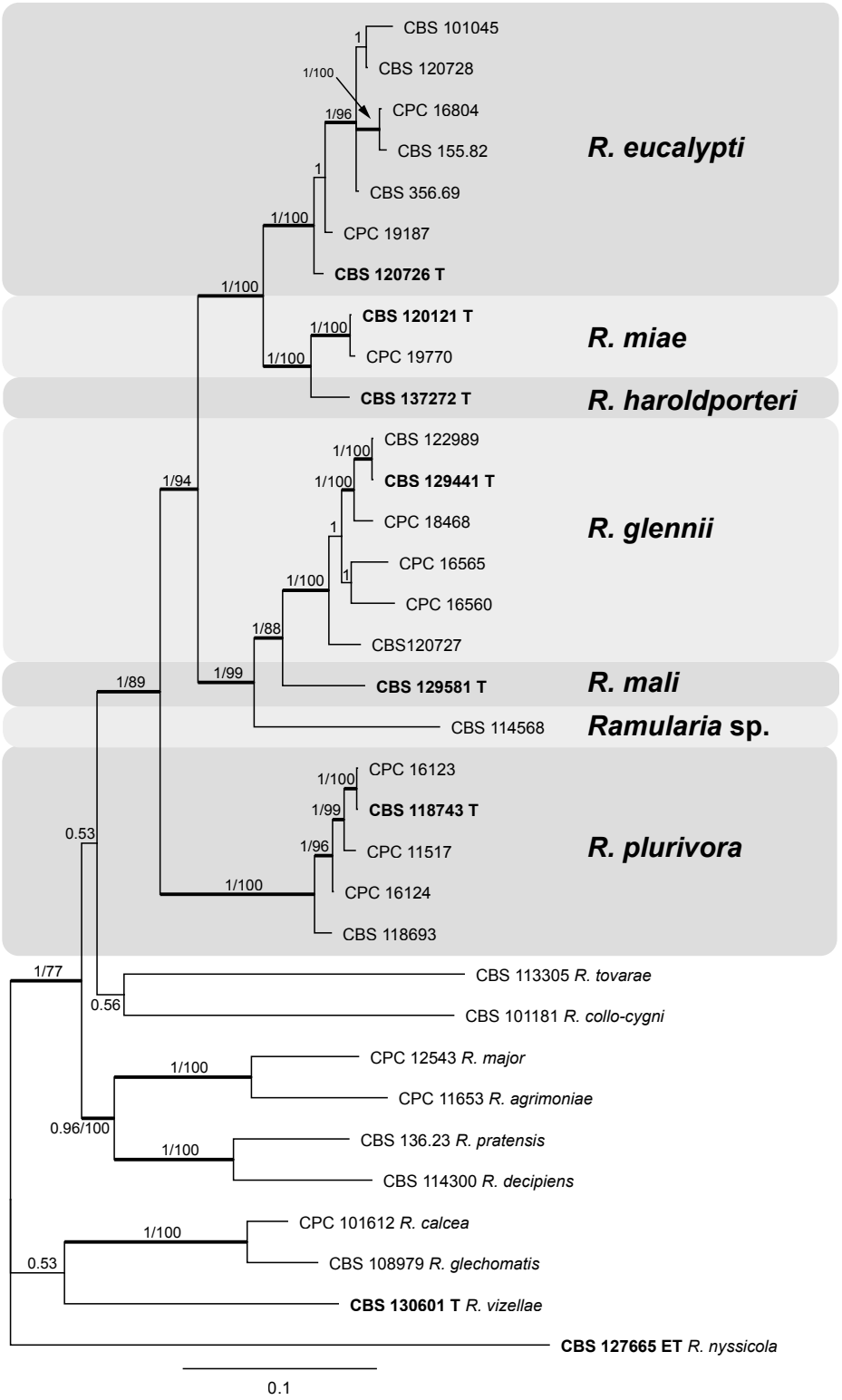

Fig. 3. Phylogenetic tree resulting from a Bayesian analysis of the combined 6-gene sequence alignment. Both Bayesian posterior probabilities (left number) and parsimony bootstrap support values > 75 % (right number) are indicated at the nodes, and the scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Species clades in the *R. eucalypti* complex are indicated in coloured blocks and species names in black text. Ex-type strains are in **bold** and indicated with the letter T while ex-epitype strains are indicated with ET. The tree was rooted to *R. nyssicola* (CBS 127665).

constant, 234 were variable and parsimony-uninformative and 707 were parsimonyinformative. A parsimony consensus tree was calculated from the equally most parsimonious trees and the branches present in the strict consensus tree are mapped with a thicker stroke on the Bayesian tree (Fig. 3). Phylogenetic trees based on the combined dataset and generated with both parsimony and Bayesian analyses (Fig. 3) separated strains into seven well-supported species within this complex: *R. eucalypti*, *R. glennii*, *R. haroldporteri*, *R. mali*, *R. miae*, *R. plurivora* and *Ramularia* sp. *Ramularia eucalypti* is no longer the only species of the genus to be found on *Eucalyptus* with the addition of the newly described *R. glennii*. The clinical isolates do not cluster in the same clade as *R. eucalypti*, and are here described as *R. glennii* and *R. plurivora*. The species causing the apple and pear fruit damage in storage is a new species as well (*R. mali*) considering both the branch length and the posterior probability value separating it from the closest species (*R. glennii*). The clades of *R. eucalypti*, *R. glennii* and *R. plurivora* show some interspecific variability within the evaluated genes, but not strong enough to support further division into additional species.

MALDI-TOF MS

A total of 22 strains from *Ramularia* were used to create the *Ramularia* in-house library. Twenty-one strains belonged to *R. eucalypti* s.lat. and one strain of *R. vizellae* was used as a reference species outside the complex while still within the same genus. It was not always possible to obtain good quality MSPs for all strains (e.g. *R. haroldporteri* and *Ramularia* sp.) as the crude protein extraction performed with the current protocol was problematic for a few strains. For the PCA dendrogram 26 MSPs were used in total, including the 22 MSPs from the *Ramularia* in-house library and four *Cladosporium* strains from the Bruker Filamentous fungi v. 1 Library that were used as an outgroup (Fig. 1). The distance level presented on the dendrogram is a relative measure of the differences among the MSP peak patterns and three clades can be observed: *R. plurivora*, *R. glennii* /*R. mali* and *R. eucalypti* /*R. miae*. The PCA dendogram topology shows a broadly similar topology to the DNA phylogeny but it is unable to separate the species *R. glennii* from *R. mali* and *R. eucalypti* from *R. miae*, which are closely related. The MALDI-TOF MS identification results of the four clinical isolates confirmed their identity as *R. plurivora* and *R. glenni*, respectively, as secure genus and species identification was attained with log-score > 2.0. The identification results showed that the top ten identification hits per tested spot per isolate were matching only with MSPs of *Ramularia* species.

Taxonomy

The multigene analysis resulted in seven well-supported species. Four new species are described, two are redescribed on different cultural media, and one new combination is proposed. Culture growth curves were not consistent among isolates within the same phylogenetic clade (Fig. 2). Lines representing isolates within the same clade are depicted with the same colour, but with different symbols. The optimal growth temperature for the majority of the isolates was 21 °C and only two isolates, CBS 18468 and CBS 129441, grew better at 18 °C. The isolates within the *R. eucalypti* clade (blue) reached diameters between 18 and 24 mm while isolates of *R. glennii* reached 18, 22 and 26 mm, respectively. The isolate CBS 118743 from the *R. plurivora* clade, isolated from human bone marrow in the Netherlands, presented morphological dimorphism (Fig. 9). The mycelium was filamentous until 27 °C, while from 30 °C upwards, the morphology switched into an arthroconidial yeast form that was even able to grow at 40

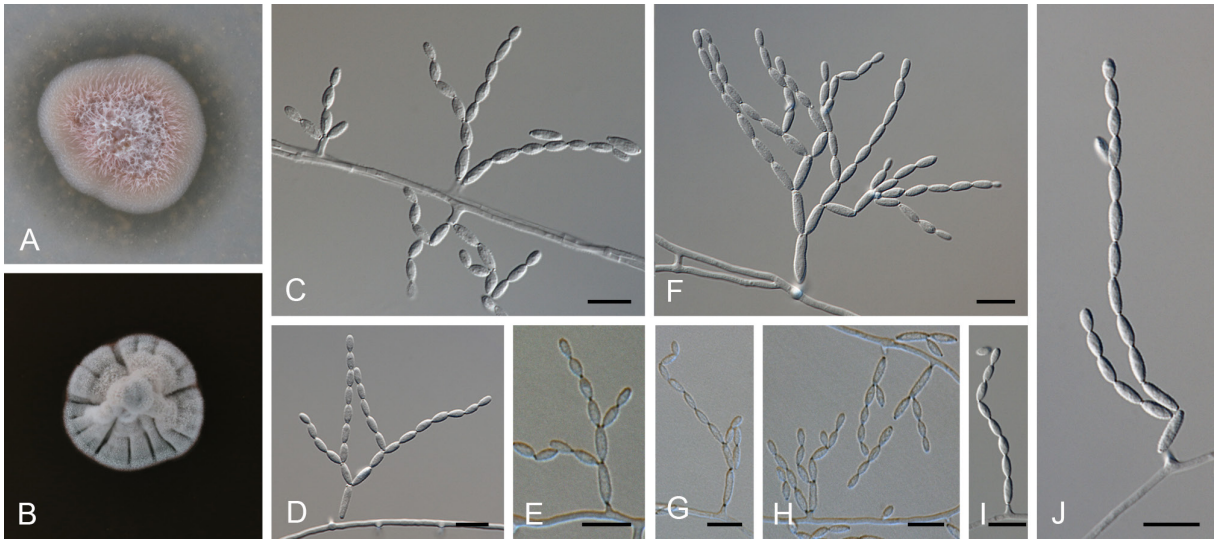

Fig. 4. *Ramularia eucalypti* (CBS 120726). A. Culture on OA; B. Culture on MEA; C–J. Hypha, conidiophores and conidia. Scale bars = 10 µm.

°C. None of the other isolates within this clade displayed morphological dimorphism and were unable to grow from 30 °C onwards.

Ramularia eucalypti Crous, Fung. Diversity 26: 174. 2007. MycoBank MB501270. Fig. 4.

Mycelium consisting of septate, branched, smooth to finely verruculose, hyaline, 1–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth to finely verruculose, terminal and lateral, (6–)11–13(–20) × 1(–2) µm, with 1–3 apical loci almost flat or short cylindrical; *scars* thickened, darkened, refractive, 0.5–1 µm diam. *Ramoconidia* hyaline, smooth to finely verruculose, subcylindrical to fusiform, aseptate, (5–)7–8(–11) × (1.5–)2(–3) µm. *Intercalary conidia* hyaline, smooth to finely verruculose, aseptate, fusiform to oval, (4–)5.5–6(–9) × (1.5–)2(–2.5) µm, in branched chains (–11). *Terminal conidia* hyaline, smooth to finely verruculose, aseptate, obovoid, (3–)3.5–4(–6) × (1–)1.5–2 µm; *hila* thickened, darkened, refractive, 0.5–1 µm diam.

Culture characteristics: On MEA surface folded, mostly dirty white but with pale greenish grey tones, radially striated with lobate, concave, feathery margin, with fluffy aerial mycelium, reverse isabeline with iron-grey patches and with small buff margin, reaching 22 mm after 2 wk at 25 °C. On OA surface with sparse fluffy aerial mycelium in the centre, rosy-buff with greenish grey patch, low convex, forming a 5 mm ring of media discoloration, reaching 20 mm after 2 wk at 25 °C. On PDA colony flat, radially striated with entire edge, mostly flat aerial mycelium, greenish grey with dirty white thin margin, reverse olivaceous-grey with dirty white margin, reaching 20 mm after 2 wk at 25 °C.

Specimens examined: **Australia**, Queensland, Cairns, Kuranda, Karoomba River Walk, on leaves of *Eucalyptus* sp., 19 Aug. 2006, P.W. Crous & J. Stone, CPC 13304 = CBS 120728. **Italy**, Norcia, on *Corymbia grandifolia*, 10 May 2006, W. Gams (holotype CBS H- 19832, ex-type cultures CPC 13043 = CBS 120726, CPC 13044, CPC 13045). **The Netherlands**, Gelderland, Wageningen, on *Phragmites* sp., 19 Feb. 2011, P.W. Crous, CPC 19187, CPC

19188; Noord-Holland, Kortenhoef, Kortenhoefse Plassen, associated with *Puccinia* sp. on *Carex acutiformis*, Jan. 1982, W. Gams & O. Constantinescu, CBS 155.82; Anloo, Pinetum Anloo, on *Pinus wallichiana*, 8 June 2009, W. Quaedvlieg, CPC 16804; unknown location, on *Malus sylvestris* (cv. Golden Delicious), Mar. 1969, Van der Scheer, CBS 356.69; Baarn, on *Geranium pusillum*, May 1998, H.A. van der Aa, CBS 101045.

Notes: Currently, *R. eucalypti* is the only confirmed member of *Ramularia* known from *Eucalyptus* since *R. pitereka* and similar species were allocated to *Quambalaria*. The specimens examined show that this is a plurivorous species, able to colonise very different hosts like *Eucalyptus* (*Myrtaceae*), *Pinus* (*Pinaceae*) and *Phragmites* (*Poaceae*). Among the examined strains, CBS 356.69 sporulated sparsely and never formed conidial chains longer than two conidia, probably due to the fact that this is an old culture (from 1969), and strain CBS 101045 produced long chains with up to 13 intercalary conidia.

Ramularia glennii Videira & Crous, **sp. nov.** MycoBank MB808138. Fig. 5.

Etymology: Named after the collector of one of the isolates, Anthony E. Glenn, a plant pathologist from the Agricultural Research Service of the United States Department of Agriculture (ARS/USDA), who found it growing in the rubber of the refrigerator where he usually stored the samples related to his *Fusarium* research.

Mycelium consisting of septate, branched, smooth, hyaline, 1–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* smooth, hyaline, terminal and lateral, (5–)13–16(–25) × 1(–2) µm, sympodial proliferation with 1–3 apical loci almost flat or protuberant, cylindrical; *scars* thickened, darkened, refractive, 0.5–1 µm diam. *Ramoconidia* hyaline, smooth to finely verruculose, subcylindrical to clavate or oval, 0–1-septate, hyaline, (6–)9–11(–15) × (2–)3(–4) µm. *Intercalary conidia* hyaline, smooth to finely verruculose, aseptate, fusiform or oval, (5–)6.5–8(–12) × (2–)2.5(–3) µm, in branched chains of up to 7. *Terminal conidia*, hyaline, smooth to finely verruculose, aseptate, obovoid, (3–)5–5.5(–8) × (1.5–)2(–3) µm; *hila* thickened, darkened, refractive, 0.5–1 µm diam.

Culture characteristics: On MEA surface folded, radially striated and sinking into the media, vinaceous-buff, undulate feathery and concave margin, reverse ochreous, reaches 27 mm after 2 wk at 25 °C. On OA surface folded and slightly depressed, rosy-buff, margin undulate and with flat mycelium while fluffy aerial mycelium covers the centre, 5 mm halo around the colony, reaches 22 mm after 2 wk at 25 °C. On PDA surface mostly flat, white, pale mouse-grey in the centre, undulate margins, reverse olivaceous-grey in the centre and buff towards the margin, reaches 24 mm after 2 wk at 25 °C.

Specimens examined: **Iraq**, Al-Kora, Basrah, on leaves of *Eucalyptus camaldulensis*, 1 Mar. 2009, A. Saadoon, CPC 16560, CPC 16561, CPC 16565. **Italy**, Viterbo, on leaves of *Corymbia grandifolia*, 1 Apr. 2006, W. Gams, CPC 13047 = CBS 120727, CPC 13048. **The Netherlands**, Rotterdam Maasstad Ziekenhuis (Clara), on human bronchial alveolar lavage, 2011, unknown collector (holotype CBS H-21617, type culture CBS 129441); Rotterdam Maasstad Ziekenhuis (Clara), on human skin tissue, 2008, unknown collector, CBS 122989. **USA**, Athens, on rubber of refrigerator, Sept. 2010, A. Glenn, CPC 18468, CPC 18469, CPC 18470.

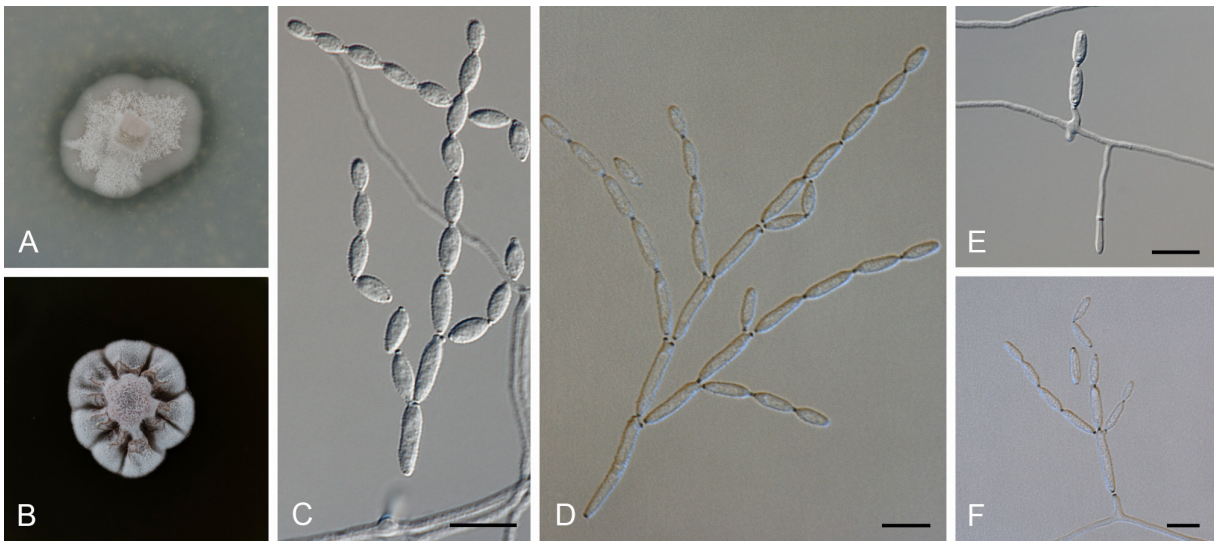

Fig. 5. *Ramularia glennii* (CBS 129441). A. Culture on OA; B. Culture on MEA; C–F. Hypha, conidiophores and conidia. Scale bars = 10 µm.

Notes: The specimens examined were collected from a wide range of substrates worldwide. The multigene phylogeny showed some internal structure that was insufficient to confidently split this group in more than one species. Morphologically, all the strains were similar but strain CBS 129441 had slightly longer ramoconidia than the rest and the isolate CPC 18468 showed an optimal growth rate at 18 °C instead of 21 °C (Fig. 2), which may reflect some intraspecific variation.

Ramularia haroldporteri Videira & Crous, **sp. nov.** MycoBank MB808136. Fig. 6.

Etymology: Named after Harold Porter, who bequeathed the land in Leopard's Kloof (Gorge in Afrikaans) to the National Botanical Gardens of South Africa, who in turn named this garden in his honour.

Mycelium consisting of septate, branched, smooth to finely verruculose, hyaline, 1–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth to finely verruculose, terminal and lateral, (7–)10–13(–19) × 1(–2) µm, sympodial proliferation with 1–3 apical loci almost flat or short cylindrical; *scars* thickened, darkened, refractive, 0.5–1 µm diam. *Ramoconidia* subcylindrical, oval or ellipsoid, aseptate, hyaline, smooth to finely verruculose, (5–)8–9(–13) × (1.5–)2 µm. *Intercalary conidia* hyaline, smooth to finely verruculose, aseptate, oval or ellipsoid, (4 –)5 – 6(– 8) × (1.5–)2(–2.5) µm, in branched chains of up to 8. *Terminal conidia*, hyaline, smooth to finely verruculose, aseptate, obovoid, (2.5–)3–4(–4.5) × (1.5–)2(–2.5) µm; *hila* thickened, darkened, refractive, 0.5–1 µm diam.

Culture characteristics: On MEA surface convex, strongly folded, smoke-grey, with undulate and concave margin, flat aerial mycelium, reverse greyish sepia, reaches 18 mm after 2 wk at 25 °C. On OA folded with undulate margins, smokegrey, flat aerial mycelium, reaches 15 mm after 2 wk at 25 °C. On PDA surface folded with undulate margins, smoke-grey, flat aerial mycelium, reverse olivaceous-grey, reaches 15 mm after 2 wk at 25 °C.

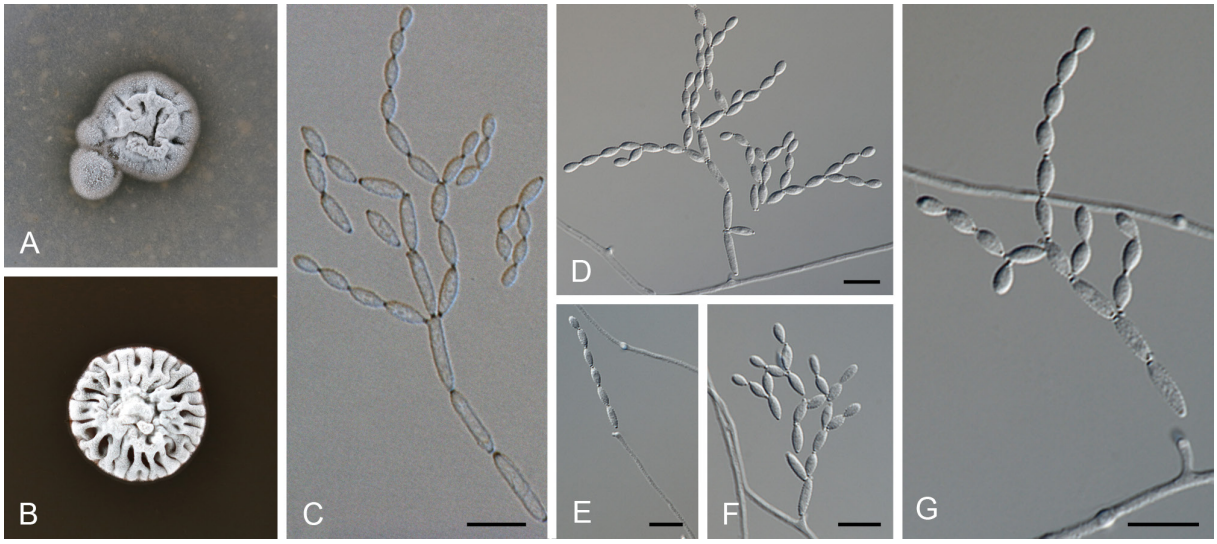

Fig. 6. *Ramularia haroldporteri* (CBS 137272). A. Culture on OA; B. Culture on MEA; C–G. Hypha, conidiophores and conidia. Scale bars = 10 µm.

Specimen examined: **South Africa**, Western Cape Province, Betties Bay, Harold Porter Botanical Garden, on leaves of unidentified bulb plant, 14 Jan. 2009, P.W. Crous (holotype CBS H-21616, ex-type culture CPC 16296 = CBS 137272).

Notes: *Ramularia haroldporteri* differs from *R. miae* by producing significantly shorter ramoconidia, intercalary and terminal conidia and by not producing exudate droplets on top of the mycelium. In the individual gene phylogenetic trees, all genes except the ITS separates *R. haroldporteri* from *R. miae*.

Ramularia mali Videira & Crous, **sp. nov.** MycoBank MB808135. Fig. 7.

Etymology: Named after its occurrence on apple (*Malus*).

Mycelium consisting of septate, branched, smooth, hyaline, (1–) 1.5(– 2) µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* finely verruculose, hyaline, terminal and lateral, (6.5–)11–13.5(–18) × (1–)1.5(–2) µm, sympodial proliferation with 1–2 apical loci flattened or protuberant cylindrical; *scars* thickened, darkened, refractive, 0.5–1 µm diam. *Ramoconidia* subcylindrical to clavate or fusoid, 0(–1)-septate, hyaline, finely verruculose, (5–)7–9(–16) × 2(–3) µm, with 1–2(–3) apical loci. *Intercalary conidia* hyaline, finely verruculose, aseptate, fusoid or ovoid, 5–6(–8) × 2(–3) µm, in branched chains of up to 6. *Terminal conidia* hyaline, finely verruculose, aseptate, obovoid, (3–)4–4.5(–6) × (1–)1.5–2(–2.5) µm; *hila* thickened, darkened, refractive, 0.5–1 µm diam.

Culture characteristics: On MEA surface folded, undulate margin, white greyish, feathery and concave margin, reverse iron-grey with greyish sepia margin, reaches 21 mm after 2 wk at 25 °C. On OA surface flat, smooth, entire edge, buff, 3 mm halo around the colony, reaches 18 mm after 2 wk at 25 °C. On PDA surface low convex, white greyish, flat aerial mycelium, slightly undulate margin, reverse iron-grey with rosy-buff patch, reaches 25 mm after 2 wk at 25 °C.

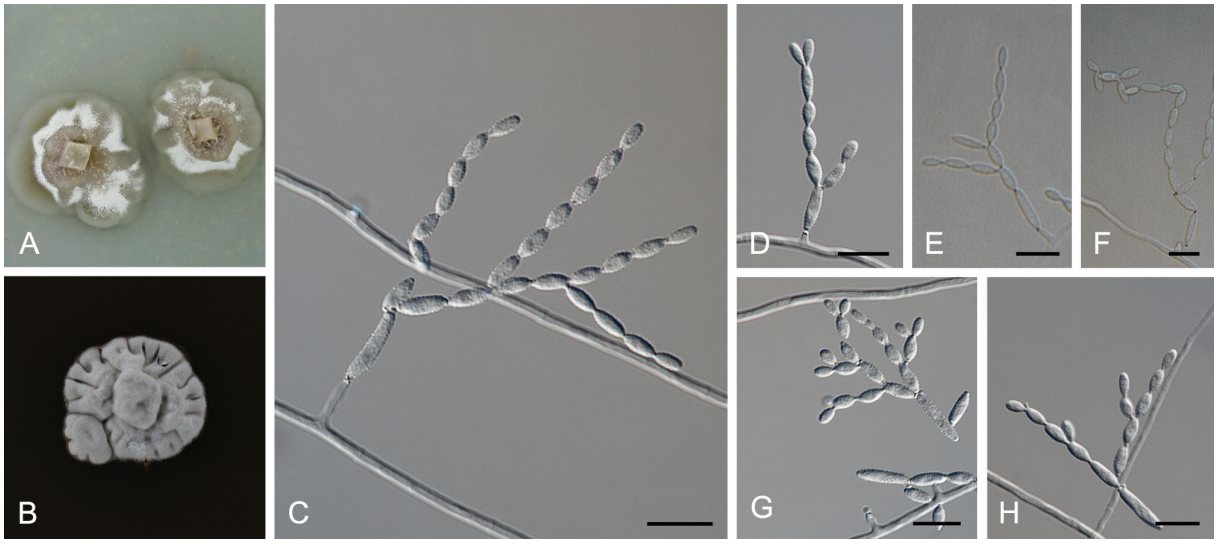

Fig. 7. *Ramularia mali* (CBS 129581). A. Culture on OA; B. Culture on MEA; C–H. Hypha, conidiophores and conidia. Scale bars = 10 µm.

Specimen examined: **Italy**, Piemont, on *Malus domestica* fruit in cold storage, May 2011, unknown collector (holotype CBS H-21618, culture extype CBS 129581).

Notes: This species, previously identified as *R. eucalypti*, is an emerging problem causing a post-harvest disorder in healthy pome fruits in cold storage, namely apple cv. Ambrosia and pear cv. Conference (Giordani *et al*. 2012). An epidemiological study reports that symptomless fruits harvested from trees showing leaf spot symptoms caused by this pathogen, developed the lenticel rot disease during the subsequent months of cold storage (Gianetti *et al*. 2012). *Ramularia mali* differs from *R. glennii* by forming shorter conidiogenous cells, shorter and thinner ramoconidia and shorter intercalary and terminal conidia.

Ramularia miae Crous, Fungal Planet 3. 2006. MycoBank MB501004. Fig. 8.

Mycelium consisting of septate, branched, smooth to finely verruculose, hyaline, 0.5–1 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth to finely verruculose, terminal and lateral, (5.5–)9–12(–24) × 1 µm, sympodial proliferation with 1–2 apical loci almost flat or short cylindrical; *scars* thickened, darkened, refractive, 0.5–1 µm diam. *Ramoconidia* hyaline, smooth to finely verruculose, subcylindrical to clavate or fusiform, 0–1-septate, (6–) 9–10(–16) × (1.5–)2 µm. *Intercalary conidia* hyaline, smooth to finely verruculose, aseptate, subcylindrical to oval, (5.5–)7– 8.5(–12.5) × (1.5–)2(–3) µm, in branched chains of up to 7. *Terminal conidia*, hyaline, smooth to finely verruculose, aseptate, obovoid, (4–)5–6(–9) × (1.5–)2(–3) µm; *hila* thickened, darkened, refractive, 0.5–1 µm diam.

Culture characteristics: On MEA surface convex, folded, dirty-white to pale olivaceous-grey, with lobate margin, short fluffy aerial mycelium, reverse iron-grey with small buff margin, reaches 15 mm after 2 wk at 25 °C, produces small droplets of slimy exudate. On OA surface flat or slightly folded with undulate margins, pale olivaceous-grey mycelium, 5 mm halo in the media, producing several droplets of colourless slimy exudates, reaches 15 mm after 2 wk

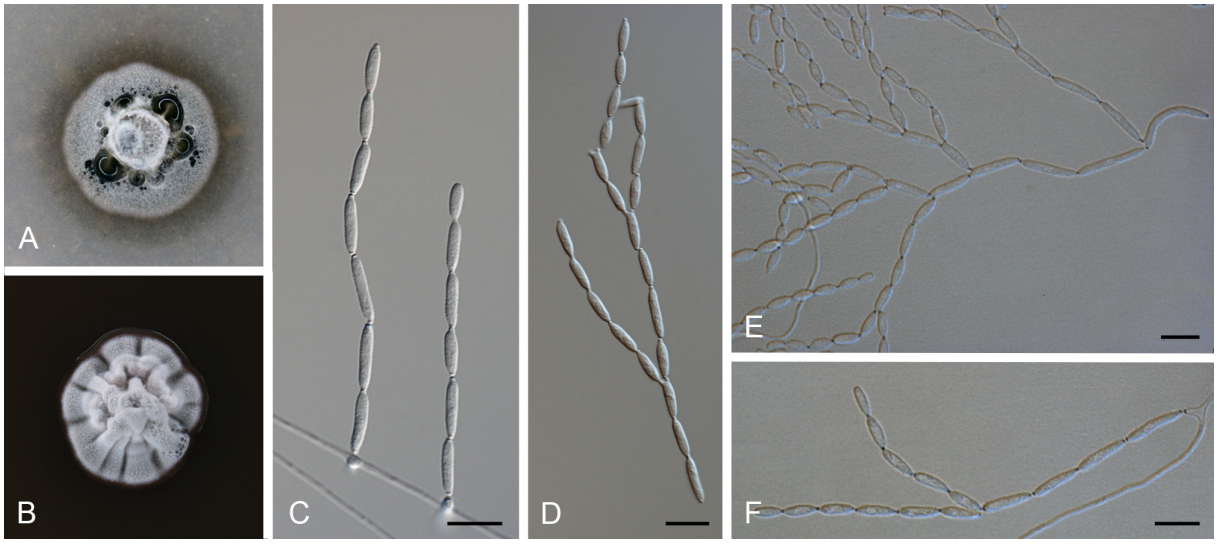

Fig. 8. *Ramularia miae* (CBS 120726). A. Culture on OA; B. Culture on MEA; C–F. Hypha, conidiophores and conidia. Scale bars = 10 µm.

at 25 °C. On PDA surface folded with lobate margins, olivaceous-grey with white-grey patch, producing large droplets of colourless slimy exudates, reaches 15 mm after 2 wk at 25 °C.

Specimens examined: **South Africa**, Western Cape Province, Betties Bay, Harold Porter Botanical Garden, on *Wachendorfia thyrsiflora*, Jan. 2006, P.W. Crous & M.K. Crous (holotype CBS H-19763, ex-type cultures CBS 120121 = CPC 12736, CPC 12737, CPC 12738); Western Cape Province, Kirstenbosch Botanical Garden, on *Gazania rigens* var. *uniflora*, 9 Aug. 2011, P.W. Crous, CPC 19835; Kirstenbosch Botanical Garden, on *Leonotis leonurus*, 30 July 2011, P.W. Crous, CPC 19770.

Notes: Morphologically, *R. miae* differs from *R. eucalypti* by having shorter conidiogenous cells and ramoconidia and longer intercalary and terminal conidia. *Ramularia miae* was first observed causing black leaf spots on *Wachendorfia thyrsiflora*, a tall evergreen geophyte with bright red roots that belongs to the Bloodwort family (*Haemodoraceae*). This host is native to South Africa and *R. miae* is likely to occur wherever it is cultivated. In addition, the specimens examined were isolated from two new hosts native to South Africa: *Gazania rigens* var. *uniflora* (*Asteraceae*), a flowering plant that is cultivated as an ornamental worldwide, and *Leonotis leonurus* (*Lamiaceae*), a broadleaf evergreen shrub that is known for its medicinal and slightly psychoactive properties, suggesting a plurivorous *Ramularia* species.

Ramularia nyssicola (Cooke) Videira & Crous, **comb. nov.** MycoBank MB809667
Basionym: *Sphaerella nyssicola* Cooke as '*nyssaecola*'. Hedwigia 17: 40. 1878.
≡ *Mycosphaerella nyssicola* (Cooke) F.A. Wolf as '*nyssaecola*'. Mycologia 32: 333. 1940.

Specimen examined: **USA**, Maryland, Prince George's County, Glen Dale, on fallen overwintered leaves of *Nyssa ogeche* × *sylvatica* hybrid, June 2009, R. Olsen, ex-epitype culture CBS 127665.

Notes: *Mycosphaerella nyssicola* has been recently epitypified from overwintered leaves of *Nyssa sylvatica* trees freshly collected in Maryland, USA (Minnis *et al*. 2011). *Nyssa sylvatica*

or black gum trees (*Cornaceae*) are cultivated as ornamental plants and *M. nyssicola* causes leaf spots that reduce their aesthetic appeal and cause early defoliation. The ITS and LSU sequences supported *M. nyssicola* as a distinct species from *R. endophylla* (= *M. punctiformis*), even though they were almost indistinguishable morphologically (Aptroot 2006). Minnis *et al*. (2011) did not propose a new combination in *Ramularia* at the time because they did not observe the asexual *Ramularia* morph, and the name *M. nyssicola* correctly adhered to the ICBN Art. 59.1. However, the previous Art. 59 has been deleted from the new International Code of Nomenclature for Algae, Fungi and Plants (ICN) and, since January 2013, both asexual and sexual morph names have equal status. We propose a new combination in *Ramularia* because the name *Ramularia* (Unger 1833) predates *Mycosphaerella* (Johanson 1884a), and species of *Mycosphaerella* s.str. have been shown to be confined to taxa with *Ramularia* asexual morphs (Crous 2009c), which is also supported by the DNA data generated in this study. Furthermore, the genus *Ramularia* has recently been monographed (Braun 1995, 1998), while *Mycosphaerella* (Aptroot 2006) contains an assemblage of more than 40 different genera (Crous 2009e).

Ramularia plurivora Videira & Crous, **sp. nov.** MycoBank MB808132. Fig. 9.

Etymology: Named after its wide host range.

Mycelium consisting of septate, branched, smooth, hyaline, (0.5–) 1–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* smooth, hyaline, terminal and lateral, (6–)10–13(–17) × (0.5–)1(–2) µm, sympodial proliferation with 1–3 apical loci flattened or protuberant cylindrical; *scars* thickened, darkened, refractive, 0.5–1 µm diam. *Ramoconidia* subcylindrical to ellipsoid, 0–1-septate, hyaline, smooth to finely verruculose, (6–)9–11(–18) × (1.5–)2 µm. *Intercalary conidia* hyaline, smooth, aseptate, ellipsoid, smooth to finely verruculose, (6–)7.5–8(–10.5) × (1.5–)2 µm, in branched chains (–7). Terminal conidia hyaline, smooth to finely verruculose, aseptate, ellipsoid, (4–)5–6(–9) × (1–)1.5–2 µm; hila thickened, darkened, refractive, 0.5–1 µm diam. On MEA, *Arthroconidia* smooth, bacilliform, oblong with apices

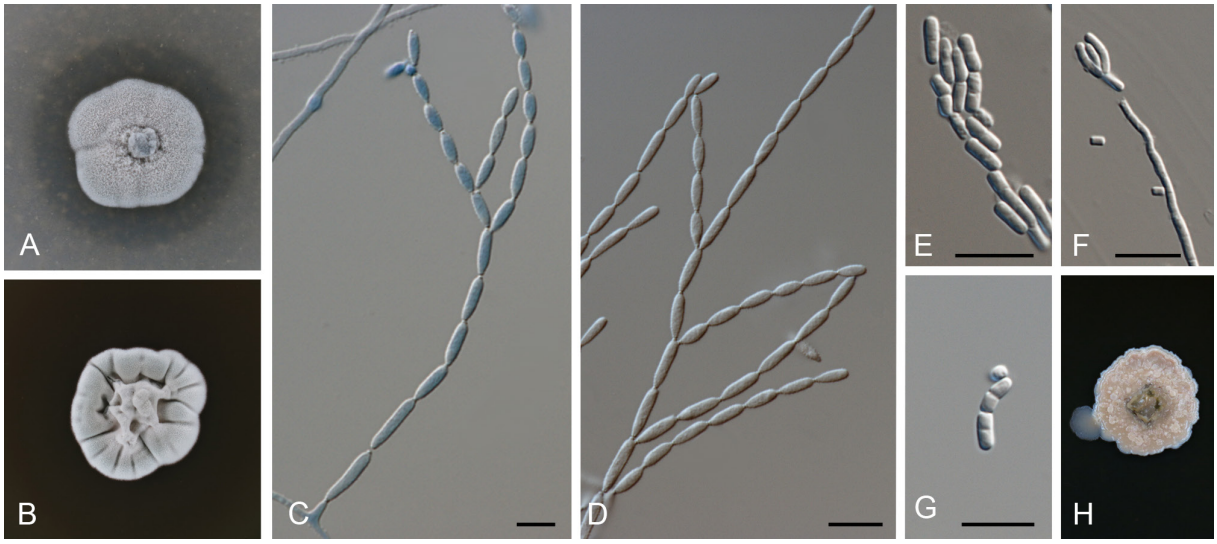

Fig. 9. *Ramularia plurivora* (CBS 118743). A. Culture on OA; B. Culture on MEA; C, D. Hypha, conidiophores and conidia; E–G. Arthroconidia formed at 33 °C; H. Culture on MEA at 33 °C. Scale bars = 10 µm.

rounded or truncate, 0–3-septate, slightly constricted at the septa, 1-septate, (3.5–)4.5–5(–7) × (1–)1.5–2 µm, 2-septate, (6–)8–9(–12) × 1.5–2 µm, 3-septate, (8–)10–11(–13.5) × (1.5–)2(–2.5) µm.

Culture characteristics: On MEA surface dirty white with a greenish grey tinge, folded, radially striated with undulate margins, reverse fuscous black with a buff margin, reaches 25 mm after 2 wk at 25 °C. On OA surface dirty white to light greenish grey, smooth, with entire edge, central area sporulating profusely and outer ring sparse in mycelium, reaches 35 mm after 2 wk at 25 °C. On PDA colonies have a dirty white and greenish grey aspect, low convex, undulate margins, central area sporulating profusely and outer ring sparse in mycelium, reaches 25–35 mm after 2 wk at 25 °C.

Specimens examined: **Republic of Korea**, on *Coleosporium plectanthri* on *Plectranthus excisus*, 2004, H.D. Shin, CPC 11517. **The Netherlands**, Den Haag, Laboratory of Medical Microbiology, Hospital Leyenburg, from human bone marrow, 2005, holotype CBS H-21619, ex-type culture CBS 118743 = CPC 12207; Hilversum, Central Biological and Serological Laboratory, on human skin from neck, 20 May 2005, CBS 118693 = CPC 12206; on melon in storage, 1 Jan. 2008, J.H. Houbraken, CPC 16123, CPC 16124.

Notes: The strain CBS 118743 presented temperature-induced morphological dimorphism being filamentous until 27 °C and an arthroconidial yeast form from 30 °C up to 40 °C. This temperature-induced dimorphism may be related with the ability to cause disease. Isolates CPC 16123, CPC 11517, CBS 118693 were not able to grow at 40 °C. However, after a week at 40 °C, when transferred back to 21 °C, they were able to grow, meaning they were able to survive at 40 °C for that period of time.

***Ramularia* sp.**

Culture characteristics: On MEA surface convex, folded, white with very few and small droplets of pale luteous exudates, margin undulate and feathery, reverse umber with ochreous margin, reaching 18 mm after 2 wk at 25 °C. On OA surface convex, white and feathery, margin undulate and without aerial mycelium, 2 mm hazel ring around the colony, reaching 20 mm after 2 wk at 25 °C. On PDA surface convex, white, margin slightly undulate and feathery, reverse dark mouse grey with pale luteus margin, reaching 18 mm after 2 wk at 25 °C; culture sterile.

Specimen examined: **Sweden**, Uppland, Knovsta, isolated from *Epilobium hirsutum* L., 22 Sept. 1989, *E. Gunnerbeck*, CBS 114568.

Notes: This strain was previously identified as *R. epilobiana*. The type specimen of *R. epilobiana* was described from *Epilobium hirsutum* in France, and no ex-type culture is available. The culture CBS 114568 was sterile and we were unable to compare its morphology with that of the type description. However, it is very doubtful that it represents the true *R. epilobiana* since all species of the *R. eucalypti* complex have catenate, narrow conidia, and *R. epilobiana* is characterised by having broadly ellipsoid-ovoid conidia that are formed singly. The DNA sequences obtained from this strain differ significantly from the sequences of the closest strain CBS 129581. Therefore, we rename it as '*Ramularia* sp.' and retain it as a potential new species pending the collection of fresh material from the same host and country.

DISCUSSION

Eucalyptus is one of the most important commercially afforested genera cultivated to meet the increasing global demand for wood and paper pulp. Over the years, more than 50 species of the family *Mycosphaerellaceae* have been described causing diseases on *Eucalyptus* trees (Quaedvlieg *et al*. 2014). However, since the introduction of molecular techniques, many wellestablished plant pathogens have been revealed to represent species complexes (Crous & Groenewald 2005, Groenewald *et al*. 2005, Damm *et al*. 2012a, b, Weir *et al*. 2012). The pathogen *R. eucalypti* has certainly proved to be no exception.

Using a polyphasic approach involving morphology, multi-gene phylogeny and MALDI-TOF MS, a total of seven species were accepted within the complex: *R. eucalypti*, *R. glennii*, *R. haroldporteri*, *R. mali*, *R. miae*, *R. plurivora* and one undescribed *Ramularia* species. Species discrimination was mostly based on the multigene phylogeny since it clearly separated them into stable and strongly supported monophyletic clades while the morphological features and the MALDI-TOF MS PCA dendrogram did not consistently discriminate all species.

Within the clades of *R. eucalypti* and *R. glennii*, some phylogenetic structure was observed that was not resolved consistently in all gene trees (data not shown) and, in accordance with the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) concept, the transition from concordance to conflict determined the limit of these species (Taylor *et al*. 2000). The isolates within these clades have been collected worldwide and the phylogenetic structure observed suggests that the isolates studied may represent populations in the process of divergence. It has been shown that *Mycosphaerella* populations can be carried within asymptomatic *Eucalyptus* trees transported and planted across the world and, given time, they have genetically diverged sometimes to the point of being recognised as distinct species (Crous & Groenewald 2005).

The ITS barcode was not sufficient to achieve species level identification, just like previously reported among other cercosporoid genera, e.g. *Cercospora* (Groenewald *et al*. 2013) and *Pseudocercospora* (Crous *et al*. 2013a). The need to use secondary barcodes to achieve species identification has been highlighted in several studies in recent years (e.g. Fitzpatrick *et al*. 2006, Aguileta *et al*. 2008, Quaedvlieg *et al*. 2012). Secondary barcodes are usually protein-coding genes since their intron sequences introduce more variability that is valuable for species discrimination. From the five protein-coding genes that were used in this study, any of the partial genes *tef1*-α, *rpb2* or *gapdh* could be used as a secondary barcode since they all delineate the seven recognised species. However, further studies are necessary to determine which of these loci would be more adequate to discriminate species within the genus *Ramularia*.

Cultural morphological traits have been used in the past for species discrimination within species complexes in other genera, e.g. *Cercospora apii* s.lat. (Groenewald *et al*. 2005). The species in this study (Fig. 2), however, showed few morphological or cultural features that could be consistently and reliably used to identify them. All the strains used in this study were cultures that were deposited in the CBS or CPC fungal collections and no fresh material was collected. Therefore, any features that may exclusively develop in association with the original host or substrate have not been examined.

Although the genus *Ramularia* is currently accepted as a hostspecific genus this assumption has not been tested experimentally. In the present study, *R. haroldporteri* and *R. mali* have been isolated from a single host while *R. eucalypti*, *R. glennii*, *R. miae* and *R. plurivora* were isolated from multiple hosts, suggesting that both host-specific and plurivorous species may occur in this genus, even within the same species complex. Some species of the *Mycosphaerellaceae* are

known to have the ability of colonising different hosts in order to disperse further in an attempt to find the host to which they are truly pathogenic (Crous & Groenewald 2005). This ability makes it more difficult to determine whether they act as true pathogens, are opportunistic and take advantage of an already debilitated host, or if they are simply saprobic.

The pathogen responsible for causing lenticel rot in fruits of apple (*Malus malus* cv. Ambrosia) and pear (*Pyrus communis* cv. Conference) in the Piemont Province in Italy (Gianetti *et al*. 2012, Giordani *et al*. 2012) is here newly described as *R. mali*. The apple tree orchards in Piemont are an important crop that in 2011 produced 140 000 t of fruit. Healthy apple fruits (*Malus domestica* cv. Ambrosia) collected from trees with leaf spots caused by *R. mali* in the orchards, exhibited disease symptoms during the subsequent months of cold storage (Gianetti *et al*. 2012). Artificial inoculations of healthy apple (*Malus domestica* cv. Ambrosia) with *R. mali* also caused the development of symptoms indicating that this is a true pathogen (Giordani *et al*. 2012). It is thought that the fungus was already present in the country and that the gradual abandonment of the use of broad-spectrum fungicides in the fruit sector allowed the emergence of this pathogen that had passed unnoticed until now. In 2013, in the Trentino Alto-Adige province in Italy, apples from a different cultivar (*Malus domestica* cv. Golden Delicious), also developed the lenticel rot in cold storage and the disease affected 50–60 % of the crop. In the same year and province, *Malus domestica* cv. Braeburn and *Malus domestica* cv. Rosy Glow were also affected. Molecular analysis of these isolates were identical to those of *R. eucalypti* (Crous *et al*. 2007c) (100 % ITS, 99–100 % LSU) deposited on GenBank. However, artificial inoculation of these isolates on ripe fruits of *Malus domestica* cv. Golden Delicious did not result in de development of disease symptoms (Lindner 2013). No isolates from this province were available in the present study. Since the ITS barcode is not sufficient for species identification, the mentioned pathogen can be *R. eucalypti*, *R. mali*, or a different species. If it is *R. mali*, it may be a mere opportunist on *Malus domestica* cv. Golden Delicious and only truly pathogenic to the Ambrosia cultivar. Information on the biology and behaviour of *R. mali* is still lacking and no preventive measures to control this fungus from spreading have been taken.

The newly described species *R. glennii* and *R. plurivora* include strains that were obtained not only from plants but also from human clinical specimens. This is the first time species of the genus *Ramularia* are reported in association with a human host and little is known about their pathogenicity. Some pathogens are able to infect hosts from different kingdoms (van Baarlen *et al*. 2007) and other plant pathogens have been reported capable of infecting humans (Mostert *et al*. 2006, Phillips *et al*. 2013). The fact that only a limited number of isolates was obtained and no previous report is known about *Ramularia* species infecting patients support the hypothesis that this is an opportunistic fungus. However, if potential host species are immunocompromised, opportunistic pathogens may turn into aggressive pathogens (van Baarlen *et al*. 2007). Furthermore, *R. plurivora* (strain CBS 118743) displayed morphological dimorphism (Fig. 9) and was able to grow at 40 °C (Fig. 2). These characteristics are similar to, for example, *Talaromyces marneffei* (syn. *Penicillium marneffei*, *Eurotiomycetes*) (Vanittanakom *et al*. 2006, Houbraken & Samson 2011), a human pathogen known to cause lethal systemic infections in immunocompromised patients. Therefore, further studies are needed to appraise the pathogenicity of *R. plurivora* in order to determine if measures for its rapid identification, containment and treatment should be taken.

MALDI-TOF MS has become a powerful tool in the clinical microbiology workflow for the identification of bacteria and yeasts (Bader 2013, Lau *et al*. 2013). The use of MALDI-TOF MS for routine filamentous fungal identification from clinical samples has only recently been standardised and validated for several species (Cassagne *et al*. 2011, Lau *et al*. 2013, L'Ollivier

et al. 2013). Filamentous fungi present some challenges when compared to yeast and bacteria. They have thicker cell walls that make the protein extraction more difficult, the presence of cell wall pigments inhibit the ionisation process and sporebased protein extractions result in a low variability of mass spectra peaks (Bader 2013). The use of Sabouraud broth as culture media has been shown to inhibit pigmentation and spore production in most species thus improving the quality of the spectra. Furthermore, filamentous fungi have complex phylogenetic relationships that make their species boundaries more difficult to define. The need to use secondary barcodes to resolve species complexes also challenges the MALDI-TOF MS to perform identifications almost at the level of intraspecies subtyping (Degenkolb *et al*. 2008, Cassagne *et al*. 2011, Welker & Moore 2011, Bader 2013, Brun *et al*. 2013).

The species in this complex are very closely related and the PCA dendrogram topology (Fig. 1) individualised only three clades containing *R. plurivora*, *R. glennii* /*R. mali* and *R. eucalypti* / *R. miae*. The dendrogram represents the relative similarity of the peak patterns and is based on a scoring algorithm that is influenced not only by the available number of MSPs that are representative of each species, but also by the intensity of the peaks. The first parameter can be improved by creating more MSPs from different strains of the same species. However, the second parameter can only be improved by preparing all the samples on the same day, using the same amount of protein and using the same settings on the machine, which is virtually impossible when building a large database. Furthermore, the protocol for the crude protein extraction recommended by the manufacturer still needs to be optimised, since it did not work for all strains in this study.

Nevertheless, the use of MALDI-TOF MS as an identification tool has still proven to be reliable not only in previous studies but also in this one. When the in-house *Ramularia* library was challenged with the identification of the clinical isolates of *R. glenni* and *R. plurivora*, a secure genus and species identification log-score (> 2.0) was attained.

In conclusion, the *R. eucalypti* species complex has been resolved with the circumscription of the *R. eucalypti* s.str. and the description of four new species. *Ramularia eucalypti* and *R. glennii* are the only species of this genus described so far from the economically important *Eucalyptus* hosts. *Ramularia mali* is an important pathogen of apple cv. Ambrosia and may become a serious pathogen on other apple cultivars. For the first time, two *Ramularia* species, *R. glennii* and *R. plurivora* have been reported from clinical specimens and *R. plurivora* has the potential of becoming an important human pathogen. The identification of the clinical isolates with MALDI-TOF MS was successful and their MSPs should be added to the commercially available Bruker database of MSPs (BDAL). This would promote a fast and accurate identification of these species in clinical laboratories and would contribute to further investigate the epidemiological relationship with the human host.

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CHAPTER 3

The rise of *Ramularia* from the *Mycosphaerella* labyrinth

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Key words: Cercosporoid, Cryptic species, Multigene, Nomenclature, Phylogeny

Abstract: In this study we aimed to resolve the *Ramularia endophylla* species-complex by applying a polyphasic approach involving morphology and multi-gene phylogeny. Eleven partial genes were targeted for amplification and sequencing for a total of 81 isolates representing *R. endophylla* s. lat. and 32 isolates representing 11 *Ramularia* species that were previously linked to a *Mycosphaerella* sexual morph in literature. A Bayesian phylogenetic analysis, as well as a parsimony analysis, was performed on a combined five-locus dataset and the resulting trees showed significant support for three species within the complex, including the previously described *R. endophylla* and *R. vizellae*, and one novel species, *Ramularia unterseheri*. A parsimony analysis was also separately performed with mating-type gene sequences (MAT1-1-1 and MAT1-2-1) and the resulting tree topologies were in accordance with that of the multigene analysis. A bibliographic review of the proposed links between *Ramularia* spp. and their purported *Mycosphaerella* sexual morphs is also presented, confirming six connections in Ramularia. In spite of more than 10 000 species having been described in *Mycosphaerella*, the majority is shown to belong to other genera, suggesting that the taxa identified as *Mycosphaerella* in much of the plant pathology literature needs to be revisited.

INTRODUCTION

Mycosphaerella s. lat. (Johanson 1884b) is one of the largest genera of *Ascomycetes* and comprises numerous economically important crop pathogens. Over the years more than 10 000 species were described in this genus mainly based on host association or simply because their fruiting bodies were spherical (Aptroot 2006; Crous 2009c; Koike *et al*. 2011). Although the morphology of the sexual morph is relatively uniform, the genus has been associated with more than 40 asexual genera (Crous *et al*. 2009e) including both coelomycetes and hyphomycetes. Early molecular work based on ITS DNA sequencing indicated that *Mycosphaerella* was monophyletic, although the subsequent introduction of additional loci and more taxa showed it was polyphyletic (Crous *et al*. 2009d, e). As a consequence, members of this genus were allocated to different families such as *Schizothyriaceae* (Batzer *et al*. 2008), *Cladosporiaceae* (Schubert *et al*. 2007; Dugan *et al*. 2008; Bensch *et al*. 2010, 2012), *Dissoconiaceae*, *Mycosphaerellaceae* and *Teratosphaeriaceae* (Crous *et al*. 2009c; Li *et al*. 2012). From these results it became evident that the mycosphaerella-like morphology had evolved multiple times and a new circumscription of *Mycosphaerella* was urgently required.

The type species *Mycosphaerella punctiformis* was epitypified from freshly collected material and its asexual morph described as *Ramularia endophylla* (Verkley *et al*. 2004). Phylogenetic analyses based on DNA sequence data of the SSU and ITS regions grouped *Mycosphaerella* species with *Ramularia* asexual morphs in a monophyletic group with high bootstrap support (Verkley *et al*. 2004; Crous *et al*. 2007a). This partly led to the proposal by Crous *et al*. (2009e) that *Mycosphaerella* s. str. should be limited to species with *Ramularia* asexual morphs, and that the remaining mycosphaerella-like species should be allocated to other genera. In order to halt the unnecessary proliferation of generic names, it was proposed at the time that it would be preferable to not continue using the traditional dual nomenclature system, and that a single generic name should be attributed to each unambiguous phylogenetic lineage such as in the case of the *Botriosphaeriaceae* (Crous *et al*. 2006b).

The widespread use of phylogenetic analyses, based on DNA sequence comparisons, has fuelled the idea that dual nomenclature in fungi is superfluous (Taylor 2012). A number of far reaching proposals were accepted at the eighteenth International Botanical Congress in Melbourne, which led to a revised and renamed International Code of Nomenclature for Algae, Fungi, and Plants (ICN), signalling the end of dual nomenclature (Hawksworth *et al*. 2011; Wingfield *et al*. 2012). In pleomorphic fungi priority should be given to the oldest name, regardless of its sexuality. However, for widely used names, particularly where the asexual morph names replace sexual morph names, additional considerations are needed as specified in ICN Art. 57.2. The name *Ramularia* (Unger 1833) is older than *Mycosphaerella* (Johanson 1884b) and, while *Mycosphaerella* sensu lato represents numerous genera distributed over different families, *Mycosphaerella* sensu strictu has *Ramularia* asexual morphs. Choosing *Ramularia* over *Mycosphaerella* requires less name changes since most established connections already have species names in *Ramularia*. Therefore, the name *Ramularia* has been selected for this genus and included in a list of protected names (Wijayawardene *et al*. 2014).

Ramularia includes species that are usually defined as hyphomycetes with hyaline conidiophores and conidia with thickened, darkened, and refractive conidial hila and conidiogenous loci (scars on conidiogenous cells). The structure and colour of conidiogenous loci were considered important characters to define the genus and distinguish it from closely allied genera (Braun 1995, 1998). Recent molecular studies indicate that these characters were not always phylogenetically informative, and that the generic concept of some asexual

genera warranted revision (Verkley *et al.* 2004; Kirschner 2009). For example, *Cercosporella* is usually distinguished from *Ramularia* by bulging, hyaline conidiogenous loci. These characters are variable and difficult to distinguish with light microscopy (Kirshner 2009). A DNA phylogeny based on sequences obtained from the large nuclear ribosomal subunit (LSU) places the type species of *Cercosporella* (*Cercosporella virgaureae*) in a sister clade to *Ramularia,* but *Cercosporella centaureicola*, for example, clustered within *Ramularia sensu stricto*. The ultrastructure of conidiogenous loci differed between these genera, with *Ramularia* having a raised rim with a central dome that is cladosporium-like, while *Cercosporella* has flat scars in the shape of a truncated cone (Kirschner 2009).

The genus *Ramularia* includes around 1000 species that vary in lifestyle from phytopathogenic to saprobic, endophytic and even hyperparasitic. Phytopathogenic species cause leaf spots, necrosis or chlorosis that lead to early defoliation and disease symptoms that usually develop under conditions of high air humidity and low temperatures. Endophytic species usually grow symptomless within the leaves and mature in overwintering leaves on the soil, releasing ascospores in spring that can re-infect young leaves in spring. *R. endophylla* (syn. *M. punctiformis*) is an endophyte often associated with broad-leaved trees, and has a worldwide distribution (Verkley *et al.* 2004). Recent DNA sequence comparisons based on sequence obtained from the intergenic nuclear ribosomal spacer region (ITS) has shown that a number of *R. endophylla* strains collected from several hosts appear to be heterogeneous, indicating the presence of cryptic species (Verkley *et al.* 2004; Minnis *et al.* 2011). This applies to *Ramularia nyssicola*, which is morphologically indistinguishable from *R. endophylla*, but based on DNA sequence comparisons and host specificity represents a distinct species on *Nyssa* (Minnis *et al.* 2011; Videira *et al.* 2015a).

Identification of closely related species based on morphology is often difficult and the ITS barcode of fungi alone (Schoch *et al.* 2012) is unreliable for species identification among several cercosporoid genera (e.g. Groenewald *et al.* 2013; Crous *et al.* 2013a; Bakhshi *et al.* 2014). Several studies in recent years have highlighted the need to use additional phylogenetic markers to achieve accurate species identification (e.g. Bensch *et al.* 2012; Damm *et al.* 2012a, b; Quaedvlieg *et al.* 2012; Phillips *et al.* 2013; Wikee *et al.* 2013). In general, protein-coding genes have higher species resolution power due to their variable intron sequences. In addition, partial sequences from the mating-type ideomorphs (MAT1-1 and MAT1-2), specifically the alpha box (MAT1-1-1) and the high mobility group (MAT1-2-1), have also been found valuable due to their high interspecific variability and low intraspecific variability (Du *et al.* 2005; Paoletti *et al.* 2005). Species delimitation is challenging and guided by several concepts but no strict rule applies. The use of concordance of multiple gene genealogies has been frequently used in mycology to determine species boundaries. This is known as the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) principle and is an adaptation of the Phylogenetic Species Concept (PSC) (Taylor *et al.* 2000). With the addition of ecological and morphological data to support the multiple gene phylogenies in a polyphasic approach, mycologists have been increasingly relying on the Consolidated Species Concept (CSC) for fungal species delimitation (Quaedvlieg *et al*. 2014). The aims of this study were to: (i) resolve the variation in the *R. endophylla* species complex by applying morphology, ecology and multi-gene phylogeny based on five partial genes and partial mating-type locus DNA sequences; (ii) to investigate all purported links between *Ramularia* and *Mycosphaerella* in literature, and (iii) provide a platform that will enable a revision of this generic complex.

MATERIALS AND METHODS

Isolates

The isolates included in this study were obtained from the culture collection of the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, the Netherlands, from the working collection of Pedro Crous (CPC), housed at CBS-KNAW, or were freshly isolated from a range of different plant hosts (Table 1). Single-conidia and single-ascospore cultures were obtained using the techniques described for species of *Mycosphaerella* and its asexual morphs (Crous *et al*. 1991; Crous 1998). Representative cultures of the new species delineated in this study were deposited in the CBS culture collection.

DNA extraction, amplification and sequencing

Fungal mycelium of strains (Table 1) was harvested with a sterile scalpel and the genomic DNA was isolated using the UltraClean™ Microbial DNA Isolation Kit (MoBio Laboratories, Solana Beach, CA, USA) following the manufacturers' protocols. Eleven partial nuclear genes were initially targeted for PCR amplification and sequencing: 28S nrRNA gene (LSU), internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS) of the nrDNA operon, actin (*actA*), translation elongation factor 1-α (*tef1*-α), histone H3 (*his3*), glyceraldehyde-3- phosphate dehydrogenase (*gapdh*), RNA polymerase II second largest subunit (*rpb2*), calmodulin (*cmdA*), β-tubulin (*tub2*), mating-type gene 1 (MAT1-1-1) and mating-type gene 2 (MAT1-2-1). The primers employed are listed in Table 2. The PCR amplifications were performed on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA). The PCR mixtures consisted of 1 mL genomic DNA, 1 x GoTaq® Flexi buffer (Promega, Madison, WI, USA), 2 mM $MgCl_2$, 40 mM of each dNTP, 0.2 mM of each primer and 0.5 Unit GoTaq® Flexi DNA polymerase (Promega) in a total volume of 12.5 mL. The PCR mixtures for *his3*, *gapdh*, *rpb2*, *cmdA* and *tub2* contained 2 mL genomic DNA. The PCR conditions were: initial denaturation (94 °C, 3 min); 35 cycles amplification (94 °C, 30 s; annealing temperature listed in Table 2, 30 s; 72 °C, 45 s), and final extension (72 °C, 5 min). For *gapdh* and *his3*, 40 amplification cycles were used. To obtain the partial *rpb2*, a touchdown PCR protocol was used: initial denaturation (94 °C, 3 min), 5 amplification cycles (94 °C, 45 s; 60 °C, 45 s; 72 °C, 2 min), 5 amplification cycles (94 °C, 45 s; 58 °C, 45 s; 72 °C, 2 min), 30 amplification cycles (94 °C, 45 s; 54 °C, 45 s; 72 °C, 2 min) and a final extension (72 °C, 8 min). The resulting fragments were sequenced in both directions using the PCR primers and the BigDye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems Life Technologies, Carlsbad, CA, USA). DNA sequencing amplicons were purified through Sephadex G-50 Superfine columns (SigmaeAldrich, St. Louis, MO) in MultiScreen HV plates (Millipore, Billerica, MA). Purified sequence reactions were analysed on an Applied Biosystems 3730xl DNA Analyzer (Life Technologies, Carlsbad, CA, USA). The DNA sequences generated were analysed and consensus sequences were computed using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium).

Phylogenetic analysis

The generated sequences for each gene were aligned with MAFFT v. 7 (Katoh & Standley 2013) and the alignments were manually checked and improved where necessary using MEGA v. 5 (Tamura *et al.* 2011). From the strains listed in Table 1, only those with the complete dataset

Table 1. Collection details and GenBank accession numbers of strains included in this study.

Species	Culture collection accession number(s)[1]	Host/isolation source	Location	Collector	GenBank Accession numbers[2]										
					LSU	ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	MAT1	MAT2
Ramularia aplospora	CBS 109014	*Alchemilla vulgaris*, leaf spot	Austria, Ötztal	G. Verkley	KP894107	KP894216	KP894322	KP894432	KP894542	KP894653	KP894764	KP894875	–	KP895037	–
	CBS 109120	*Alchemilla vulgaris*, leaf spot	Austria, Tirol	G. Verkley	KP894108	KP894217	KP894323	KP894433	KP894543	KP894654	KP894765	KP894876	–	–	KP895066
	CBS 114118; UPSC 2679	*Alchemilla vulgaris*	Sweden, Uppland	E. Gunnerbeck	KP894109	KP894218	KP894324	KP894434	KP894544	KP894655	KP894766	KP894877	–	–	KP895067
	CBS 545.82	mildew on *Alchemilla vulgaris*	Germany, Gössweinstein	T. Hijwegen	KP894110	EU402328	KP894325	KP894435	KP894545	KP894656	KP894767	KP894878	KP894965	KP895038	–
Ramularia calcea	CBS 101612	*Symphytum* sp., leaf spot	Germany, Thüringen	G. Arnold	KP894111	KP894219	KP894326	KP894436	KP894546	KP894657	KP894768	KP894879	KP894966	KP895039	–
	CBS 101613	*Symphytum* sp., leaf spot	Germany, Thüringen	G. Arnold	KP894112	KP894220	KP894327	KP894437	KP894547	KP894658	KP894769	–	KP894967	KP895040	–
Ramularia endophylla	CBS 101680	*Castanea sativa*, dead leaf	Netherlands, Utrecht	A. Aptroot	KP894126	KP894233	KP894341	KP894451	KP894561	KP894672	KP894783	KP894887	KP894974	KP895044	–
	CBS 113265 eepTy	*Quercus robur*, dead leaf	Netherlands, Utrecht	G. Verkley	AY490776	AY490763	KF903461	KF253276	KP894562	KP894673	KP207603	KF253981	KP894975	KP895045	–
	CBS 113868	*Quercus robur*, living leaf	Netherlands, Utrecht	G. Verkley	KP894127	KP894234	KP894342	KP894452	KP894563	KP894674	KP894784	KP894888	–	KP895046	–
	CBS 113869	*Quercus robur*, living leaf	Netherlands, Utrecht	G. Verkley	KP894128	KP894235	KP894343	KP894453	KP894564	KP894675	KP894785	KP894889	–	KP895047	–
	CBS 113870	*Quercus robur*, living leaf	Netherlands, Utrecht	G. Verkley	KP894129	KP894236	KP894344	KP894454	KP894565	KP894676	KP894786	KP894890	KP894976	–	–
	CBS 113871	*Quercus robur*, fallen leaf	Netherlands, Utrecht	G. Verkley	KP894130	KP894237	KP894345	KP894455	KP894566	KP894677	KP894787	KP894891	KP894977	KP895048	–
	CBS 115299	*Quercus robur*, living leaf	Netherlands, Utrecht	G. Verkley	KP894131	KP894238	KP894346	KP894456	KP894567	KP894678	KP894788	KP894892	–	KP895049	–
	CBS 115302	*Quercus robur*, living leaf	Netherlands, Utrecht	–	KP894132	KP894239	KP894347	KP894457	KP894568	KP894679	KP894789	KP894893	KP894978	–	KP895073
	CBS 115303	*Quercus robur*, living leaf	Netherlands, Utrecht	–	KP894133	KP894240	KP894348	KP894458	KP894569	KP894680	KP894790	KP894894	–	KP895050	–
	CBS 115304	*Quercus robur*, living leaf	Netherlands, Utrecht	–	KP894134	KP894241	KP894349	KP894459	KP894570	KP894681	KP894791	KP894895	–	–	KP895074
	CBS 115310	*Quercus robur*, dead leaf	Netherlands, Utrecht	–	KP894135	KP894242	KP894350	KP894460	KP894571	KP894682	KP894792	–	KP894979	KP895051	–
	CBS 115311	*Quercus robur*, dead leaf	Netherlands, Utrecht	–	KP894136	KP894243	KP894351	KP894461	KP894572	KP894683	KP894793	KP894896	KP894980	KP895052	–
	CBS 117876; CPC 11203	*Quercus robur*	Netherlands, Utrecht	G. Verkley	KP894137	KP894244	KP894352	KP894462	KP894573	KP894684	KP894794	KP894897	KP894981	KP895053	–

Table 1. (Continued).

Species	Culture collection accession number(s)[1]	Host/isolation source	Location	Collector	GenBank Accession numbers[2]										
					LSU	ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	MAT1	MAT2
	CBS 117877; CPC 11204	*Quercus robur*	Netherlands, Utrecht	G. Verkley	KP894138	KP894245	KP894353	KP894463	KP894574	KP894685	KP894795	KP894898	KP894982	–	KP895075
	CBS 942.97	*Quercus* sp., leaves	Belgium, Namur	A. Aptroot	KP894139	KP894246	KP894354	KP894464	KP894575	EU874860	KP894796	KP894899	KP894983	–	–
	CPC 11503	–	South Korea	H.D. Shin	KP894140	KP894247	KP894355	KP894465	KP894576	KP894686	KP894797	KP894900	KP894984	KP895054	–
Ramularia grevilleana	CBS 114732; UPSC 3244	*Fragaria ananassa*	Sweden, Uppland	E. Gunnerbeck	KP894113	KP894221	KP894328	KP894438	KP894548	KP894659	KP894770	–	KP894968	–	–
	CBS 259.36	–	Netherlands	–	KP894114	KP894222	KP894329	KP894439	KP894549	KP894660	KP894771	–	–	–	KP895068
	CBS 298.34	–	Netherlands	–	KP894115	KP894223	KP894330	KP894440	KP894550	KP894661	KP894772	KP894880	KP894969	–	–
	CBS 719.84	*Fragaria* x *ananassa* 'Tioga'	New Zealand, Auckland	–	KP894116	EU167605	KP894331	KP894441	KP894551	KP894662	KP894773	KP894881	–	–	–
Ramularia inaequalis	CBS 250.96	*Taraxacum officinale*	Canada, Nova Scotia	S. Green	KP894117	KP894224	KP894332	KP894442	KP894552	KP894663	KP894774	KP894882	KP894970	–	KP895069
	CPC 15752	*Taraxacum* sp.	Mexico, Montecillo	M. de J. Yanez-Morales	KP894118	KP894225	KP894333	KP894443	KP894553	KP894664	KP894775	–	–	KP895041	–
	CPC 15753	*Taraxacum* sp.	Mexico, Montecillo	M. de J. Yanez-Morales	KP894119	KP894226	KP894334	KP894444	KP894554	KP894665	KP894776	KP894883	KP894971	–	–
	CPC 25741; X39	*Taraxacum officinale*	Netherlands, Utrecht	U. Damm	KP894120	KP894227	KP894335	KP894445	KP894555	KP894666	KP894777	–	–	–	KP895070
	CPC 25742; X40	*Taraxacum officinale*	Netherlands, Utrecht	U. Damm	KP894121	KP894228	KP894336	KP894446	KP894556	KP894667	KP894778	–	–	–	KP895071
Ramularia lactea	CBS 114442; UPSC 2727	*Viola hirta*	Sweden, Uppland	E. Gunnerbeck	KP894122	KP894229	KP894337	KP894447	KP894557	KP894668	KP894779	KP894884	KP894972	KP895042	–
	CBS 135.23	*Viola odorata*	–	–	KP894123	KP894230	KP894338	KP894448	KP894558	KP894669	KP894780	–	KP894973	–	–
Ramularia nyssicola	CBS 127664; AR 4629	*Nyssa ogeche* x *sylvatica* hybrid	USA, Maryland	R. Olsen	KP894124	KP894231	KP894339	KP894449	KP894559	KP894670	KP894781	KP894885	–	–	–
	CBS 127665 epTy; AR 4656; DM 2	*Nyssa ogeche* x *sylvatica* hybrid	USA, Maryland	R. Olsen	KJ504724	KJ504765	KJ504429	KJ504680	KJ504548	KJ504636	KJ504592	KJ504496	KJ504473	KP895043	–
Ramularia phacae-frigidae	**CBS 234.55 eTy**	*Phaca frigida*	Switzerland, Corveglia	E. Müller	KP894125	KP894232	KP894340	KP894450	KP894560	KP894671	KP894782	KP894886	–	–	KP895072
Ramularia pusilla	CBS 124973; RoKi 3143	*Poa annua*, leaves	Germany, Frankfurt	R. Kirshner	KP894141	KP894248	KP894356	KP894466	–	KP894687	KP894798	KP894901	–	–	–

Table 1. (Continued).

Species	Culture collection accession number(s)[1]	Host/isolation source	Location	Collector	GenBank Accession numbers[2]										
					LSU	ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	MAT1	MAT2
Ramularia tricherae	CBS 108973	*Knautia arvensis*, leaf spot	Netherlands, Limburg	G. Verkley	KP894142	KP894249	KP894357	KP894467	KP894577	KP894688	KP894799	KP894902	KP894985	KP895055	–
	CBS 108989	*Knautia dipsacifolia*, leaf spot	Austria, Ötztal	G. Verkley	KP894143	KP894250	KP894358	KP894468	KP894578	KP894689	KP894800	KP894903	KP894986	–	KP895076
	CBS 108990	*Knautia dipsacifolia*, leaf spot	Austria, Ötztal	G. Verkley	KP894144	KP894251	KP894359	KP894469	KP894579	KP894690	KP894801	KP894904	–	–	–
	CBS 108994	*Knautia arvensis*, leaf spot	Netherlands, Limburg	G. Verkley	KP894145	KP894252	KP894360	KP894470	KP894580	KP894691	KP894802	KP894905	KP894987	KP895056	–
	CBS 236.73; CCM F-369	*Knautia drymeia*	Czechoslovakia	–	KP894146	KP894253	KP894361	KP894471	KP894581	KP894692	KP894803	KP894906	–	KP895057	–
Ramularia unterseheri	CBS 117801; CPC 12091	*Fagus sylvatica*, dead leaves	Netherlands, Utrecht	G. Verkley	KP894147	KP894254	KP894362	KP894472	KP894582	KP894693	KP894804	KP894907	KP894988	–	–
	CBS 117807; CPC 12095	*Fagus sylvatica*, dead leaves	Netherlands, Utrecht	G. Verkley	KP894148	KP894255	KP894363	KP894473	KP894583	KP894694	KP894805	KP894908	KP894989	–	KP895077
	CBS 117878; CPC 11206	*Acer pseudoplatanus*, decaying leaves	Netherlands, Utrecht	G. Verkley	KP894149	KP894256	KP894364	KP894474	KP894584	KP894695	KP894806	KP894909	KP894990	–	–
	CBS 117879; CPC 11207	*Acer pseudoplatanus*, decaying leaves	Netherlands, Utrecht	G. Verkley	KP894150	KP894257	KP894365	KP894475	KP894585	KP894696	KP894807	KP894910	–	–	–
	CBS 117880; CPC 11209	*Tilia* sp.	Netherlands, Utrecht	G. Verkley	KP894151	KP894258	KP894366	KP894476	KP894586	KP894697	KP894808	KP894911	KP894991	–	–
	CBS 117881; CPC 11211	*Tilia* sp.	Netherlands, Utrecht	G. Verkley	KP894152	KP894259	KP894367	KP894477	KP894587	KP894698	KP894809	KP894912	KP894992	–	KP895078
	CBS 124827	*Fagus sylvatica*, living leaves	Germany, Greifswald	M. Unterseher	KP894153	KP894260	KP894368	KP894478	KP894588	KP894699	KP894810	KP894913	KP894993	–	–
	CBS 124830	*Fagus sylvatica*, living leaves	Germany, Greifswald	M. Unterseher	KP894154	KP894261	KP894369	KP894479	KP894589	KP894700	KP894811	KP894914	KP894994	–	–
	CBS 124831	*Fagus sylvatica*, living leaves	Germany, Greifswald	M. Unterseher	KP894155	KP894262	KP894370	KP894480	KP894590	KP894701	KP894812	KP894915	KP894995	–	–
	CBS 124834	*Fagus sylvatica*, living leaves	Germany, Greifswald	M. Unterseher	KP894156	KP894263	KP894371	KP894481	KP894591	KP894702	KP894813	KP894916	KP894996	–	KP895079
	CBS 124836	*Fagus sylvatica*, living leaves	Germany, Greifswald	M. Unterseher	KP894157	KP894264	KP894372	KP894482	KP894592	KP894703	KP894814	KP894917	KP894997	–	–
	CBS 124838	*Fagus sylvatica*, living leaves	Germany, Greifswald	M. Unterseher	KP894158	KP894265	KP894373	KP894483	KP894593	KP894704	KP894815	KP894918	–	–	–

Table 1. (Continued).

Species	Culture collection accession number(s)[1]	Host/isolation source	Location	Collector	GenBank Accession numbers[2]										
					LSU	ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	MAT1	MAT2
	CBS 124844	*Fagus sylvatica*, leaf litter	Germany, Greifswald	M. Unterseher	KP894159	KP894266	KP894374	KP894484	KP894594	KP894705	KP894816	KP894919	KP894998	–	–
	CBS 124846	*Fagus sylvatica*, leaf litter	Germany, Greifswald	M. Unterseher	KP894160	KP894267	KP894375	KP894485	KP894595	KP894706	KP894817	KP894920	KP894999	–	–
	CBS 124852	*Fagus sylvatica*, leaf litter	Germany, Greifswald	M. Unterseher	KP894161	KP894268	KP894376	KP894486	KP894596	KP894707	KP894818	KP894921	KP895000	–	–
	CBS 124867	*Fagus sylvatica*, leaf litter	Germany, Greifswald	M. Unterseher	KP894162	KP894269	KP894377	KP894487	KP894597	KP894708	KP894819	KP894922	KP895001	–	KP895080
	CBS 124884 eTy	*Fagus sylvatica*, leaf litter	Germany, Greifswald	M. Unterseher	KP894163	KP894270	KP894378	KP894488	KP894598	KP894709	KP894820	KP894923	KP895002	–	–
	CBS 130721; DTO 162-C2	Room inside castle (probably air sample)	Germany, Munich	–	KP894164	KP894271	KP894379	KP894489	KP894599	KP894710	KP894821	KP894924	–	–	–
	CBS 355.90	*Fagus sylvatica*, seed	Germany, former west Germany	U. Delfs-Siemer	KP894165	KP894272	KP894380	KP894490	KP894600	KP894711	KP894822	–	KP895003	–	–
	CPC 25739; W6	*Alnus* sp., leaf	Germany, Hesse	W. Quaedvlieg	KP894166	KP894273	KP894381	KP894491	KP894601	KP894712	KP894823	–	–	–	–
	CPC 25740; X2	*Fagus* sylvatica, decaying leaves	Netherlands, Utrecht	S.I.R. Videira	KP894167	KP894274	KP894382	KP894492	KP894602	KP894713	KP894824	KP894925	KP895004	–	KP895081
Ramularia urticae	CBS 105.26	–	–	–	KP894169	KP894276	KP894384	KP894494	KP894604	KP894715	KP894826	–	–	–	–
	CBS 113974; UPSC 2359	*Urtica dioica*	Sweden, Uppland	E. Gunnerbeck	KP894168	KP894275	KP894383	KP894493	KP894603	KP894714	KP894825	KP894926	KP895005	–	–
	CBS 162.91	*Urtica dioica*, leaf spot	Germany, Weimar	G. Arnold	KP894170	KP894277	KP894385	KP894495	KP894605	KP894716	KP894827	–	KP895006	–	–
Ramularia variabilis	CPC 16865	*Verbascum* sp.	Canada, Ontario	K. Seifert	KP894171	KP894278	KP894386	KP894496	KP894606	KP894717	KP894828	–	KP895007	–	–
	CPC 16866	*Verbascum* sp.	Canada, Ontario	K. Seifert	KP894172	KP894279	KP894387	KP894497	KP894607	KP894718	KP894829	–	KP895008	–	–
	CPC 25967	*Verbascum* sp.	Austria, Graz	C. Scheuer	KP894173	KP894280	KP894388	KP894498	KP894608	KP894719	KP894830	–	–	–	–
Ramularia vizellae	CBS 113267	*Quercus robur*, dead fallen leaves	Netherlands, Utrecht	G. Verkley	KP894174	KP894281	KP894389	KP894499	KP894609	KP894720	KP894831	KP894927	KP895009	–	–
	CBS 115980	*Malus* sp., dead leaf litter	Netherlands, Gelderland	–	KP894175	KP894282	KP894390	KP894500	KP894610	KP894721	KP894832	–	–	KP895058	–
	CBS 115981	*Malus* sp., dead leaf litter	Netherlands, Gelderland	–	KP894176	KP894283	KP894391	KP894501	KP894611	KP894722	KP894833	KP894928	KP895010	–	–

Table 1. (Continued).

Species	Culture collection accession number(s)[1]	Host/isolation source	Location	Collector	GenBank Accession numbers[2]										
					LSU	ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	MAT1	MAT2
	CBS 115982	*Malus* sp., dead leaf litter	Netherlands, Gelderland	–	KP894177	KP894284	KP894392	KP894502	KP894612	KP894723	KP894834	KP894929	KP895011	–	–
	CBS 115983	*Malus* sp., dead leaf litter	Netherlands, Gelderland	–	KP894178	KP894285	KP894393	KP894503	KP894613	KP894724	KP894835	KP894930	KP895012	–	KP895082
	CBS 115984	*Malus* sp., dead leaf litter	Netherlands, Gelderland	–	KP894179	KP894286	KP894394	KP894504	KP894614	KP894725	KP894836	KP894931	KP895013	–	KP895083
	CBS 116015	*Malus* sp., dead leaf litter	Netherlands, Gelderland	–	KP894180	KP894287	KP894395	KP894505	KP894615	KP894726	KP894837	KP894932	KP895014	–	KP895084
	CBS 116069	*Malus* sp., dead leaf litter	Netherlands, Gelderland	–	KP894181	KP894288	KP894396	KP894506	KP894616	KP894727	KP894838	KP894933	KP895015	–	KP895085
	CBS 117798; CPC 12088	*Carpinus betulus*, fruit scales	Netherlands, Utrecht	G. Verkley	KP894182	KP894289	KP894397	KP894507	KP894617	KP894728	KP894839	–	–	–	KP895086
	CBS 117799; CPC 12089	*Acer pseudoplatanus*, dead leaves	Netherlands, Utrecht	G. Verkley	KP894183	KP894290	KP894398	KP894508	KP894618	KP894729	KP894840	KP894934	KP895016	–	–
	CBS 117802; CPC 12092	*Carpinus betulus*, dead leaves	Netherlands, Utrecht	G. Verkley	KP894184	KP894291	KP894399	KP894509	KP894619	KP894730	KP894841	KP894935	KP895017	–	–
	CBS 117805; CPC 12094	*Aesculus hippocastanum*, dead leaves	Netherlands, Utrecht	G. Verkley	KP894185	KP894292	KP894400	KP894510	KP894620	KP894731	KP894842	KP894936	KP895018	–	KP895087
	CBS 117806; CPC 12096	*Tilia* sp., dead leaves	Netherlands, Utrecht	G. Verkley	KP894186	KP894293	KP894401	KP894511	KP894621	KP894732	KP894843	KP894937	KP895019	–	KP895088
	CBS 117870; CPC 11193	*Quercus rubra*, deacaying leaves	Netherlands, Utrecht	G. Verkley	KP894187	KP894294	KP894402	KP894512	KP894622	KP894733	KP894844	KP894938	KP895020	–	KP895089
	CBS 117871; CPC 11194	*Quercus rubra*, deacaying leaves	Netherlands, Utrecht	G. Verkley	KP894188	KP894295	KP894403	KP894513	KP894623	KP894734	KP894845	KP894939	KP895021	–	–
	CBS 117872; CPC 11197	*Amelanchier lamarckii*	Netherlands, Utrecht	G. Verkley	KP894189	KP894296	KP894404	KP894514	KP894624	KP894735	KP894846	KP894940	KP895022	–	KP895090
	CBS 117873; CPC 11198	*Amelanchier lamarckii*	Netherlands, Utrecht	G. Verkley	KP894190	KP894297	KP894405	KP894515	KP894625	KP894736	KP894847	KP894941	KP895023	–	–
	CBS 117874; CPC 11200	*Aesculus hippocastanum*	Netherlands, Utrecht	G. Verkley	KP894191	KP894298	KP894406	KP894516	KP894626	KP894737	KP894848	KP894942	KP895024	–	KP895091
	CBS 117875; CPC 11201	*Aesculus hippocastanum*	Netherlands, Utrecht	G. Verkley	KP894192	KP894299	KP894407	KP894517	KP894627	KP894738	KP894849	KP894943	KP895025	–	–
	CBS 117882; CPC 11212	*Sorbus aucuparia*, decaying leaves	Netherlands, Utrecht	G. Verkley	KP894193	KP894300	KP894408	KP894518	KP894628	KP894739	KP894850	KP894944	KP895026	KP895059	–

Table 1. (Continued).

Species	Culture collection accession number(s)[1]	Host/isolation source	Location	Collector	GenBank Accession numbers[2]										
					LSU	ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	MAT1	MAT2
	CBS 117883; CPC 11213	*Sorbus aucuparia*, decaying leaves	Netherlands, Utrecht	G. Verkley	KP894194	KP894301	KP894409	KP894519	KP894629	KP894740	KP894851	KP894945	KP895027	KP895060	–
	CBS 124861	*Fagus sylvatic*a, leaf litter from 2007	Germany, Greifswald	M. Unterseher	KP894195	KP894302	KP894410	KP894520	KP894630	KP894741	KP894852	KP894946	–	–	KP895092
	CBS 130601 eTy; CPC 18283	*Protea* sp., leaves	South Africa	P.W. Crous	JN712567	KJ504808	KJ504472	KJ504723	KJ504591	KJ504679	KJ504635	–	KJ504495	KP895061	–
	CBS 184.97	*Acer pseudoplatanus*, dead leaves	Netherlands, Utrecht	H.A. van der Aa	KP894196	KP894303	KP894411	KP894521	KP894631	KP894742	KP894853	KP894947	KP895028	KP895062	–
	CBS 185.97	*Acer pseudoplatanus*, dead leaves	Netherlands, Utrecht	H.A. van der Aa	KP894197	KP894304	KP894412	KP894522	KP894632	KP894743	KP894854	KP894948	KP895029	KP895063	–
	CBS 324.87	*Brassica* sp., in leaf spot	Netherlands	–	GU214581	GU214581	KP894413	KP894523	KP894633	KP894744	KP894855	KP894949	KP895030	–	KP895093
	CBS 367.64	*Malus sylvestris*, fruit	France	C. Moreau	KP894198	KP894305	KP894414	KP894524	KP894634	KP894745	KP894856	KP894950	KP895031	–	KP895094
	CBS 369.67	*Lotus uliginosus*, young leaves	Netherlands, Utrecht	H.A. van der Aa	KP894199	KP894306	KP894415	KP894525	KP894635	KP894746	KP894857	KP894951	–	–	KP895095
	CBS 428.74; IHEM 3995	*Phaseolus* sp.	Switzerland	–	KP894200	KP894307	KP894416	KP894526	KP894636	KP894747	KP894858	KP894952	KP895032	–	–
	CBS 515.69	*Acer pseudoplatanus*	Netherlands, Utrecht	H.A. van der Aa	KP894201	AY490759	KP894417	KP894527	KP894637	KP894748	KP894859	KP894953	KP895033	–	KP895096
	CBS 724.79	*Tilia* sp., overwintering leaf on the ground	Germany, Munchen	A.John	KP894202	KP894308	KP894418	KP894528	KP894638	KP894749	KP894860	KP894954	KP895034	–	KP895097
	CBS 943.97	*Quercus* sp., leaves	Netherlands	A. Aptroot	KP894203	KP894309	KP894419	KP894529	KP894639	KP894750	KP894861	KP894955	KP895035	–	–
	CPC 15541	*Acer campestre*	Ukraine, Seversky Donets river	A. Akulov	KP894204	KP894310	KP894420	KP894530	KP894640	KP894751	KP894862	–	–	–	–
	CPC 25728; MP19	*Corylus* sp.	Netherlands, Utrecht	S.I.R. Videira	KP894205	KP894311	KP894421	KP894531	KP894641	KP894752	KP894863	KP894956	–	–	–
	CPC 25729; MP20	*Quercus* sp.	Netherlands, Utrecht	S.I.R. Videira	KP894206	KP894312	KP894422	KP894532	KP894642	KP894753	KP894864	KP894957	–	KP895064	–
	CPC 25730; MP21	*Carpinus* sp.	Netherlands, Utrecht	S.I.R. Videira	KP894207	KP894313	KP894423	KP894533	KP894643	KP894754	KP894865	KP894958	–	–	KP895098
	CPC 25731; MP23	*Quercus* sp.	Netherlands, Utrecht	S.I.R. Videira	KP894208	KP894314	KP894424	KP894534	KP894644	KP894755	KP894866	KP894959	–	–	KP895099
	CPC 25732; MP24	*Fagus* sp., decaying leaves	Netherlands, Utrecht	S.I.R. Videira	KP894209	KP894315	KP894425	KP894535	KP894645	KP894756	KP894867	KP894960	–	KP895065	–

Table 1. (Continued).

Species	Culture collection accession number(s)[1]	Host/isolation source	Location	Collector	GenBank Accession numbers[2]										
					LSU	ITS	*actA*	*tef1-α*	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	MAT1	MAT2
	CPC 25733; W7	Leaf of unidentified plant	Germany, Hesse	W. Quaedvlieg	KP894210	KP894316	KP894426	KP894536	KP894646	KP894757	KP894868	–	–	–	–
	CPC 25734; X1	*Fagus* sp., decaying leaves	Netherlands, Utrecht	S.I.R. Videira	KP894211	KP894317	KP894427	KP894537	KP894647	KP894758	KP894869	KP894961	KP895036	–	KP895100
	CPC 25735; X3	*Fagus* sp., decaying leaves	Netherlands, Utrecht	S.I.R. Videira	KP894212	KP894318	KP894428	KP894538	KP894648	KP894759	KP894870	KP894962	–	–	–
	CPC 25738; X31	*Sambucus nigra*	Austria, Graz	C. Scheuer	KP894215	KP894321	KP894431	KP894541	KP894651	KP894762	KP894873	–	–	–	–
	CPC 25736; X4	*Corylus* sp., decaying leaves	Netherlands, Utrecht	S.I.R. Videira	KP894213	KP894319	KP894429	KP894539	KP894649	KP894760	KP894871	KP894963	–	–	–
	CPC 25737; X5	*Aesculus hipocastanum*, decaying leaves	Netherlands, Utrecht	S.I.R. Videira	KP894214	KP894320	KP894430	KP894540	KP894650	KP894761	KP894872	KP894964	–	–	KP895101
Zymoseptoria passerini	**CBS 120382 eepTy**	*Hordeum vulgare*	USA, North Dakota	S. Goodwin	JQ739843	JF700877	JF701046	JQ739787	KP894652	KP894763	KP894874	JF701114	JF700978	–	–

[1] AR: Personal culture collection of Amy Rossman; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CCM: Czech Collection of Microorganisms, Masaryk University, Brno, Czech Republic; CPC: Personal culture collection of Pedro Crous, housed at CBS; DTO: Personal culture collection of the Applied and Industrial Mycology, housed at CBS; IHEM: Collection of the Laboratorium voor Microbiologie en Microbiele Genetica, Gent, Belgium; IPO: Research Institute for Plant Protection, Wageningen; RoKI: Personal culture collection of Roland Kirschner; UPSC: Uppsala University Culture Collection of Fungi, Botanical Museum University of Uppsala, Uppsala, Sweden.

[2] LSU: large subunit (28S) of the nrRNA gene operon; ITS: internal transcribed spacers and intervening 5.8S nrDNA; *actA*: partial actin gene; *tef1-α*: partial translation elongation factor 1-alpha gene; *gapdh*: partial glyceraldehyde-3-phosphate dehydrogenase gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *his3*: partial histone H3 gene; *cmdA*: partial calmodulin gene; *tub2*: partial beta-tubulin gene; MAT1: partial *MAT1-1-1* mating type gene; MAT2: partial *MAT1-2* mating type gene. eTy: ex-type; eepTy: ex-epitype; "X" represents a DNA sequence that will be submitted to Genbank and "–" a DNA sequence that was not generated.

Table 2. Details of primers used for amplification and sequencing in this study.

Locus[1]	Primer Name	Primer sequence (5'→3')	Annealing temperature (°C)	Orientation	Reference
actA	ACT-512F	ATG TGC AAG GCC GGT TTC GC	55	Forward	Carbone & Kohn (1999)
	ACT-783 R	TAC GAG TCC TTC TGG CCC AT	55	Reverse	Carbone & Kohn (1999)
	ACT-2Rd	ARR TCR CGD CCR GCC ATG TC	55	Reverse	Groenewald *et al*. (2013)
tub2	T1	AAC ATG CGT GAG ATT GTA AGT	52	Forward	O'Donnell & Cigelnik (1997)
	β-Sandy-R	GCR CGN GGV ACR TAC TTG TT	52	Reverse	Stukenbrock *et al*. (2012)
	Bt2a	GGT AAC CAA ATC GGT GCT GCT TTC	52	Forward	Glass & Donaldson (1995)
	Bt2b	ACC CTC AGT GTA GTG ACC CTT GGC	52	Reverse	Glass & Donaldson (1995)
cmdA	CAL-228F	GAG TTC AAG GAG GCC TTC TCC C	58	Forward	Carbone & Kohn (1999)
	CAL-737R	CAT CTT TCT GGC CAT CAT GG	58	Reverse	Carbone & Kohn (1999)
	CAL2Rd	TGR TCN GCC TCD CGG ATC ATC TC	58	Reverse	Groenewald *et al*. (2013)
gapdh	gpd1	CAA CGG CTT CGG TCG CAT TG	55	Forward	Berbee *et al*. (1999)
	gpd2	GCC AAG CAG TTG GTT GTG C	55	Reverse	Berbee *et al*. (1999)
his3	CylH3F	AGG TCC ACT GGT GGC AAG	52	Forward	Crous *et al*. (2004d)
	CylH3R	AGC TGG ATG TCC TTG GAC TG	52	Reverse	Crous *et al*. (2004d)
ITS	V9G	TTA CGT CCC TGC CCT TTG TA	52	Forward	Hoog & Gerrits van den Ende (1998)
	ITS4	TCC TCC GCT TAT TGA TAT GC	52	Reverse	White *et al*. (1990)
LSU	LSU1Fd	GRA TCA GGT AGG RAT ACC CG	52	Forward	Crous *et al*. (2009a)
	LR5	TCC TGA GGG AAA CTT CG	52	Reverse	Vilgalys & Hester (1990)
MAT1-1-1	MgMfSpMat1-1f1	CATTNGCNCATCCCTTTG	54	Forward	Groenewald *et al.* (2006)
	MgMfSpMat1-1r2	GGCTTNGANACCATGGTGAG	54	Reverse	Groenewald *et al.* (2006)
MAT1-2-1	MgMfSpMat1-2f2	CAAAGAANGCNTTCNTGATCT	54	Forward	Groenewald *et al.* (2006)
	MgMfSpMat1-2r1	TTCTTCTCNGATGGCTTGC	54	Reverse	Groenewald *et al.* (2006)
rpb2	RPB2-5F	GAY GAY MGW GAT CAY TTY GG	60→58→54	Forward	Liu *et al*. (1999)
	RPB2-7cR	CCC ATR GCT TGY TTR CCC AT	60→58→54	Reverse	Liu *et al*. (1999)
	Rpb2-F1	GGTGTCAGTCARGTGYTGAA	60→58→54	Forward	Videira *et al*. (2015a)
	Rpb2-R1	TCC TCN GGV GTC ATG ATR ATC AT	60→58→54	Reverse	Videira *et al*. (2015a)
tef1-α	EF1-728F	CAT CGA GAA GTT CGA GAA GG	54	Forward	Carbone & Kohn (1999)
	EF-2	GGA RGT ACC AGT SAT CAT GTT	54	Reverse	O'Donnell *et al*. (1998)
	TEF-1R	CTT GAT GAA ATC ACG GTG ACC	54	Reverse	Videira *et al*. (2015a)

[1] *actA*: partial actin gene; *tub2*: partial beta-tubulin gene; *cmdA*: partial calmodulin gene; *gapdh*: partial glyceraldehyde-3-phosphate dehydrogenase gene; *his3*: partial histone H3 gene; ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: large subunit (28S) of the nrRNA gene operon; MAT1: partial MAT1-1-1 mating type gene; MAT2: partial MAT1-2 mating type gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *tef1*-α: partial translation elongation factor 1-alpha gene.

of genes were used in the phylogenetic analyses, with the exception of *Ramularia pusilla*, which was missing the sequence of *gapdh* and was considered as missing data in the alignment. Phylogenetic analyses of sequence data consisted of both Neighbour-Joining analysis and parsimony analysis performed with PAUP v. 4.0b10 (Swofford 2003) and also a Bayesian analysis performed with MrBayes v. 3.2.1 (Ronquist *et al.* 2011).

The Neighbour-Joining analysis using the HKY85 substitution model was applied to each gene partition individually. The single gene trees were manually compared in order to check the stability of each species clade and exclude incongruent genes from the multigene analysis (data not shown, individual gene trees deposited on TreeBASE). Alignment gaps were treated as missing data and all characters were unordered and of equal weight. Any ties were broken randomly when encountered. The selected genes for the multigene parsimony and Bayesian analysis were concatenated with Mesquite v. 2.75 (Maddison & Maddison 2011).

The parsimony analysis was performed on three datasets, namely the concatenated alignment of five genes and the individual alignments of the mating-type sequences (MAT1-1-1 and MAT1-2-1). The analysis used a heuristic search with 100 random taxa additions and the branch-swapping algorithm for tree bisection and reconstruction. Alignment gaps were treated as fifth base and all characters were unordered and of equal weight. Branches of zero length were collapsed and all multiple, equally parsimonious trees were saved. The robustness of the trees obtained was evaluated by 1000 bootstrap replications (Hillis & Bull 1993). Other measures calculated included tree length (TL), consistency index (CI), retention index (RI) and rescaled consistency index (RC). The resulting trees were printed with Geneious v. 7.0.6 (Kearse *et al.* 2012).

The Bayesian analysis was performed on the combined multigene alignment only. MrModeltest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model settings for each data partition in order to perform a model-optimized Bayesian phylogenetic reconstruction using MrBayes v. 3.2.1 (Ronquist *et al.* 2011). The heating chain was set to 0.15 and the Markov Chain Monte Carlo (MCMC) analysis of four chains was started in parallel from a random tree topology and lasted until the average standard deviation of split frequencies reached 0.01. Burn-in was set to 25 % after which the likelihood values were stationary. Trees were saved each 250 generations and the resulting phylogenetic tree was printed with Geneious v. 7.0.6 (Kearse *et al*. 2012). All new sequences generated in this study were deposited in NCBI's GenBank nucleotide database (www.ncbi.nlm.nih.gov) and the accession numbers of the sequences used for the phylogenetic analyses are listed in Table 1. The alignments and respective phylogenetic trees were deposited in TreeBASE (www.treeBASE.org).

Taxonomy

Isolates were cultivated for 7 d at 21 °C. Microscopic observations of the conidiogenous structures were performed using a Nikon Eclipse 80i light microscope with differential interference contrast (DIC) illumination. Slides were prepared using the inclined coverslip method (Kawato & Shinobu 1959, revised in Nugent *et al*. 2006) and also transparent adhesive tape (Titan Ultra Clear Tape, Conglom Inc., Toronto, Canada) (Bensch *et al*. 2012). Clear lactic acid was used as mounting medium for the measurements. The morphological structure terminology followed those used for Ramularia species by Crous *et al*. (2011c). The recorded measurements represent the minimum value followed by the 95 % confidence interval of 30 individual measurements and the maximum value, for both length and width. For culture characterization the isolates were inoculated on 2 % potato dextrose agar (PDA), oatmeal agar (OA) and 2 % malt extract

agar (MEA) (recipes according to Crous *et al*. 2009f), and incubated in the dark at 25 °C. After 14 d, the colony diameter was measured and the colony colour described according to the mycological colour charts of Rayner (1970). Nomenclatural novelties and descriptions were deposited in MycoBank (Crous *et al*. 2004a).

RESULTS

DNA amplification and phylogenetic analysis

Of the 11 loci tested in this study, seven were successfully amplified for most strains (LSU, ITS, *actA*, *tef1*-α, *his3*, *gapdh*, *rpb2*). The amplification of *cmdA* and *tub2* often resulted in multiple bands, despite the attempts of protocol optimization and were not used in the multigene analysis. The amplification of the mating-type loci was not successful for all the strains (Table 1) and was particularly challenging for the MAT1-2-1 with the use of the degenerate primers (Table 2) that were reported successful for other *Mycosphaerellaceae* (Groenewald *et al*. 2006, 2007). Due to the observed variation of the position of these loci in other species, an attempt was made to amplify the loci using the forward primer for MAT1-1-1 and the reverse primer of MAT1-2-1 and vice-versa. A sequence of approximately 670 bp was obtained for several strains with the combination of the primers MgMfSpMat1-1f1 (MAT1-1-1 forward) and MgMfSpMat1-2r1 (MAT1-2-1 reverse) for which the last portion of approximately 200 bp corresponded to the MAT1-2-1 conserved high mobility group. When sequences of the MAT1-2-1 obtained with the regular primer combination were compared with the ones obtained with the described uncommon combination, they matched exactly. The mating-type genes were not used in the combined analysis since all isolates with a successful sequence had either the MAT1-1-1 or MAT1-2-1 amplicon. In addition, no sequences of MAT1-1-1 were obtained for any of the *Ramularia unterseheri* strains available in this study. All the obtained sequences were deposited in GenBank (Table 1).

The Neighbour-joining analysis using the HKY85 substitution model used to check the stability and robustness of clades for the individual loci (data not shown) revealed that the both the LSU and ITS locus separated *Ramularia endophylla* strains in a unique clade but were not able to separate *Ramularia vizellae* from *R. unterseheri* (newly described). The single gene trees for *actA*, *his3*, *rpb2* and *gapdh* could separate three species within the complex, namely *R. endophylla*, *R. vizellae*, and *R. unterseheri*. The partial sequences of *tef1*-α were very heterogeneous and the resulting phylogenetic tree was not congruent with the other genes. The *tef1*-α sequences were, therefore, not used in the multigene analysis.

The multigene analysis was based on a concatenated alignment of five loci (ITS, *actA*, *rpb2*, *gapdh* and *his3*) and contained 114 taxa, of which 81 belonged to the *R. endophylla* species complex, 32 represented other *Ramularia* species and the outgroup sequence of *Zymoseptoria passerini*. The final alignment contained a total of 2618 characters divided in five partitions containing 515 (ITS), 236 (*actA*), 897 (*rpb2*), 575 (*gapdh*) and 375 (*his3*) characters respectively, including alignment gaps. From the total alignment, 81 characters were excluded from the phylogenetic analysis: 20 characters that were artificially introduced as spacers between the genes; 10 characters (ITS) and 17 characters (*gapdh*) that represented a longer sequence in the outgroup compared to the ingroup sequences; 20 characters (*gapdh*) representing a longer intron that only existed for *Ramularia nyssicola*; 14 characters (*actA*) representing a repetition in an intron on the strains in *Ramularia grevilleana* (see alignment in TreeBASE).

The results of the MrModelTest analyses for the multigene dataset indicated that the ITS

partition had fixed (equal) base frequencies, whereas all the other partitions had dirichlet base frequencies. The optimised models for this alignment were SYM + I + G for ITS and GTR + I + G for all the other data partitions. The Bayesian analysis of the concatenated five-locus alignment generated 104 082 trees from which 26 020 trees were discarded (25 % burnin). The 50 % majority rule consensus tree (Fig. 1) and posterior probabilities (values ≤1) were calculated from the remaining 78 062 trees. The alignment contained a total of 959 unique site patterns: 100 (ITS), 123 (*actA*), 413 (*rpb2*), 209 (*gapdh*), 114 (*his3*). The parsimony analysis on the multigene dataset generated 1000 equally most parsimonious trees. From the analysed characters, 1559 were constant, 205 were variable and parsimony-uninformative and 772 were parsimony-informative. A parsimony consensus tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 1; bootstrap support values >75). The overall parsimony phylogeny supported the same species clades as those presented in the Bayesian phylogeny (Fig. 1). Phylogenetic trees based on the combined dataset (Fig. 1) and generated with both parsimony and Bayesian analyses, separated strains into three well supported species within the original complex: *R. endophylla*, *R. vizellae*, and *R. unterseheri.* The other *Ramularia* strains represent species that, in literature, have been associated with a *Mycosphaerella* sexual morph (Table 3). The MAT1-1-1 alignment contained 30 taxa, including the outgroup *Cercospora beticola* (GenBank DQ192581), and 570 characters, including alignment gaps, from which 175 were constant, 74 were variable and parsimony-uninformative, and 321 were parsimony-informative. The MAT1-2-1 alignment contained 37 taxa, including the outgroup *Cercospora beticola* (GenBank DQ192582), and 233 characters, including alignment gaps. Of these characters, 67 were constant, 31 were variable and parsimony-uninformative, and 135 were parsimony-informative. Similar trees were obtained with both neighbour-joining and parsimony methods. Two most parsimonious trees were obtained from the MAT-1-1-1 sequence alignment and nine most parsimonious trees were obtained from the MAT1-2-1 sequence alignment. The most parsimonious trees differed slightly in the arrangement of the taxa within the clades of *R. vizellae* (Fig. 2 and Fig. 3) and of *R. unterseheri* (Fig. 3) but the global tree topology was identical. The trees obtained for both MAT1-1-1 (Fig. 2) and MAT1-2-1 (Fig. 3) datasets showed that *R. endophylla* and *R. vizellae* cluster in separate clades with bootstrap support values of 100 % (MAT1-1-1) and 100 % and 97 % (MAT1-2-1), respectively. In the tree obtained for MAT1-2-1 the clade of *R. unterseheri* is supported with 98 % bootstrap. Strict consensus trees were calculated for each locus and the branches present were depicted in thicker lines (Figs. 2 and 3). The phylogenetic trees obtained from the mating-type sequences are in agreement with the parsimony and Bayesian analyses of the multigene dataset.

Taxonomy

Ramularia endophylla Verkley & U. Braun, Mycol. Res. 108: 1276 (2004)
Synonyms: *Sphaeria punctiformis* Pers., Ann. Bot. (Usteri) 11: 26 (1794), non *Ramularia punctiformis* Sacc. (Saccardo, 1904).
Astoma punctiforme (Pers.) Gray, Nat. Arr. Brit. Pl. (London) 1: 524 (1821)
Sphaerella punctiformis (Pers.) Rabenh., Klotzschii Herb. Viv. Mycol., ed. nov.: no. 264 (1856)
Mycosphaerella punctiformis (Pers.) Starbäck, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 15 (2): 9 (1889)
Diatrype punctiformis (Pers.) Zahlbr., Cat. Lich. Univers. 7: 780 (1931)
For further synonyms, see Tomilin (1979) and Aptroot (2006).

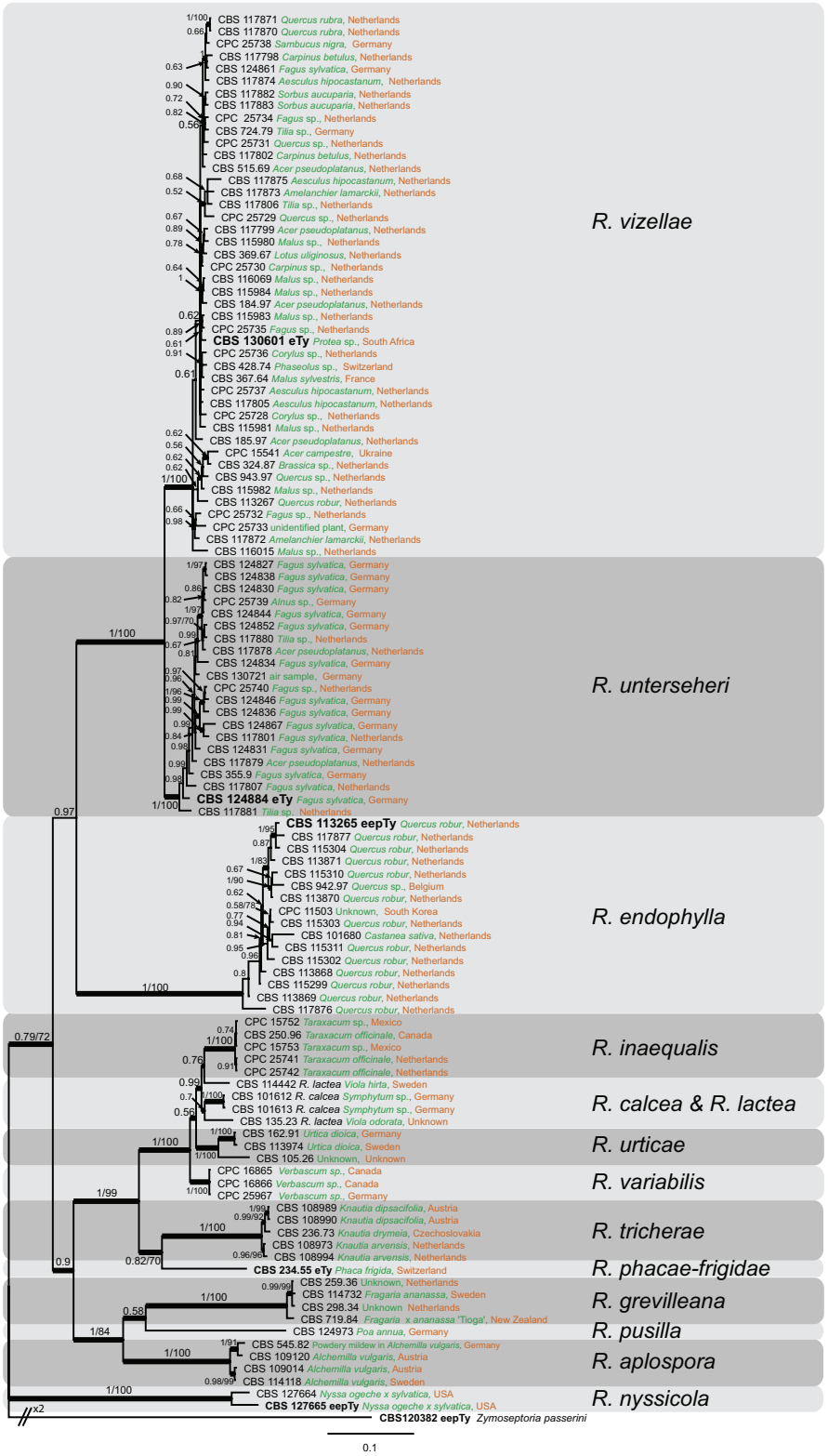

Fig. 1. Phylogenetic tree resulting from a Bayesian analysis of the combined 5-gene sequence alignment. Both Bayesianposterior probabilities (left number) and parsimony bootstrap support values > 70 % (right number) are indicated at the nodes; the scale bar represents the expected number of changes per site. Branches depicted in a thicker represent thebranches present in the strict consensus parsimony tree. Strains in bold and marked as 'eTy' are ex-types and those markedas 'eepTy' are ex-epitypes. The tree was rooted to *Zymoseptoria passerini* (CBS 120382).

Table 3. Relations between *Ramularia* asexual morphs and their *Mycosphaerella* sexual morphs reported in literature. References in **bold** represent the reference where a link was experimentally proven.

Asexual morph[1]	Sexual morph[1]	Current name	CA[2]	References	Sexual link[3]	Notes
R. endophylla Verkley & U. Braun (2004)	***M. punctiformis*** (Pers.) Starbäck (1889) [bas. *Sphaeria punctiformis* Pers. (1794)]	***R. endophylla*** Verkley & U. Braun (2004)	Y	**Verkley et al. (2004)**	EP	Verkley et al. (2004) epitypified *M.punctiformis* and linked it with *R. endophylla* morphologically and genetically.
R. grevilleana (Oudem.) Jørst. (1945) [bas. *Cylindrosporium grevilleanum* Oudem. (1873)]	***M. fragariae*** (Tul.) Lindau (1897) [bas. *Sphaeria fragariae* Tul. & C. Tul. (1856)]	***R. grevilleana*** (Oudem.) Jørst. (1945)	Y	**Dudley (1889)**; Potebnja (1908); Schellenberger (1917); Plakidas (1941); Klebahn (1918); Tomilin (1979); Sivanesan (1984); Braun (1998), Braun (2003)	EP	Dudley (1889) used conidia from pure cultures to infect strawberry leaves and observed perithecia formed in these lesions and that the ascospores germinated within the ascus, shot out through the ostiole and gave rise to conidia.
R. inaequalis (Preuss) U. Braun (1998) [bas. Fusoma inaequale Preuss (1855)]	***M. hieracii*** (Sacc. & Briard) Jaap (1908) [bas. *Sphaerella nebulosa* var. *hieracii* Sacc.&Briard (1885)]	***R. inaequalis*** (Preuss) U. Braun (1998)	Y	Jaap (1908); **Klebahn (1918)**; Sivanesan (1984)	EP	Klebahn (1948) isolated ascospores and obtained a culture in which the conidiogenous stage was observed.
R. variabilis Fuckel (1870)	***M. mariae*** (Sacc. & E. Bommer) Lindau (1903) [bas. *Sphaerella mariae* Sacc.&E. Bommer (1886)]	***R. variabilis*** Fuckel (1870)	Y	**Arx (1949)**; Tomilin (1979); Sivanesan (1984); Braun (1998); Aptroot (2006)	EP	Ascospores were isolated from perithecia in overwintered leaves into pure cultures from which the conidial forms developed.
R. nyssicola(Cooke) Videira & Crous (2014)	***M. nyssicola*** (Cooke) F.A. Wolf (1940)	***R. nyssicola*** (Cooke) Videira & Crous (2014)	Y	Minnis et al. (2011); **Videira et al. (2015a)**	EP	The asexual morph has not observed but the available strains obtained from the sexual morph are genetically placed within the *Ramularia* clade.
Ramularia sp.	***M. phacae-frigidae*** E. Müll. & Wehm. (1954)	***R. phacae-frigidae*** (E. Müll. & Wehm.) Videira & Crous (2015), **this study**	Y	**Müller & Wehmeyer (1954);** Aptroot (2006); Present study	EP	Müller & Wehmeyer (1954) observed ramularia-like spores when he described the species, but did not name the conidial form.
R. atropae Allesch. (1892)	**?** ***M. montellica*** (Sacc.) Guyot (1946)	–	N	Tomilin (1979); Braun (1998)	DB	Aptroot (2006) states the type belongs to *Davidiella*.
R. chamerionis Rostr. [as '*chamaenerii*'] (1885)	***M. chamaenerii*** Savile (1962)	–	N	Savile (1962); Sivanesan (1984); Aptroot (2006)	DB	Aptroot (2006) stated this belongs to *Davidiella*.

Table 3. (Continued).

Asexual morph[1]	Sexual morph[1]	Current name	CA[2]	References	Sexual link[3]	Notes
R. evanida (J. G. Kühn) Sacc. (1886)	***M. gentianae*** (Niessl) Lindau (1897) [syn. *M. galatea* (Sacc.) Jacz. (1917)]	–	N	Petrak (1940a); Tomilin (1979); Braun (1998)	DB	Aptroot (2006) states the type and additional material studied belong to *Davidiella*.
R. pteridiicola Petr. (1927)	**?** ***M. aquilina*** (Fr.) J. Schröt (1894)	–	N	Petrak (1927); Eriksson 1992); Braun (1998); Aptroot (2006)	DB	Aptroot (2006) studied material from India (IMI 152515) and states it belongs to *M. punctiformis*.
R. trifolii Jaap (1910)	***M. carinthiaca*** Jaap (1908)	–	N	Jaap (1910); Tomilin (1979); Braun (1998), Aptroot (2006)	DB	Aptroot (2006) studied authentic material, states it is a parasitic species of *Davidiella* and proposed a new combination *Davidiella carinthiaca* (Jaap) Aptroot.
Ramularia sp.	***M. nawae*** Hiura & Ikata (1929)	–	N	Kwon & Park (2004); Berbegal et al. (2013)	DB	Asexual ramularia-like morph observed but ITS closely related to *Phaeopleospora* (*Mycosphaerellaceae*). LSU not available.
R. aplospora Speg. (1879)	***M. alchemillicola*** Vassiljevsky 1925	–	Y	Vasil'evskij & Karakulin (1937); Tomilin (1979); Braun (1998)	NEP	
R. brunnea Peck (1878)	***M. tussilaginis*** (Rehm) Lindau (1903)	–	N	Wolf (1912); Vasil'evskij & Karakulin (1937); Tomilin (1979); Braun (1998); Aptroot (2006)	NEP	
R. lactea (Desm.) Sacc. (1882)	***M. violae*** Potebnia 1910	–	Y	Tomilin (1979); Braun (1998)	NEP	
R. obducens Thüm. (1881)	***M. pedicularis*** (P. Karst.) Lind (1913)	–	N	Savile (1968); Braun (1998)	NEP	Aptroot (2006) could not locate the type but after observing other Scandinavian material states that it belongs to section Caterva.
R. onobrychidis Allesch. (1892)	**?** ***M. onobrychidis*** (Hollós) Tomilin (1968)	–	N	Švarcman (1973); Braun (1998)	NEP	Aptroot (2006) states the type may have been destroyed during the war.
R. sambucina Sacc. (1882)	***M. ebulina*** Petr. (1915)	–	N	Petrak (1915); Tomilin (1979); Aptroot (2006)	NEP	Aptroot (2006) states the isotype in L belongs to section Caterva.

Table 3. (Continued).

Asexual morph[1]	Sexual morph[1]	Current name	CA[2]	References	Sexual link[3]	Notes
R. tricherae Lindr. (1902)	**? *Sphaerella sylvatica*** Sacc. & Speg. (1878) [syn. *M. scabiosae* Tomilin (1971)]	–	Y	Laibach (1921); Braun (1998); Aptroot (2006)	NEP	Aptroot (2006) states the type belongs to section Caterva.
R. ulmariae Cooke (1876)	***M. filipendulae-denudatae*** Kamilov (1973)	–	N	Tomilin (1979); Braun (1998)	NEP	
R. urticae Ces. (1863)	***M. superflua*** (Fuckel) Petr. (1940)	–	Y	Tomilin (1979); Sivanesan (1984); Petrak (1940b)	NEP	

[1] bas.: basionym; syn.: synonym.

[2] CA: Cultures of the *Ramularia* morph available; Y - Yes, N - No

[3] Sexual link; EP - Experimentally Proven; DB - Doubtfull; NEP - Not Experimentally Proven

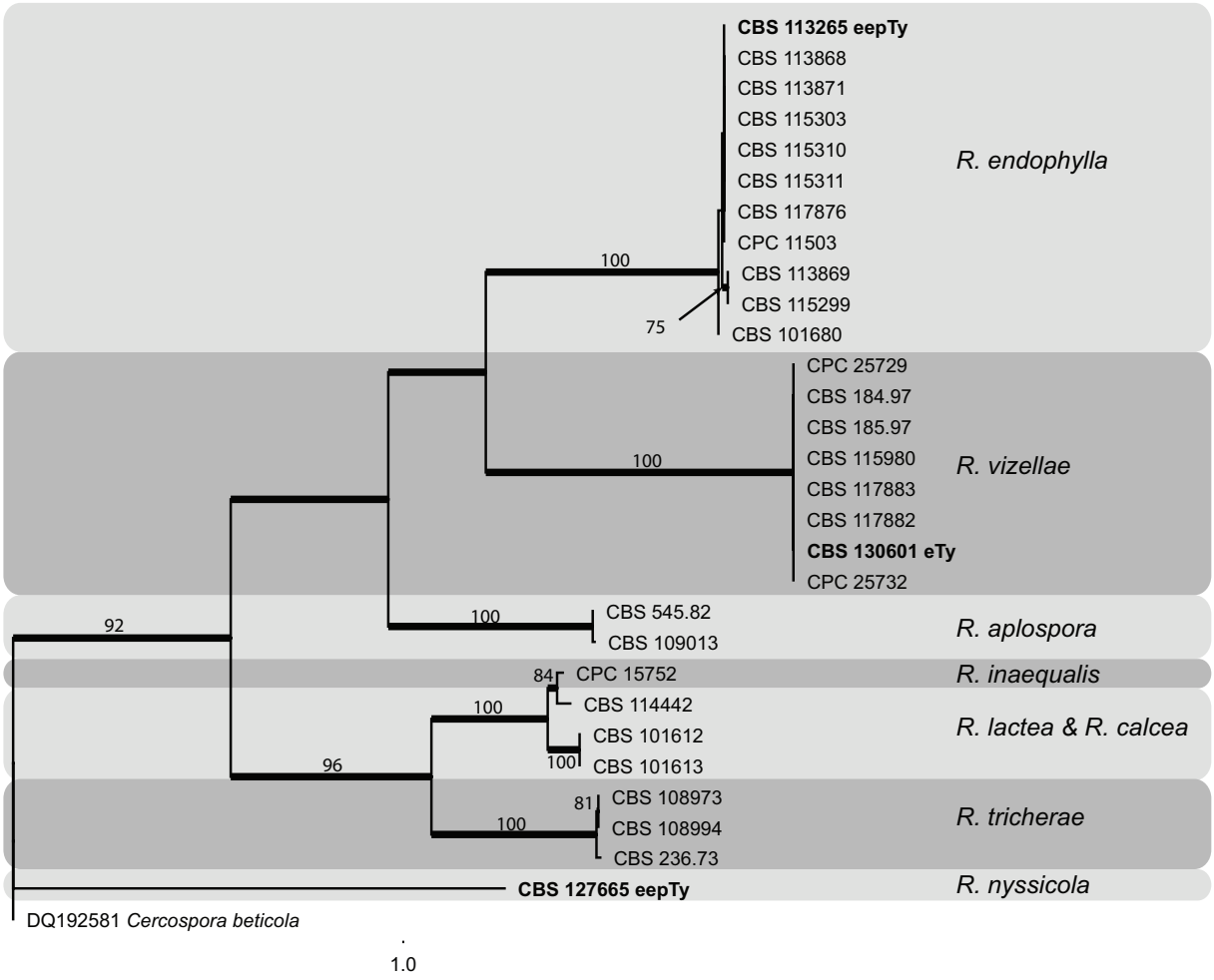

Fig. 2. The first of two equally most parsimonious trees obtained from the MAT1-1-1 sequence alignment. Bootstrap supportvalues from 1000 replicates are shown at the nodes. The tree was rooted to *Cercospora beticola* (GenBank DQ192581). TL= 912 steps, CI = 0.760, RI = 0.919, RC = 0.698, HI = 0.240. Strains in bold and marked as 'eTy' are ex-types and those marked as'eepTy' are ex-epitypes.

Specimens examined: **Belgium**, Namur, on leaves of *Quercus* sp., 7 May 1997, A. Aptroot (CBS 942.97). **Netherlands**, Utrecht, on dead leaves of *Castanea sativa*, 23 Feb. 1999, A. Aptroot (CBS 101680); on dead leaves of *Quercus robur*, Apr. 2003, G. Verkley (CBS H-7949, epitype; ex-epitype culture CBS 113265); on living leaf of *Quercus robur*, G. Verkley (CBS 113868; CBS 113869; CBS 113870); on fallen leaf of *Quercus robur*, G. Verkley (CBS 113871); on living leaves of *Quercus robur*, Sep. 2008, G. Verkley (CBS 115299; CBS 115302); on living leaf of *Quercus robur*, May 2013 (CBS 115303; CBS 115304); on dead leaf of *Quercus robur*, Aug. 2002, (CBS 115310; CBS 115311); on *Quercus robur*, G. Verkley (CBS 117876); on *Quercus robur*, 18 Jun. 2009, G. Verkley (CBS 117877). **South Korea**, unknown host, 1 Jan. 2004, H.D. Shin (CPC 11503).

Notes: The link between *Ramularia endophylla* (Verkley *et al.* 2004) and *Mycosphaerella punctiformis* (Starbäck 1889), initially described as *Sphaeria punctiformis* (Persoon 1794), was experimentally proven by Verkley *et al.* (2004) with morphological and phylogenetic data. Although the oldest epithet among these two names is '*punctiformis*' (Persoon 1794), the name *Ramularia punctiformis* Sacc. (Saccardo, 1904) is already in use. Several possible epithets

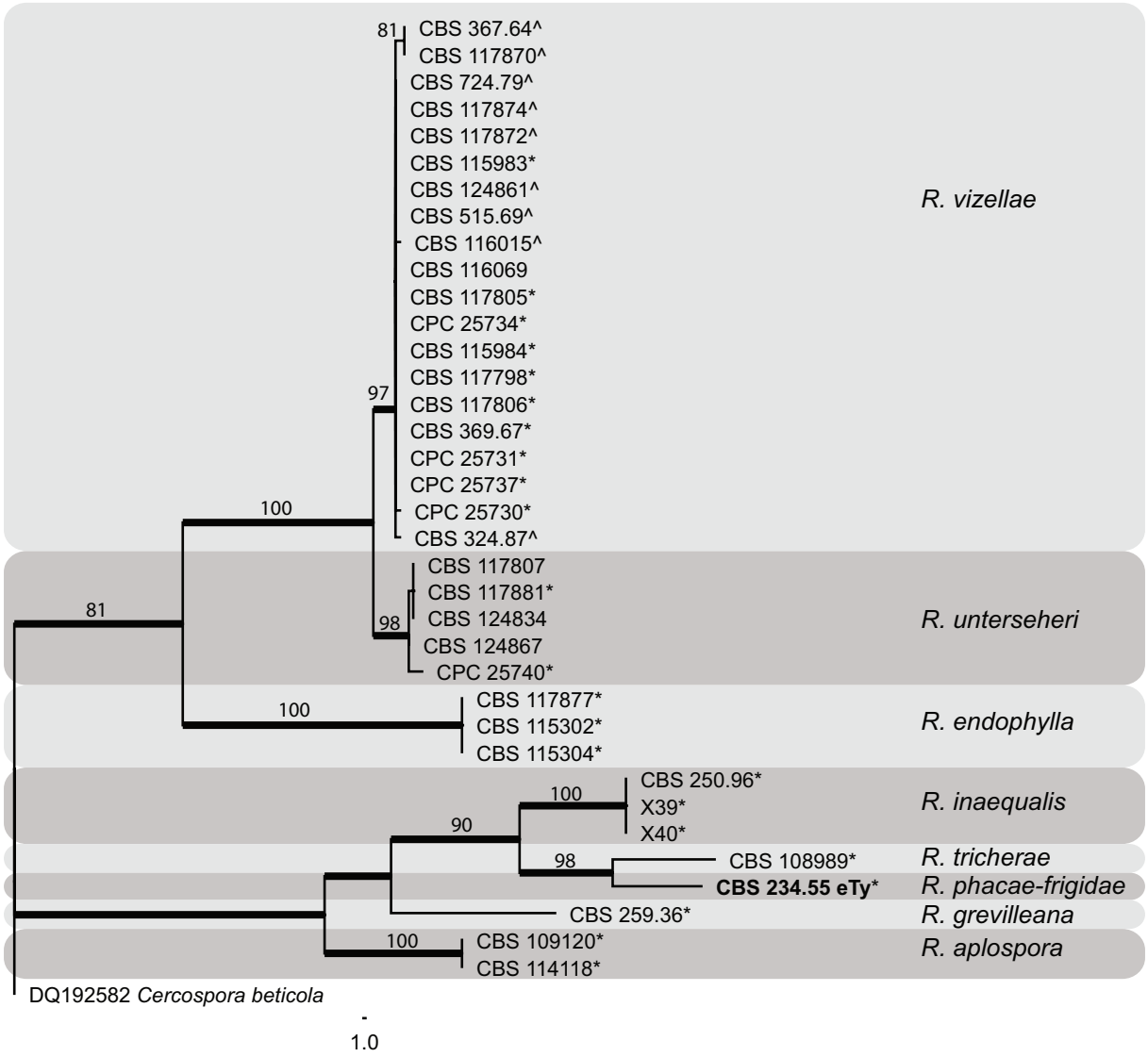

Fig. 3. The first of nine equally most parsimonious trees obtained from the MAT1-2-1 sequence alignment. Bootstrap support values from 1000 replicates are shown at the nodes. The tree was rooted to *Cercospora beticola* (GenBank DQ192582).TL = 379 steps, CI = 0.736, RI = 0.873, RC = 0.643, HI = 0.264. Strains in bold and marked as 'eTy' are ex-types and those marked as 'eepTy' are ex-epitypes. The asterisk (*) represents sequences obtained with the primer combination MAT1-1-1 forward and MAT1-2-1 reverse (Table 2) and the caret (^) represents strains obtained with both the usual primer combination MAT1-2-1 forward and reverse and the unusual primer combination MAT1-1-1 forward and MAT1-2-1 reverse (Table 2). Strains without these symbols represent sequences obtained only with the regular primer combination MAT1-2-1 forward and reverse (Table 2).

can be found among the synonyms proposed by Tomilin (1979) and Aptroot (2006). However, these specimens are often in poor state, contain immature perithecia or represent species never collected or observed after their first description (Aptroot 2006). In addition, several type specimens of other *Mycosphaerella* species have been found to be indistinguishable from *M. punctiformis* (Aptroot 2006) and the names represent valid epithets in case this material is recollected and prove to be the same species. With the objective to clarify and stabilize

the taxonomy of this species, we propose that the epithet '*endophylla*' is conserved since it represents an unequivocally proven link between sexual and asexual stage of this species, both biologically and phylogenetically.

Ramularia grevilleana (Oudem.) Jørst., Meld. Stat. Plantepatol. Inst. 1: 17 (1945)
Basionym: *Cylindrosporium grevilleanum* Oudem., Arch. Neerl. Sci. Exact. Nat. 8: 392 (1873), asexual morph [*Cylindrosporium* sp., in Tulasne & Tulasne (1863: 288)].
Synonyms: *Sphaeria fragariae* Tul. & C. Tul., Ann. Sci. Nat., Bot. 5: 112 (1856), nom. illeg., non Schwein. 1832.
Stigmatea fragariae Tul. & C. Tul., Select. Fung. Carpol. 2: 288 (1863).
Ramularia fragariae Peck, Ann. Rep. N.Y. State Mus. Nat. Hist.32: 43 (1880).
Sphaerella fragariae (Tul. & C. Tul.) Sacc., Syll. Fung. 1: 505 (1882).
Mycosphaerella fragariae (Tul. & C. Tul.) Lindau, Nat. Pflanzenfam., Teil 1, 1(1): 424 (1897).
Ramularia punctiformis Sacc., Alaska Exp. Crypt.: 16 (1904).
For further synonyms based on asexual morphs, see Braun (1995: 248).

Specimens examined: **Sweden**, Uppland, Alsike, on *Fragaria ananassa*, 4 Oct. 1989, E. Gunnerbeck (CBS 114732 = UPSC 3244). **Netherlands**, unknown district, host, collector and date (CBS 259.36; CBS 298.34). **New Zealand**, Auckland, on *Fragaria* × *ananassa* 'Tioga' (CBS 719.84).

Notes: This pathogen is known for causing leaf spot disease in strawberry, both cultivated and wild species, and has a worldwide distribution (Braun 1998). The link between *Ramularia grevilleana* (Jørstad 1945) and *Mycosphaerella fragariae* (Lindau 1897) was experimentally proven by Dudley (1889) who observed the ascospores germinating within the ascus inside the perithecium, developing into mycelium that grew out through the perithecium wall and ostiolum, and produced conidia. Since then, most authors have treated this link as reliable and both names have appeared together in several publications (Maas 1984; Crous *et al*. 2000; Braun & Pennycook 2003; Kirshner 2009). *Ramularia grevilleana* (Jørstad 1945) was initially described as *Cylindrosporium grevilleanum* by Oudemans (1873a). The confused nomenclatural history of this asexual morph name, previously attributed to Tulasne & Tulasne (1863), was discussed and clarified by Braun & Pennycook (2003). *Mycosphaerella fragariae* (Lindau 1897) was first described as *Sphaeria fragariae* (Tulasne 1856), which is a nom. illeg. (homonym). *Stigmatea fragariae* Tul. & Tul. (Tulasne & Tulasne 1863) is the first valid name for this species but a reallocation of this name to *Ramularia* is not possible because *R. fragariae* already exists. *Cylindrosporium grevilleanum* (Oudemans 1873a) is the oldest available epithet among the synonyms and the basionym of the current name *Ramularia grevilleana* (Jørstad 1945), which is the nomenclaturally correct denomination for this species.

Ramularia phacae-frigidae (E. Müll. & Wehm.) Videira & Crous, **comb. nov.** MycoBank MB812600
Basionym: *Mycosphaerella phacae-frigidae* E. Müll. & Wehm., Sydowia 8: 190 (1954).

Specimens examined: **Switzerland**, Corveglia, above St. Moritz, from *Phaca frigida*, 20 Jul. 1953, E. Müller (ex-type culture CBS 234.55).

Notes: When *Mycoshaerella phacae-frigidae* was originally described (Müller & Wehmeyer

1954), the ascospores were isolated, producing a *Ramularia* state that was not named at that time. Based on morphological and molecular evidence we propose a new combination for this name in *Ramularia*. Culture CBS 234.55 was deposited by E. Müller in the CBS culture collection in May 1955 and is from the same host, locality and date as the original material used for the description of *M. phacae-frigidae*, which indicates that it is an ex-type strain.

Ramularia unterseheri Videira & Crous, **sp. nov.** MycoBank MB812599 Fig. 4.

Etymology. Named after Martin Unterseher, whose research focus on biodiversity and ecology of endophytic fungi, and the person who collected most of the strains of this species currently deposited at the CBS-KNAW collection.

Description: *Mycelium* consisting of septate, branched, smooth, hyaline hyphae, (1–)1.5–2 µm diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* smooth, hyaline, arising from hyphae, terminal and lateral, (5.5–)11–14(–20) × (1.5–)2 µm, sympodially proliferating with 1–3 apical loci, flattened or protuberant, cylindrical; scars thickened, darkened, refractive, 0.5–1 µm diam. *Ramoconidia* subcylindrical to oval or ovoid, 0–1-septate, hyaline, smooth, (8–)10–12(–18) × (1.5–)2–2.5(–3) µm. *Intercalary conidia* hyaline, smooth, aseptate, oval to ovoid, (6–)8–9(–13) × (2–)2.5–3 µm, in branched chains of up to six conidia. *Terminal conidia* hyaline, smooth, aseptate, obovoid to oval (3.5–)5–6(–7) × (1.5–)2–2.5(–3) µm; hila thickened, darkened, refractive, 0.5–1 µm diam.

Culture characteristics: On MEA surface raised, radially striated, with smooth mycelium, rosy

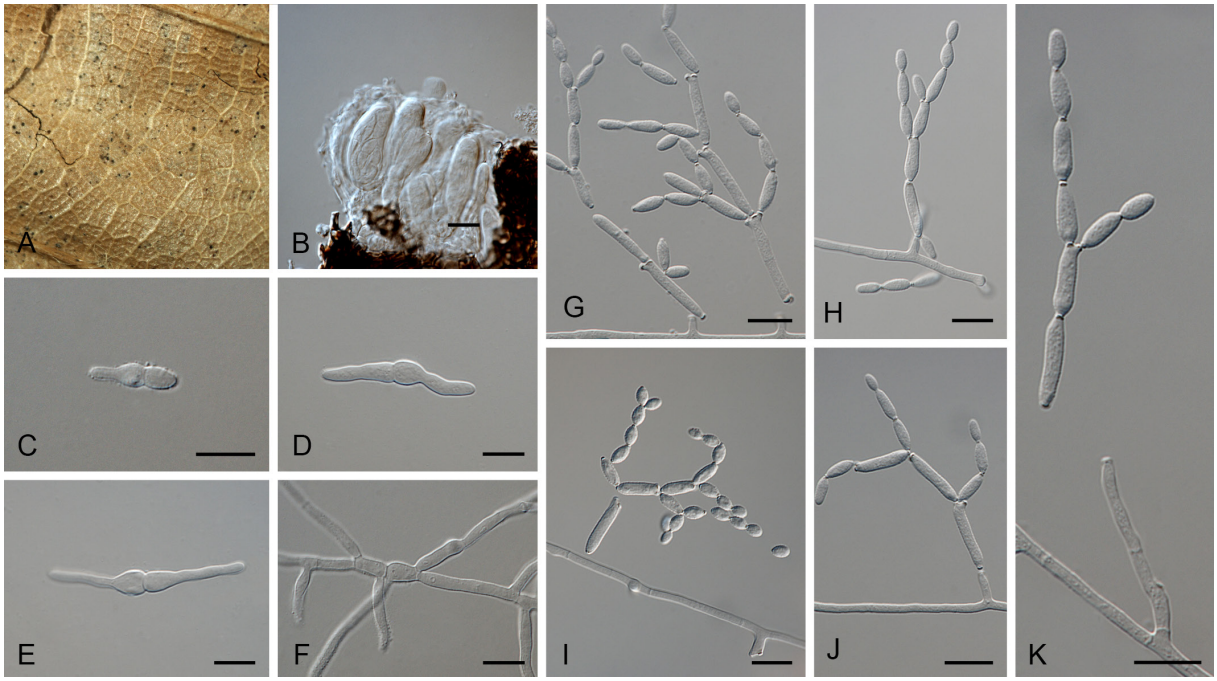

Fig. 4. *Ramularia unterseheri*. A. Leaf of *Fagus sylvatica* (CPC 25740); B. Broken ascoma bearing asci with ascospores (CPC25740); C–F. Germinating ascospores (CPC 25740); G–K. Hypha, conidiophores and conidia (CBS 124884). Scale bars = 10 µm.

vinaceus, with undulate margins and reverse cinnamon, reaching 10 mm after 2 wk at 25 °C. On OA surface flat, smooth mycelium, with undulate edge, reaching 15 mm after 2 wk at 25 °C. On PDA radially striated, smooth mycelium, rosy buff with undulate margins, reverse cinnamon, reaching 12 mm after 2 wk at 25 °C.

Specimens examined: **Germany**, Mecklenburg-Vorpommern, Greifswald, Elisenhain, on leaf litter of *Fagus sylvatica*, 4 Jan. 2008, M. Unterseher (holotype CBS H-22285, ex-type culture CBS 124884), additional collections with same details (CBS 124844, 124846, 124852, CBS 124867); on living leaves from understorey of *Fagus sylvatica*, 8 Jan. 2008, M. Unterseher (CBS 124826, CBS 124827, CBS 124830, CBS 124831, CBS 124834, CBS 124836, CBS 124838); without locality, on seed of *Fagus sylvatica*, date unknown, U. Delfs-Siemer (CBS 355.90); Hessen, Schlangenbad, on leaf of *Alnus* sp., 2012, W. Quaedvlieg (CPC 25739 = W6); Mecklenburg-Vorpommern, Bornhof, on *Lupinus* sp., U. Feiler 1993 (CBS 588.93); Bavaria, Munich, room inside a castle, May 2011, unknown collector (CBS 130721). **Netherlands**, Utrecht, Amelisweerd, on dead leaves of *Fagus sylvatica*, 25 Apr. 2005, G. Verkley (CBS 117801 = CPC 12091); Amersfoort, dead leaves of *Fagus sylvatica*, 25 Jul. 2005, G. Verkley (CBS 117807 = CPC 12095); Baarn, Baarnsche Bos, on *Tilia* sp., 26 Apr. 2004, G. Verkley (CBS 117880 = CPC 11209, CBS 117881 = CPC 11211); Baarn, decaying leaves of *Acer pseudoplatanus*, 26 Apr. 2004, G. Verkley (CBS 117878 = CPC 11206, CBS 117879 = CPC 11207); Rhijnauwen forest, decaying leaves of *Fagus sylvatica*, 17 May 2012, S.I.R. Videira (CPC 25740 = X2).

Notes: *Ramularia unterseheri* is a plurivorous species that is often found in *Fagus sylvatica* leaves in Germany and the Netherlands. It differs from *R. vizellae* by shorter and narrower ramoconidia [(8–)10–12(–18) × (1.5–)2–2.5(–3) µm versus (8–)10–12(–23) × (2.5–)3–3.5(–5) µm] and longer and narrower terminal conidia [(3.5–)5–6(–7) × (1.5–)2–2.5(–3) versus 4–5 (–5.5) × (2–)3(–3.5) µm]. It has been previously isolated from dead overwintered leaves as well as from living leaves (Verkley *et al*. 2004). In this study, a mycosphaerella-like sexual morph was observed (Fig. 4, A–F) in newly collected samples of overwintered leaves in the Netherlands, but the available material was too scarce to provide a description.

Ramularia vizellae Crous, Persoonia 27: 37 (2011) MycoBank MB560566 Fig. 5.

Specimens examined: **France**, on fruit of *Malus sylvestris*, C. Moreau (CBS 367.64). **Austria**, Graz, Innere Ragnitz, on *Sambucus nigra*, 12 Oct. 2012, C. Scheuer (CPC 25738 = X31). **Germany**, Mecklenburg-Vorpommern, Greifswald, Elisenhain, on leaf litter from *Fagus sylvatica*, 4 Jan. 2008, M. Unterseher (CBS 124861); Hessen, Schlangenbad, on leaf of unidentified plant, W. Quaedvlieg (CPC 25733 = W7); Bavaria, München, on overwintering leaves of *Tilia* sp., Jul. 1979, A. John (CBS 724.79). **Netherlands**, in leaf spot caused by *Mycosphaerella* sp. on *Brassica* sp. (CBS 324.87); Gelderland, Randwijk, on dead leaf litter of *Malus* sp. (CBS 115980); Randwijk, on dead leaf litter of *Malus* sp. (CBS 115981, CBS 115982, CBS 115983, CBS 115984, CBS 116015, CBS 116069); Utrecht, Amelisweerd, on dead leaves of *Acer pseudoplatanus*, 25 Apr. 2005, G. Verkley (CBS 117799 = CPC 12089); on dead leaves of *Carpinus betulus*, 25 Apr. 2005, G. Verkley (CBS 117802 = CPC 12092); Amersfoort, on dead leaves of *Tilia* sp., 25 Apr. 2005, G. Verkley (CBS 117806 = CPC 12096); Baarn, Park Kasteel Groeneveld, on decaying leaves of *Quercus rubra*, 26 Apr. 2004, G. Verkley (CBS 117870 = CPC 11193), on decaying leaves of *Quercus rubra*, G. Verkley (CBS 117871 =

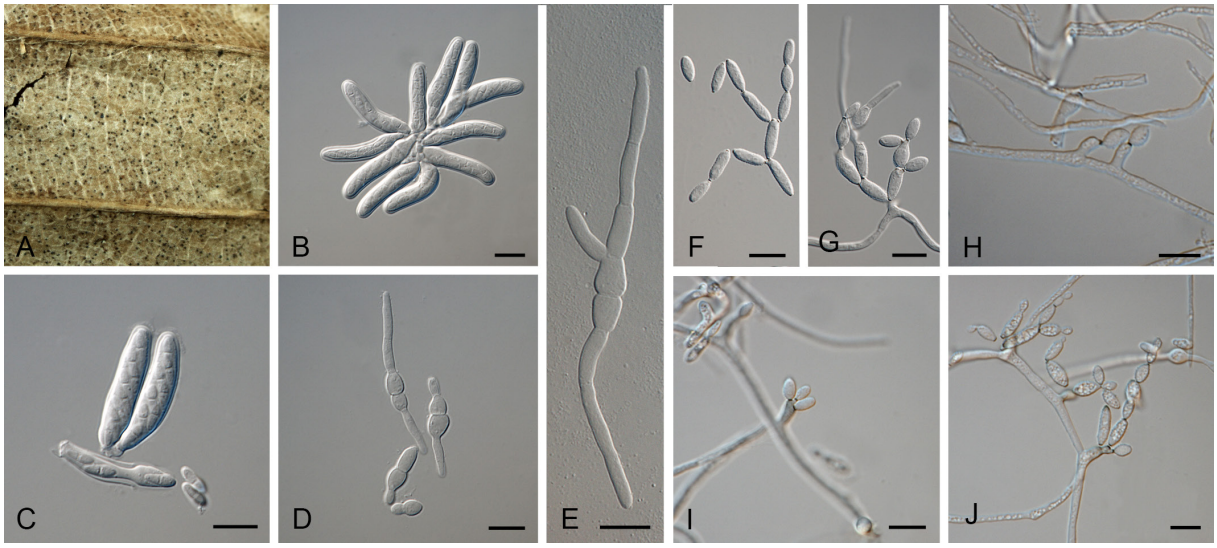

Fig. 5. *Ramularia vizellae*. A. Leaf of *Carpinus* sp. (CPC 25730); B, C. Asci bearing ascospores (CPC 25730). D, E. Germinating ascospores (CPC 25730); F–J. Hypha, conidiophores and conidia (F, G. CPC 25729; H. CBS 117871; I, J. CBS 117799). Scale bars = 10 µm.

CPC 11194), on *Amelanchier lamarckii*, 26 Apr. 2004, G. Verkley (CBS 117872 = CPC 11197, CBS 117873 = CPC 11198); Lage Vuursche, on *Aesculus hippocastanum*, G. Verkley (CBS 117874 = CPC 11200, CBS 117875 = CPC 11201), on decaying leaves of *Sorbus aucuparia*, 26 Apr. 2004, G. Verkley (CBS 117882 = CPC 11212, CBS 117883 = CPC 11213); garden, Eemnesserweg 90, on dead leaves of *Acer pseudoplatanus*, 7 May 1996, H.A. van der Aa (CBS 184.97, CBS 185.97), on *Acer pseudoplatanus*, 15 Oct. 1968, H.A. van der Aa (CBS 515.69); Baarn, ruderal terrain at Drakenburgerweg, on young leaves of *Lotus uliginosus*, 18 Jun. 1967, H.A. van der Aa (CBS 369.67); Utrecht Botanical Garden, on overwintered leaves of *Corylus* sp., 21 Apr. 2012, S.I.R. Videira (CPC 25728 = MP19), on overwintered leaves of *Quercus* sp., 21 Apr. 2012, S.I.R. Videira (CPC 25729 = MP20), on overwintered leaves of *Carpinus* sp., 21 Apr. 2012, S.I.R. Videira (CPC 25730 = MP21), on overwintered leaves of *Quercus* sp., 21 Apr. 2012, S.I.R. Videira (CPC 25731 = MP23), on overwintered leaves of *Fagus* sp., 21 Apr. 2012, S.I.R. Videira (CPC 25732 = MP24); Utrecht Rhijnauwen park, on *Aesculus hippocastanum*, 25 Apr. 2005, G. Verkley (CBS 117805 = CPC 12094), on overwintered leaves of *Fagus* sp., 17 May 2012, S.I.R. Videira (CPC 25734 = X1, CPC 25735 = X3), on fruit scales of *Carpinus betulus*, 25 Apr 2005, G. Verkley (CBS 117798 = CPC 12088), on overwintered leaves of *Corylus* sp., 17 May 2012, S.I.R. Videira (CPC 25736 = X4), on overwintered leaves of *Aesculus hipocastanum*, 17 May 2012, S.I.R. Videira (CPC 25737 = X5); Soesterberg 'De Stompert', on dead fallen leaves of *Quercus robur*, G. Verkley (CBS 113267). **South Africa**, on leaves of *Protea* sp. in association with *Vizella interupta*, 2 May 2010, P.W. Crous (ex-type culture CBS 130601 = CPC 18283). **Switzerland**, on *Phaseolus* sp. (CBS 428.74 = IHEM 3995). **Ukraine**, Seversky Donets river, NNP Svjatie Gory, on *Acer campestre*, 21 Jul. 2008, A. Akulov (CPC 15539, CPC 15541).

Notes: This species was recently described from leaves of *Protea* sp. from South Africa (Crous *et al*. 2011) in association with lesions caused by *Vizella interrupta* in what was deemed as either a chance encounter, as sporulation was not observed in the leaf itself, or an indication

that the species was a secondary invader of the diseased leaf tissue. *Ramularia vizellae* is now known from numerous hosts in many European countries (Fig. 1, Table 1) as well as in South Africa. A mycosphaerella-like sexual morph was observed in freshly collected samples in the Netherlands (Fig. 5, A–E), but a description is not provided due to the scarcity of material examined.

DISCUSSION

Based on the epitypification of *Mycosphaerella punctiformis* (now *Ramularia endophylla*) (Verkley *et al*. 2004), and the molecular characterization of *Ramularia pusilla* (type species of *Ramularia*) by Kirschner (2009), the names *Mycosphaerella* and *Ramularia* are confirmed as congeneric. This means it is now possible to separate species closely allied to *R. endophylla*, such as *R. nyssicola* (Minnis *et al*. 2011). Based on the multigene phylogeny generated in this study (Fig. 1), the host range and distribution of *R. endophylla* has been narrowed, since most of the strains were isolated from *Quercus* leaves collected in the Netherlands, with the exception of one strain collected from *Castanea sativa* and another strain collected from Korea.

The heterogeneity observed in the ITS sequences in the past was further accentuated when protein coding genes were added to the analysis and both the Bayesian and parsimony analyses based on five genes in the present study split this species complex into three species: *R. endophylla*, *Ramularia vizellae* and the newly described species, *Ramularia unterseheri*. The identification of these closely related species based on morphology alone is difficult, and the ITS barcode alone is insufficient for species level identification. Based on the individual gene trees, each of the partial gene sequences of *actA*, *rpb2* and *gapdh* are good phylogenetic markers to use in addition to the ITS barcode since they successfully separate the three species.

The new species described in this study, *R. unterseheri* (Fig. 4), is only known from the Netherlands and Germany, but with a rather broad host range, namely *Acer* (*Sapindaceae*), *Alnus* (*Betulaceae*), *Fagus* (*Fagaceae*) and *Tilia* (*Malvaceae*). The intraspecific variation observed in each clade (Fig. 1) is a result of the variation observed in the gene sequences among the strains. The internal structure of this variation was not consistent between different loci and cryptic speciation is unlikely to account for these genetic differences.

In this study, a mycosphaerella-like sexual morph was observed for both *R. unterseheri* (Fig. 4) and *R. vizellae* (Fig. 5) in overwintered leaves collected in the Netherlands. In addition, several of the strains of *R. unterseheri* were isolated from living material as endophytes in the previous work of Verkley *et al.* (2004). These observations indicate that these species most likely have a life cycle similar to that of *R. endophylla* but more work needs to be done in order to fully understand these fungal life-cycles. Even though the life-cycle of *R. endophylla* is well known (Verkley *et al.* 2004), some questions still remain unanswered, e.g. the role played by the *Asteromella* spermatial state in the development of the species.

Sexual reproduction plays an important role in the dynamics and fitness of a species by introducing variability through genetic recombination and the mating type genes are essential for the sexual cycle to occur. The similarity of homologous mating-type genes is usually very low except for the high mobility group and the alpha domains (Turgeon 1998). These conserved domains were successfully used to clarify the phylogenetic relationships among closely related species (Du *et al.* 2005; Paoletti *et al.* 2005) but were not effective in resolving the *Cercospora apii* complex (Groenewald *et al.* 2006). The MAT1-2-1 tree showed that *R. vizellae*, *R. unterseheri* and *R. endophylla* strains cluster in separate well supported clades and the same can be observed in the MAT1-1-1 tree for the strains of *R. endophylla* and *R. vizellae*. In this

study, the mating-type loci were effective in the separation of this complex. The complete characterization of the mating-type genes in *Ramularia* species has not been performed before and the evidence indicates these species are heterothallic since the strains with a MAT1-1-1 sequence did not amplify the MAT1-2-1 locus and vice-versa. However, transitions between heterothallic (self-sterile) and homothallic (self-fertile) sexual cycles are common among fungi and which represents the ancestral state is unknown. Experimentally proven links in literature between *Ramularia* and *Mycosphaerella* are limited (Table 3). There are six cases where the authors reported they observed the complete life cycle of the fungus from ascospore to conidia.

Experimentally confirmed links include *R. endophylla*/*M. punctiformis* (= *R. endophylla*) (Verkley *et al.* 2004), *Ramularia grevilleana*/*Mycosphaerella fragariae* (= *R. grevilleana*) (Oudemans 1873a; Braun 2003), *Ramularia variabilis*/*Mycosphaerella mariae* (= *R. variabilis*) (Arx 1949), and *Ramularia inaequalis*/*Mycosphaerella hieracii* (= *R. inaequalis*) (Klebahn 1918). In the case of *Mycosphaerella nyssicola*, no *Ramularia* morph has been observed, but based on molecular evidence the species belongs in *Ramularia,* and a new combination (= *R. nyssicola*) was made for this species (Videira *et al.* 2015a). When *Mycosphaerella phacae-frigidae* was described (Müller & Wehmeyer 1954), the ascospores that were isolated produced a *Ramularia* state in culture that was not named at the time, and hence a new combination is introduced for this name in *Ramularia* (= *Ramularia phacae-frigidae*).

Sivanesan (1984) reported the links *Ramularia gossypi*/*M. areola*, *Ramularia nigromaculans*/*Mycosphaerella nigromaculans*, and *Ramularia urticae*/*Mycosphaerella superflua*, among others. *Ramularia gossypii* has been reassigned to the genus *Ramulariopsis* (Braun & Pennycook 1993) and *R. nigromaculans* has been excluded from *Ramularia* based on its pigmented conidia (Braun 1998). *Ramularia urticae*/*M. superflua*, and at least eight other links (Table 3), have not been experimentally proven, and await further collections and study.

Other existing links have been considered doubtful since Aptroot (2006) examined the herbarium type specimens of some *Mycosphaerella* that he considered belonged to *Davidiella* (Table 3). An interesting case is that of *Mycosphaerella nawae*, a pathogen causing circular leaf spot of persimmon that was originally reported from Japan (Ikata & Hitomi 1929) but has now spread worldwide (Berbegal *et al*. 2013). In Korea, a ramularia-like morph was observed (Kwon & Park 2004) but its importance during the infection processes was not established (Berbegal *et al*. 2013). Despite its importance as a plant pathogen, no cultures of this species are available in public culture collections. A recent study by Berbegal *et al*. (2013) generated two ITS sequences (GenBank GQ465767 & GQ465768) of *M. nawae* that, when compared with other dothideomyceteous ITS sequences in NCBI's GenBank, places the species near or in *Phaeophleospora* within the *Mycosphaerellaceae* (Quaedvlieg *et al*. 2014). This link is considered doubtful, awaiting further collections of fresh material.

In conclusion, we have shown that the *R. endophylla* species complex consists of three species, namely *R. endophylla*, *R. vizellae*, and a novel species described in this paper, *R. unterseheri*. We show that *R. vizellae* has a much wider host range and geographical distribution than originally assumed and observed its sexual stage. In spite of close to 1000 species names in *Ramularia*, and more than 10 000 species that have been described in *Mycosphaerella* s. lat., the present study could only confirm six connections in *Ramularia*, and one new combination was proposed to accommodate *R. phacae-frigidae*. Additional collections of other names in *Mycosphaerella* may reveal more species that are true members of *Ramularia*, but presently the majority appears to belong to other genera (Quaedvlieg *et al*. 2014). In much of the plant pathology literature the name *Mycosphaerella* has been applied in a broad morphological and non-phylogenetic sense. For these fungi, the term mycosphaerella-like sexual morph is more

appropriate. In accordance with the newly revised ICN code, the generic name *Ramularia* has been protected over that of *Mycosphaerella* and will be applied to this genus in the future.

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CHAPTER 4

All that glitters is not *Ramularia*

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Key words: Barcoding, Cercosporoid, Multilocus phylogeny, *Mycosphaerella*, Plant pathogen.

Abstract: *Ramularia* is a species-rich genus that harbours plant pathogens responsible for yield losses to many important crops, including barley, sugar beet and strawberry. Species of *Ramularia* are hyphomycetes with hyaline conidiophores and conidia with distinct, thickened, darkened, refractive conidiogenous loci and conidial hila, and *Mycosphaerella* sexual morphs. Because of its simple morphology and general lack of DNA data in public databases, several allied genera are frequently confused with *Ramularia*. In order to improve the delimitation of *Ramularia* from allied genera and the circumscription of species within the genus *Ramularia*, a polyphasic approach based on multilocus DNA sequences, morphological and cultural data were used in this study. A total of 420 isolates belonging to *Ramularia* and allied genera were targeted for the amplification and sequencing of six partial genes. Although *Ramularia* and *Ramulariopsis* proved to be monophyletic, *Cercosporella* and *Pseudocercosporella* were polyphyletic. *Phacellium* isolates clustered within the *Ramularia* clade and the genus is thus tentatively reduced to synonymy under *Ramularia*. *Cercosporella* and *Pseudocercosporella* isolates that were not congeneric with the ex-type strains of the type species of those genera were assigned to existing genera or to the newly introduced genera *Teratoramularia* and *Xenoramularia*, respectively. *Teratoramularia* is a genus with ramularia-like morphology belonging to the *Teratosphaeriaceae*, and *Xenoramularia* was introduced to accommodate hyphomycetous species closely related to *Zymoseptoria*. The genera *Apseudocercosporella*, *Epicoleosporium*, *Filiella*, *Fusidiella*, *Neopseudocercosporella*, and *Mycosphaerelloides* were also newly introduced to accommodate species non-congeneric with their purported types. A total of nine new combinations and 24 new species were introduced in this study.

Taxonomic novelties: New genera: *Apseudocercosporella* Videira & Crous, *Epicoleosporium* Videira & Crous, *Filiella* Videira & Crous, *Fusoidiella* Videira & Crous, *Mycosphaerelloides* Videira & Crous, *Neopseudocercosporella* Videira & Crous, *Teratoramularia* Videira, H.D. Shin & Crous, *Xenoramularia* Videira, H.D. Shin & Crous; **New combinations:** *Filiella pastinacae* (P. Karst.) Videira & Crous, *Fusoidiella depressa* (Berk. & Broome) Videira & Crous, *Mycosphaerelloides madeirae* (Crous & Denman) Videira & Crous, *Neopseudocercosporella brassicae* (Chevall.) Videira & Crous, *Neopseudocercosporella capsellae* (Ellis & Everh.) Videira & Crous, *Ramularia cerastiicola* (Crous) Videira & Crous, *Ramularia stellariicola* (M.J. Park *et al.*) Videira, H.D. Shin & Crous, *Sphaerulina chaenomelis* (Y. Suto) Videira, U. Braun, H.D. Shin & Crous, *Sphaerulina koreana* (Crous *et al.*) Videira, H.D. Shin & Crous.; **New names:** *Ramularia alangiicola* Videira, H.D. Shin & Crous, *Ramularia veronicicola* Videira & Crous; **New species:** *Acrodontium fagicola* Videira & Crous, *Acrodontium luzulae* Videira & Crous, *Acrodontium pigmentosum* Videira & Crous, *Apseudocercosporella trigonotidis* Videira, H.D. Shin & Crous, *Cercosporella catenulata* Videira & Crous, *Epicoleosporium ramularioides* Videira, H.D. Shin & Crous, *Ramularia euonymicola* Videira, H.D. Shin, U. Braun & Crous, *Ramularia gaultheriae* Videira & Crous, *Ramularia geraniicola* Videira & Crous, *Ramularia malicola* Videira & Crous, *Ramularia neodeusta* Videira & Crous, *Ramularia osterici* Videira, H.D. Shin & Crous, *Ramularia rumicicola* Videira, H.D. Shin & Crous, *Ramularia trigonotidis* Videira, H.D. Shin & Crous, *Ramularia weberiana* Videira & Crous, *Ramulariopsis pseudoglycines* Videira, Crous & Braun, *Teratoramularia infinita* Videira & Crous, *Teratoramularia kirschneriana* Videira & Crous, *Teratoramularia persicariae* Videira, H.D. Shin & Crous, *Teratoramularia rumicicola* Videira, H.D. Shin & Crous, *Xenoramularia arxii* Videira & Crous, *Xenoramularia neerlandica* Videira & Crous, *Xenoramularia polygonicola* Videira, H.D. Shin & Crous. **Typifications: Epitypifications:** *Cercosporella gossypii* Speg., *Cylindrosporium heraclei* Oudem., *Fusoma inaequale* Preuss, *Ovularia tovarae* Sawada, *Ramularia acroptili* Bremer, *Ramularia aplospora*

Speg., *Ramularia armoraciae* Fuckel, *Ramularia beticola* Fautrey & Lambotte, *Ramularia geranii* Fuckel, *Ramularia lamii* Fuckel var. *lamii*, *Ramularia pusilla* Unger, *Ramularia vallisumbrosae* Cavara, *Ramularia variabilis* Fuckel; **Neotypifications:** *Crocysporium rubellum* Bonord., *Ramularia collo-cygni* B. Sutton & J.M. Waller; **Lectotypification:** *Ramularia kriegeriana* Bres.

INTRODUCTION

Ramularia (Unger 1833) is a species-rich genus (1 220 names listed in MycoBank, accessed 6 Nov. 2015) that belongs to the family *Mycosphaerellaceae* in the order *Capnodiales*. *Ramularia* species are mostly phytopathogenic and associated with leaf spots, necrosis or chlorosis, but some species can be saprobic or even mycophilic. The genus was monographed by Braun (1995, 1998) who defined *Ramularia* as genus of hyphomycetous species with hyaline conidiophores and conidia with distinct, thickened, darkened and refractive conidiogenous loci and conidial hila. *Ramularia* and allied genera were traditionally described based on the colour (hyaline or pigmented) and the structure of conidiophores (simple or branched), the structure of conidiogenous loci and conidial hila (conspicuous or inconspicuous, by being thickened and darkened or not). Genera with hyaline structures and conspicuous conidial loci include *Cercosporella*, *Hawksworthiana*, *Neoovularia*, *Phacellium*, *Pseudodidymaria*, *Ramularia* and *Ramulariopsis*, while genera with inconspicuous conidial loci include *Monodidymaria*, *Neoramularia* and *Pseudocercosporella*.

Although these morphological characters have been considered important to define these genera, molecular studies have indicated that they are not always phylogenetically informative, and that the generic concepts need to be revised (Crous *et al.* 2001b, Verkley *et al.* 2004, Kirschner 2009). The genus *Cercosporella* was usually distinguished from *Ramularia* by having bulging and hyaline conidiogenous loci. However, these characters are minute and difficult to observe with light microscopy, resulting in frequent transfers of species between both genera. Based on 28S nrDNA sequence data the type species of *Cercosporella* (*C. virgaureae*) was shown to cluster in a sister clade to *Ramularia s. str.* (Kirschner 2009), and two additional characters were observed: *Cercosporella* has flat conidiogenous loci shaped as a truncated cone and produces cup-shaped appressoria. In contrast, *Ramularia* has conidiogenous loci with a raised rim with a tall central dome and a crater in between (resembling *Cladosporium*, see Bensch *et al.* 2012), and does not form appressoria.

Species of *Ramularia* have *Mycosphaerella* sexual morphs, but only a few lifecycles have been experimentally proven, and some species may be asexual holomorphs (Braun 1995, 1998, Verkley *et al.* 2004, Videira *et al.* 2015b). *Mycosphaerella s. lat.* species have been associated with more than 30 genera, including both hyphomycetes and coelomycetes (*Mycosphaerellaceae*) (Crous 2009). *Mycosphaerella s. str.*, however, was shown to be confined to taxa with *Ramularia* asexual morphs (Verkley *et al.* 2004, Crous *et al.* 2009c, Videira *et al.* 2015b). In agreement with the new rules for naming of pleomorphic fungi in the *International Code of Nomenclature for algae, fungi and plants* (ICN; Hawksworth 2011, Hawksworth *et al.* 2011, Wingfield *et al.* 2012, Crous *et al.* 2015b), the older name *Ramularia* was selected over that of *Mycosphaerella* (see Videira *et al.* 2015b for more details), and is included in a list of protected generic names (Kirk *et al.* 2013, Wijayawardene *et al.* 2014, Rossman *et al.* 2015).

The genus *Ramularia* includes important plant pathogens such as *R. collo-cygni* and *R. beticola* that cause severe economic losses to barley and sugar beet crops, respectively. Protecting crops from damage by weeds, animal pests and pathogens is a major prerequisite to increase productivity to meet the global increase in demand for food, feed and bioenergy.

Ramularia collo-cygni is responsible for yield losses of 15–25 % in winter barley in northern European countries and New Zealand (Cromey *et al.* 2004). Yield losses in sugar beet due to plant pathogens and pests are estimated in general to be 26 % with, and more than 80 % without, crop protection (Oerke & Dehne 2004).

As plant pathogens, some cercosporoid species have shown potential as biocontrol agents of weeds, but no commercial application is yet available. *Acroptilon repens* and *Centaurea solstitiales* are both invasive weeds in the eastern USA. The fungi *Cercosporella acroptili* and *Cercosporella centaureicola* cause significant damage to *A. repens* and *C. solstitiales*, respectively (Berner *et al.* 2005). *Crupina vulgaris* is an invasive weed of pastures in the western USA that is susceptible to leaf blight caused by *Ramularia crupinae*. *Myrica faya* is considered an invasive plant in Hawaii but, in its natural habitat, is susceptible to *Ramularia* dieback caused by *Phacellium rufibasis* (= *Ramularia destructiva*) (Gardner & Hodges 1990). The necrotrophic fungus *Ramularia rubella* is also effective against *Rumex obtusifolius*, an invasive plant of pastures, by causing severe defoliation, shoot and root weight loss (Zaller 2004).

Plant pathogenic fungi are known to produce toxic metabolites that contribute to symptom development in the host. Some phytotoxins induce the formation of reactive oxygen molecules in the plant cells such as superoxide, hydrogen peroxide or hydroxyl radicals that induce oxidative processes of membrane fatty acids. The phytopathogenic species *Ramularia rubella* was the first species of this genus observed producing rubellin metabolites (Arnone *et al.* 1986), a photodynamically active anthraquinone derivative (Heiser *et al.* 2003). More recently, also *Ramularia collo-cygni* (Miethbauer *et al.* 2003) and the mycophilic species *R. uredinicola* (Khodaparast & Braun 2005) were documented as producing rubellins, with *R. rosea* also being a candidate for rubellin biosynthesis. Although a few *Ramularia* species use the photodynamically active rubellins as non-host-specific phytotoxins, most of the species in this genus are unable to produce these compounds (Miethbauer *et al.* 2006).

Given the importance of the genus *Ramularia* to agriculture as outlined above, the aims of the present study were: (i) to resolve the phylogenetic placement of *Ramularia* and allied genera within the order *Capnodiales*, and (ii) to apply a polyphasic approach based on multilocus DNA sequence, morphological and cultural data to delimit species within the genus *Ramularia* and allied genera.

MATERIALS AND METHODS

Isolates

Isolates included in this study were obtained from the culture collection of the CBS-KNAW Fungal Biodiversity Centre (CBS), Utrecht, the Netherlands, from the working collection of Pedro Crous (CPC), housed at CBS, or were freshly isolated from a range of different plant hosts (Table 1). Single-conidium and ascospore cultures were obtained using the techniques described for species of *Mycosphaerella* and its asexual morphs (Crous *et al.* 1991, Crous 1998). Representative cultures of the new species delineated in this study were deposited in the CBS culture collection.

DNA extraction, amplification and sequencing

Fungal mycelia of strains (Table 1) were harvested with a sterile scalpel and the genomic DNA isolated using the UltraClean™ Microbial DNA Isolation Kit (MoBio Laboratories, Inc., Solana

Beach, CA, USA) following the manufacturers' protocols. The DNA was initially targeted for the amplification and sequencing of 11 partial nuclear genes: 28S nrRNA gene (LSU), internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS) of the nrDNA operon, actin (*actA*), translation elongation factor 1-α (*tef1*-α), histone H3 (*his3*), glyceraldehyde-3-phosphate dehydrogenase (*gapdh*), RNA polymerase II second largest subunit (*rpb2*), calmodulin (*cmdA*), β-tubulin (*tub2*), chitin-synthase 1 (*chs-1*) and a gene encoding a minichromosome maintenance protein (*mcm7*). The primers employed for PCR amplification of each partial gene region are listed in Table 2, with the respective annealing temperatures used. During the course of this study, new primers were designed to amplify *rpb2*. The primer positions based on GenBank accession KT216537.1 are: Rpb2-F4 34–56, Rpb2-F1 247–266, Rpb2-R1 937–959. A new forward primer was also designed for the amplification of *gapdh* and its position based on GenBank accession KJ504580.1 is: Gapdh-F1 14–32. The PCR amplifications were performed on a GeneAmp® PCR System 9700 (Applied Biosystems, Foster City, CA, USA). The PCR mixtures consisted of 1 μL genomic DNA, 1× NH4 reaction buffer (Bioline, Luckenwalde, Germany), 2 mM $MgCl_2$, 40 μM of each dNTP, 0.2 μM of each primer and 0.5 U *Taq* DNA polymerase (Bioline) in a total volume of 12.5 μL. The PCR mixtures for *his3*, *gapdh*, *rpb2*, *cmdA* and *tub2* contained 2 μL genomic DNA. The general PCR conditions were: initial denaturation (94 °C, 3 min); 35 cycles amplification [denaturation 94 °C, 30 s; locus-specific annealing temperature (Table 2), 30 s; extension 72 °C, 45 s], and final extension (72 °C, 5 min). For *gapdh* and *his3*, 40 amplification cycles were used. To obtain the partial *rpb2*, a touchdown PCR protocol was used: initial denaturation (94 °C, 3 min), 5 amplification cycles (denaturation 94 °C, 45 s; annealing 60 °C, 45 s; extension 72 °C, 2 min), 5 amplification cycles (denaturation 94 °C, 45 s; annealing 58 °C, 45 s; extension 72 °C, 2 min), 30 amplification cycles (denaturation 94 °C, 45 s; annealing 54 °C, 45 s; extension 72 °C, 2 min) and a final extension (72 °C, 8 min). In a few cases that double bands were obtained in the amplification of *gapdh* and *his3*, the band of correct size was purified from the agarose gel using the QIAquick® ording to the manufacturer's instructions. These purified samples underwent a second round of PCR amplification following the protocol originally used to amplify that fragment. The amplified DNA fragments were sequenced in both directions using the PCR primers and the BigDye® Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems Life Technologies, Carlsbad, CA, USA). DNA sequencing amplicons were purified through Sephadex G-50 Superfine columns (Sigma-Aldrich, St. Louis, MO) in MultiScreen HV plates (Millipore, Billerica, MA). Purified sequence reactions were analysed on an Applied Biosystems 3730xl DNA Analyzer (Life Technologies, Carlsbad, CA, USA). The DNA sequences generated were analysed and consensus sequences were computed using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium).

Phylogenetic analyses

The generated sequences for each gene were aligned with the online version of MAFFT v. 7 (Katoh & Standley 2013). The alignments were manually checked and improved where necessary using MEGA v. 5 (Tamura *et al.* 2011) and were concatenated with Mesquite v. 2.75 (Maddison & Maddison 2011). From the strains listed in Table 1, only those with the complete dataset of genes were used in the subsequent phylogenetic analyses, with the exception of *R. pusilla* (missing *gapdh* sequence) and *R. primulae* (missing *rpb*2 sequence), in which cases they were considered as missing data in the alignments. The phylogenetic methods used in this study included Neighbour-Joining and Parsimony analyses, both performed with PAUP v. 4.0b10 (Swofford 2003), a Maximum-Likelihood analysis performed with RAxML v. 8

Table 1. Collection details and GenBank accession numbers of isolates included in this study.[3]

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
Acrodontium crateriforme	**CBS 144.33[T]**; ATCC 15679; MUCL 15748; MUCL 8978		Associated with *Tuberculina maxima*	Netherlands	–	KX286952	FN666565	–	–	–	KX288399	–	–	–	–
	CBS 151.58; MUCL 15750		Human sputum	Netherlands	–	KX286953	KX287266	–	–	–	KX288400	–	–	–	–
	CBS 985.70		*Fraxinus excelsior*	UK, Westmorland	J.C. Frankland	KX286954	KX287267	–	–	–	KX288401	–	–	–	–
	CBS 840.71		Foodstuff	Netherlands	–	KX286955	KX287268	–	–	–	KX288402	–	–	–	–
	CBS 842.71		*Citrus* sp.	Indonesia, Java	J.H. van Emden	KX286956	KX287269	–	–	–	KX288403	–	–	–	–
	CPC 11509	*P. fraxini*	*Fraxinus rhynchophylla*	South Korea	H.D. Shin	GU214682	GU214682	(GU320413)	(GU384425)	–	KX288404	KX288727	KX289011	–	–
	CPC 11519	*Pseudocercosporella* sp.	*Agrimonia pilosa*	South Korea	H.D. Shin	KX286957	KX287270	KX287558	–	KX288123	KX288405	KX288728	KX289012	–	–
	CPC 25894		*Ranunculus* sp.	Germany	W. Quaedvlieg	KX286958	KX287271	KX287559	–	KX288124	KX288406	KX288729	–	–	–
	CPC 25895		*Betula* sp.	Germany	W. Quaedvlieg	KX286959	KX287272	KX287560	–	–	KX288407	KX288730	–	–	–
	CBS 137975; CPC 22172	*A. neolitsiae*	*Neolitsea australiensis*	Australia	B.A. Summerell	KJ869184	KJ869127	–	–	–	KX288408	–	–	–	–
A. fagicola	**CBS 714.79[T]**	*Acrodontium* sp.	*Fagus sylvatica*	Germany	–	KX286960	–	–	–	–	KX288409	–	–	–	–
A. luzulae	CBS 841.71	*A. crateriforme*	*Puccinia* sp., on leaf of *Carex* sp.	Netherlands	–	KX286961	KX287273	–	–	–	KX288410	–	–	–	–
	CBS 839.71[T]	*A. crateriforme*	*Luzula sylvatica*	UK, England	–	KX286962	KX287274	–	–	–	KX288411	–	–	–	–
A. pigmentosum	**CBS 111111[T]**	*A. griseum*	Outdoor air	Finland	S. Haatainen	KX286963	KX287275	–	–	–	KX288412	–	–	–	–
Apseudocercosporella trigonotidis	CPC 10865	*Pseudocercosporella* sp.	*Trigonotis peduncularis*	South Korea	H.D. Shin	KX286964	KX287276	KX287561	–	–	KX288413	–	–	–	–
	CBS 131890[T]; CPC 10864	*Pseudocercosporella* sp.	*Trigonotis peduncularis*	South Korea	H.D. Shin	JQ324972	GU269858	(JQ325029)	(GU384569)	–	KX288414	–	–	–	–
Caryophylloseptoria lychnidis	CBS 109102		*Silene pratensis*	Austria	G. Verkley	KF251793	KF251289	(KF253598)	(KF253237)	–	KX348048	–	(KF253952)	(KF252771)	–
Caryophylloseptoria pseudolychnidis	CBS 128614; KACC 42904; SMKC 22691		*Lychnis cognata*	South Korea	–	KF251794	KF251290	(KF253599)	(KF253238)	–	KX348049	–	(KF253953)	(KF252772)	–
Cercospora campi-silii	CBS 132625; CPC 14585		*Impatiens noli-tangere*	South Korea	H.D. Shin	KX286965	JX143561	(JX143069)	(JX143315)	–	KX288415	(JX142577)	(JX142823)	–	–
Cercospora cf. *chenopodii*	CBS 132677; CPC 15599	*Ce. chenopodii*	*Chenopodium* sp.	Mexico	M. de Jesús Yáñez-Morales	KX286966	JX143573	(JX143083)	(JX143329)	–	KX288416	(JX142591)	(JX142837)	–	–
	CPC 12450	*Pa. dubia*	*Chenopodium ficifolium*	South Korea	H.D. Shin	KX286967	JX143574	(JX143084)	(JX143330)	–	KX288417	(JX142592)	(JX142838)	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
Ce. dubia	CPC 15600	*Cercosporella* sp.	*Chenopodium* sp.	Mexico	M. de Jesús Yáñez-Morales	KX286968	KX287277	–	–	–	KX288418	–	–	–	–
Ce. sojina	**CBS 132615[NT]**; CPC 11353		*Glycine soja*	South Korea	H.D. Shin	KX286969	JX143659	(JX143173)	(JX143419)	–	KX288419	(JX142681)	(JX142927)	–	–
Ce. sorghi	CBS 478.92; INIFAT C91/204	*Ramulispora sorghi*	–	–	–	KX286970	KX287278	–	–	–	KX288420	–	–	–	–
Cercospora sp.	CBS 220.31	*Pa. personata*	–	–	–	KX286971	KX287279	–	–	–	KX288421	–	–	–	–
Cercospora sp.	CPC 11422	*Pa. sojina*	*Glycine soja*	South Korea	H.D. Shin	KX286972	KX287280	–	–	–	KX288422	–	–	–	–
Cercosporella dolichandrae	**CBS 138101[T]**;CPC 22948		*Dolichandra unguiscati*	South Africa	A. King	KJ869197	KJ869140	KX287562	–	–	KX288423	–	–	–	–
C.catenulata	**CBS 355.73[T]**	*R. deusta* var. *alba*	*Phaseolus vulgaris*	Rwanda	D. Froment	KX286973	KX287281	KX287563	–	–	KX288424	KX288731	KX289013	–	–
C. virgaureae	CPC 11456		*Erigeron annuus*	South Korea	H.D. Shin	KX286974	–	KX287564	KX287838	KX288125	KX348050	KX288732	KX289014	–	–
	CPC 11457		*Erigeron annuus*	South Korea	H.D. Shin	KX286975	KX287282	KX287565	KX287839	KX288126	KX288425	KX288733	KX289015	–	–
	CPC 11460		*Erigeron annuus*	South Korea	H.D. Shin	KX286976	KX287283	KX287566	KX287840	KX288127	KX288426	KX288734	KX289016	–	–
	CPC 11461		*Erigeron annuus*	South Korea	H.D. Shin	KX286977	KX287284	KX287567	KX287841	–	KX288427	KX288735	KX289017	–	–
	CPC 10286		*Erigeron annuus*	South Korea	H.D. Shin	KX286978	KX287285	KX287568	KX287842	KX288128	KX288428	KX288736	KX289018	–	–
	CPC 10287		*Erigeron annuus*	South Korea	H.D. Shin	KX286979	KX287286	KX287569	KX287843	KX288129	KX288429	KX288737	KX289019	–	–
	CPC 10288		*Erigeron annuus*	South Korea	H.D. Shin	KX286980	KX287287	KX287570	KX287844	–	KX288430	KX288738	–	–	–
	CBS 113304		*Erigeron annuus*	–	H.D. Shin	KF251805	GU214658	(KF253610)	(KF253249)	KX288130	KX348051	KX288739	(KF253964)	–	–
	CPC 19492	*Cercosporella* sp.	*Conyza canadensis*	Brazil	B.S. Vieira	KX286981	KX287288	KX287571	KX287845	KX288131	KX288431	KX288740	KX289020	–	–
Cladosporium cladosporioides	**CBS 112388[NT]**		Indoor air	Germany	Ch. Traumann	KX286982	HM148003	(HM148490)	(HM148244)	–	KX288432	–	–	–	–
Epicoleosporium ramularioides	**CBS 141103[T]**; CPC 10672	*R. coleosporii*	*Coleosporium phellodendri*on *Phellodendron amurense*	South Korea	H.D. Shin	GU214688	GU214688	–	KX287846	–	KX288433	–	–	–	–
	CPC 10673	*R. coleosporii*	*Coleosporium phellodendri*on *Phellodendron amurense*	South Korea	H.D. Shin	X	KX287289	–	KX287847	–	KX288434	–	–	–	KX289242
Dissoconium aciculare	CBS 204.89		*Astragalus* sp.	Germany	T. Hijwegen	GU214419	AY725520	–	–	–	KX288435	–	–	–	–
Dothistroma pini	CBS 121005; CMW 24852		*Pinus pallasiana*	Russia	T.S. Bulgakov	KF251659	KF251155	(JX902075)	(KF253115)	–	KX348052	–	(JX901514)	(KF252653)	–
	CBS 116486		*Pinus nigra*	USA, Michigan	G. Adams	JX901823	JX901735	(JX902070)	(JX901621)	–	KX348053	–	(JX901509)	(JX902192)	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
D. septosporum	CBS 128782; CPC 16798		*Pinus mugo* subsp. *rostrata*	Netherlands	W. Quaedvlieg	JX901829	JX901741	(JX902076)	(JX901627)	–	KX348054	–	(JX901515)	(JX902198)	–
Fusoidiella depressa	CBS 141335; CPC 14915	*Pa. depressa*	*Angelica gigas*	South Korea	H.D. Shin	KF251813	KF251309	–	(KF253256)	–	KX348055	–	(KF253972)	(KF252788)	–
Filiella pastinacae	CBS 114116; UPSC 2633	*P. pastinacae*	*Laserpitium latifolium*	Sweden	K. & L. Holm	KF251832	KF251328	(KF253633)	(KF253275)	–	KX348056	–	(KF253980)	(KF252803)	–
Microcyclosporella mali	**CBS 126136[T]**; CPC 16184; HJS 300-07		*Malus domestica*	Slovenia	J. Frank	GU570547	GU570535	KX287572	(HM177424)	–	KX288436	–	–	–	–
Microcyclosporella sp.	CBS 118960; CUD3b	*Pseudocercosporella* sp.	–	USA, Illinois	J. Batzer	KX286985	KX287290	KX287573	KX287848	KX288132	KX288437	KX288741	–	–	–
	CBS 125654; RH7; GA3 3D1b	*Pseudocercosporella* sp.	*Malus* sp.	USA, Georgia	M. Wheeler	FJ031995	FJ425202	KX287574	KX287849	KX288133	KX288438	KX288742	–	–	–
	CBS 119461; RH2.2	*Pseudocercosporella* sp.	–	USA, Illinois	J. Batzer	KX286986	KX287291	KX287575	KX287850	KX288134	KX288439	KX288743	KX289021	–	–
	CBS 125653; RH6; MI3 20F1a	*Pseudocercosporella* sp.	*Malus* sp.	USA, Michigan	G. Sundin	FJ031994	FJ425201	KX287576	KX287851	KX288135	KX288440	–	–	–	–
	CBS 118969; UMD1a	*Pseudocercosporella* sp.	–	USA, Missouri	J. Batzer	KX286987	KX287292	KX287577	KX287852	KX288136	KX288441	KX288744	–	–	–
	CBS 125651; RH1; OH1 34D2a	*Pseudocercosporella* sp.	*Malus* sp.	USA, Ohio	M. Ellis	FJ031989	FJ425196	KX287578	KX287853	KX288137	KX288442	KX288745	KX289022	–	–
Mycosphaerelloides madeirae	**CBS 112895[T]**; CMW 14458; CPC 3745	*M. madeirae*	*Eucalyptus globulus*	Portugal	S. Denman	KF902017	AY725553	–	(KF903109)	–	KX348057	KX288746	(KF902545)	–	–
	CBS 115936	*Ramularia* sp.	–	Netherlands	–	KX286988	AY853187	KX287579	KX287854	KX288138	KX288443	–	KX289023	–	–
	CBS 116066	*Ramularia* sp.	*Quercus robur*	Netherlands	–	KX286989	AY853188	KX287580	KX287855	KX288139	KX288444	KX288747	KX289024	–	–
	CBS 116068	*Ramularia* sp.	*Quercus robur*	Netherlands	–	KX286990	AY853189	KX287581	KX287856	KX288140	KX288445	KX288748	KX289025	–	–
Neocercospora ammicola	**CBS 136450[T]**; CCTU 1186	*Cercospora* sp.	*Ammi majus*	Iran	M. Arzanlou	KR232405	KR232407	(KR232411)	(KR232409)	–	KX288446	(KR232413)	–	–	–
Neopseudocercosporella brassicicola	CBS 228.32	*M. brassicicola*	*Brassica oleraceae*	Denmark	–	KF251808	KF251304	(KF253613)	(KF253252)	–	KX348058	–	(KF253967)	(KF252783)	–
	CBS 173.88	*M. brassicicola*	*Brassica oleracea*	Germany	–	KX286991	KX287293	KX287582	KX287857	–	KX288447	–	–	–	–
	CBS 267.53	*M. brassicicola*	*Brassica oleraceae* var. *acephala* subvar. *sabelica*	Netherlands	–	KF251809	KF251305	(KF253614)	(KF253253)	–	KX348059	–	(KF253968)	(KF252784)	–
N. capsellae	CBS 135464; CPC 11677	*Mycosphaerella* sp.	*Draba nemorosa* var. *hebecarpa*	South Korea	H.D. Shin	KX286992	DQ303091	(KF253616)	KX287858	–	KX288448	–	(KF253970)	(KF252786)	–
	CPC 14774	*P. capsellae*	*Raphanus sativus*	South Korea	H.D. Shin	KX286993	KX287294	KX287583	KX287859	KX288141	KX288449	–	–	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CBS 131896; CPC 14773	*P. capsellae*	*Raphanus sativus*	South Korea	H.D. Shin	GU253714	GU269666	(GU320372)	(GU384383)	KX288142	KX288450	KX288749	–	–	–
	CBS 112032; HJS 601	*P. capsellae*	*Brassica* sp.	–	–	KF251824	KF251320	(KF253627)	(KF253267)	–	KX348060	–	(KF253975)	(KF252797)	–
	CBS 112033; HJS 600	*P. capsellae*	*Brassica* sp.	–	–	KF251810	KF251306	(KF253615)	(KF253254)	–	KX348061	–	(KF253969)	(KF252785)	–
	CPC 12518		*Capsella bursa-pastoris*	South Korea	H.D. Shin	KX286994	KX287295	KX287584	KX287860	–	KX288451	KX288750	–	–	–
	CPC 12519		*Capsella bursa-pastoris*	South Korea	H.D. Shin	KX286995	KX287296	KX287585	KX287861	–	KX288452	KX288751	–	–	–
Pallidocercospora acaciigena	**CBS 112515[T]**; CPC 3837		*Acacia mangium*	Venezuela	M.J. Wingfield	KF902166	KF901805	(KF903455)	(KF903125)	–	KX348062	–	(KF902564)	(KF902828)	–
Pal. crystallina	CBS 111045; CPC 1179		*Eucalyptus grandis*	South Africa	M.J. Wingfield	KF902051	KF901704	(KF903424)	(KF903129)	–	KX348063	–	(KF902568)	(KF902832)	–
Pal. heimii	CPC 11716	*M. parkii*	–	Brazil	A.C. Alfenas	KF901937	KF901612	(KF903605)	(KF903134)	–	KX348064	–	(KF902573)	(KF902837)	–
Pal. irregulariramosa	CBS 111211; CPC 1362		*Eucalyptus saligna*	South Africa	M.J. Wingfield	KF902053	KX287297	(KF903441)	(KF903139)	–	KX348065	–	(KF902578)	(KF902842)	–
Pal. konae	CBS 111028; CPC 2125; JT 526		*Leucadendron* cv. Safari Sunset	USA, Hawaii	P.W. Crous	KF902158	KF901798	(KF903422)	(KF903140)	–	KX348066	–	–	(KF902843)	–
Parapenidiella pseudotasmaniensis	CBS 111681; CPC 1539	*Mycovellosiella* sp.	–	–	–	KX286996	KX287298	–	–	–	KX288453	–	–	–	–
	CBS 124991[T]; CPC 12400		*Eucalyptus globulus*	Australia	I.W. Smith	KF901844	KF901522	(KF903562)	(KF903152)	–	KX348067	–	(KF902589)	(KF902855)	–
Pp. tasmaniensis	**CBS 111687[T]**; CMW 14780; CPC 1555		*Eucalyptus nitens*	Australia	–	KF901843	DQ267591	(KF903451)	(KF903150)	–	KX348068	–	(KF902587)	(KF902853)	–
Pseudocercospora dingleyae	CBS 114645	*P. dingleyae*	*Haloragis erecta*	New Zealand	–	KX286997	KX287299	–	–	–	KX288454	–	–	–	–
Ps. eucalyptorum	CBS 132015; CPC 11713		*Eucalyptus globulus*	Spain	P. Mansilla	KF902096	KF901743	(KF903604)	(GU384523)	–	KX348069	–	(KF902615)	(KF902884)	–
	CBS 114866; CPC 11		*Eucalyptus nitens*	South Africa	P.W. Crous	KF902067	KF901720	(KF903474)	(KF903195)	–	KX348070	–	(KF902627)	(KF902897)	–
Ps. flavomarginata	CBS 124990; CPC 13492		*Eucalyptus camaldulensis*	Thailand	W. Himaman	GU253817	KF251323	(KF253629)	(KF253270)	–	KX348071	–	–	(JX902274)	–
Ps. fori	CBS 113286; CMW 9096		*Eucalyptus* sp.	South Africa	J. Roux	KF902068	KF901721	(KF903463)	(KF903197)	–	KX348072	–	(KF902628)	(KF902899)	–
Ps. macadamiae	**CBS 133432[ET]**; BRIP 55526a		*Macadamia integrifolia*	Australia, Queensland	O.A. Akinsanmi	KX286998	KX287300	–	–	–	KX288455	–	–	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
Ps. metrosideri	CBS 114294	*P. metrosideri*	*Metrosideros excelsa*	New Zealand	–	KX286999	KX287301	–	–	–	KX288456	–	–	–	–
Ps. myopori	CBS 114644	*Cercospora* sp.	*Myoporum laetum*	New Zealand	–	KX287000	KX287302	–	–	–	KX288457	–	–	–	–
Ps. norchiensis	**CBS 120738**[T]; CPC 13049		*Eucalyptus* sp.	Italy	W. Gams	GU253780	KF901665	(KF903531)	(GU384464)	–	KX348073	–	(KF902633)	(KF902906)	–
Ps. pistacina	CPC 23118	Pseudocercospora-like sp.	*Pistacia vera*	Turkey	K. Sarpkaya	KF442674	KF442647	–	KF442637	–	KX348074	–	–	(KF442733)	–
Ps. robusta	**CBS 111175**[T]; CMW 5151; CPC 1269		*Eucalyptus robur*	Malaysia	M.J. Wingfield	KF902020	KF442500	(JX902150)	(JX901694)	–	KX348075	–	(KF902640)	(KF442463)	–
Pseudocercospora sp.	CPC 19535	*Cercosporella* sp.	*Eichhornia azurea*	Brazil	D.J. Soares	KX287001	KX287303	–	–	–	KX288458	–	–	–	–
	CBS 113386	*Mycovellosiella* sp.	*Chromolaena odorata*	Guatemala	M.J. Morris	KX287002	DQ676532	–	–	–	KX288459	(DQ676557)	–	–	–
	CPC 19537	*Cercosporella* sp.	*Eichhornia azurea*	Brazil	D.J. Soares	KX287003	KX287304	–	–	–	KX288460	–	–	–	–
	CBS 110780; CPC 204	*Pseudocercosporella* sp.	*Syzygium cordatum*	South Africa	P.W. Crous	KX287004	KX287305	–	–	–	KX288461	–	–	–	–
Ps. vitis	CBS 132012; CPC 11595		*Vitis vinifera*	South Korea	–	KF902011	KF901669	(KF903603)	(GU384541)	–	KX348076	–	(KF902649)	(KF902927)	–
Pseudocercosporella bakeri	CBS 119488; Lynfield 1252		*Ipomoea indica*	New Zealand	C.F. Hill	KX287005	KX287306	KX287586	KX287862	–	KX288462	–	–	–	–
	CBS 125685[ET]; CPC 17570		*Ipomoea aquatica*	Laos	P. Phengsintham	GU570553	GU570542	KX287587	KX287863	–	KX288463	KX288752	–	–	–
Ramichloridium apiculatum	CBS 400.76; IMI 088021		Soil	Pakistan	–	EU041851	EU041794	–	–	–	KX348077	–	–	–	–
	CBS 156.59[T]; ATCC 13211; IMI 100716; JCM 6972; MUCL 15753; MUCL 7991; QM 7716		Forest soil	USA, Georgia	–	EU041848	EU041791	–	–	–	–	–	–	–	–
Ramichloridium sp.	CPC 12310	*Pseudocercosporella* sp.	Vicia amurensis	South Korea	H.D. Shin	GU214687	GU214687	–	–	–	KX288464	–	–	–	–
Ramularia abscondita	CBS 114727; UPSC 3341		*Arctium tomentosum*	Sweden	E. Gunnerbeck	KX287006	KX287307	KX287588	KX287864	KX288143	KX288465	KX288753	KX289026	KX289126	–
R. acris	CPC 25898		*Ranunculus acris*	Netherlands	S.I.R. Videira	KX287007	KX287308	KX287589	KX287865	KX288144	KX288466	KX288754	–	–	–
	CPC 25899		*Ranunculus acris*	Netherlands	S.I.R. Videira	KX287008	KX287309	KX287590	KX287866	KX288145	KX288467	KX288755	–	–	–
	CPC 25900		*?Ranunculus* sp.	Netherlands	U. Damm	KX287009	KX287310	KX287591	KX287867	KX288146	KX288468	KX288756	–	–	–
	CBS 109794	*R. didyma* var. *didyma*	*Ranunculus* sp.	Netherlands	G. Verkley	KX287010	KX287311	KX287592	KX287868	KX288147	KX288469	KX288757	–	KX289127	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
R. acroptili	CPC 18723	*Ramularia* sp.	*Cynara cardunculus*	USA, California	L. Davenport	KX287011	KX287312	KX287593	KX287869	KX288148	KX288470	KX288758	–	KX289128	–
	CPC 18724	*Ramularia* sp.	*Cynara cardunculus*	USA, California	L. Davenport	KX287012	KX287313	KX287594	KX287870	KX288149	KX288471	KX288759	–	KX289129	–
	CBS 120252[ET]; 98-001		*Acroptilon repens*	Turkey	R. Sobhian	GU214689	GU214689	KX287595	KX287871	KX288150	KX288472	KX288760	KX289027	–	–
	CBS 120253; 04-011	*C. centaureicola*	*Centaurea solstitialis*	Greece	D. Berner	EU019257	EU019257	KX287596	KX287872	KX288151	KX288473	KX288761	KX289028	KX289130	–
R. actinidiae	CPC 11674*	*Ramularia* sp.	*Actinidia polygama*	South Korea	H.D. Shin	KX287013	KX287314	–	–	–	–	–	–	–	–
	CPC 11675	*Ramularia* sp.	*Actinidia polygama*	South Korea	H.D. Shin	KX287014	KX287315	KX287597	KX287873	KX288152	KX288474	KX288762	–	–	–
R. agastaches	CPC 10819	*R. lamii*	*Agastache rugosa*	South Korea	H.D. Shin	KX287015	KX287316	KX287598	KX287874	KX288153	KX288475	KX288763	–	KX289131	–
	CPC 10820	*R. lamii*	*Agastache rugosa*	South Korea	H.D. Shin	KX287016	KX287317	KX287599	KX287875	KX288154	KX288476	KX288764	KX289029	KX289132	–
	CPC 10821	*R. lamii*	*Agastache rugosa*	South Korea	H.D. Shin	KX287017	KX287318	KX287600	KX287876	KX288155	KX288477	KX288765	KX289030	KX289133	–
R. agrimoniae	CPC 11450	*Ramularia* sp.	*Agrimonia pilosa*	South Korea	H.D. Shin	KX287018	KX287319	KX287601	KX287877	KX288156	KX288478	KX288766	–	KX289134	–
	CPC 11451	*Ramularia* sp.	*Agrimonia pilosa*	South Korea	H.D. Shin	KX287019	KX287320	KX287602	KX287878	KX288157	KX288479	KX288767	–	KX289135	–
	CPC 11452	*Ramularia* sp.	*Agrimonia pilosa*	South Korea	H.D. Shin	KX287020	KX287321	KX287603	KX287879	KX288158	KX288480	KX288768	–	KX289136	–
	CPC 11651		*Agrimonia pilosa*	South Korea	H.D. Shin	KX287021	KX287322	KX287604	KX287880	KX288159	KX288481	KX288769	–	KX289137	KX289243
	CPC 11652		*Agrimonia pilosa*	South Korea	H.D. Shin	KX287022	KX287323	KX287605	KX287881	KX288160	KX288482	KX288770	–	KX289138	–
	CPC 11653		*Agrimonia pilosa*	South Korea	H.D. Shin	KJ504743	KJ504784	KJ504448	KJ504699	KJ504567	KJ504655	KJ504611	–	KJ504481	–
R. alangiicola	CPC 10299	*Ph. alangii*	*Alangium platanifolium* var. *macrophylum*	South Korea	H.D. Shin	KX287023	KX287324	–	KX287882	KX288161	KX288483	KX288771	–	–	–
R. aplospora	**CBS 545.82[ET]**	*Cladosporium* sp.	Mildew on *Alchemilla vulgaris*	Germany	–	KP894110	EU040238	KP894325	KP894435	KP894545	KP894656	KP894767	KP894878	KP894965	–
	CBS 109120		*Alchemilla vulgaris*	Austria	G. Verkley	KP894108	KP894217	KP894323	KP894433	KP894543	KP894654	KP894765	KP894876	–	–
	CBS 109121		*Alchemilla vulgaris*	Austria	G. Verkley	KX287024	KX287325	KX287606	KX287883	KX288162	KX288484	KX288772	KX289031	–	–
	CBS 237.73; CCM F-367		*Alchemilla xanthochlora*	former Czechoslovakia	–	KX287025	KX287326	KX287607	KX287884	KX288163	KX288485	KX288773	KX289032	KX289139	–
	CBS 109013		*Alchemilla vulgaris*	Austria	G. Verkley	KX287026	KX287327	KP894322	KX287885	KX288164	KX288486	KX288774	KX289033	KX289140	–
	CBS 109014		*Alchemilla vulgaris*	Austria	G. Verkley	KP894107	KP894216	KP894322	KP894432	KP894542	KP894653	KP894764	KP894875	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CBS 114118; UPSC 2679		*Alchemilla vulgaris*	Sweden	E. Gunnerbeck	KP894109	KP894218	KP894324	KP894434	KP894544	KP894655	KP894766	KP894877	–	–
R. archangelicae	CBS 108991		*Angelica sylvestris*	Austria	G. Verkley	KX287027	KX287328	KX287608	KX287886	KX288165	KX288487	KX288775	KX289034	–	–
	CBS 108992		*Angelica sylvestris*	Austria	G. Verkley	KX287028	KX287329	KX287609	KX287887	KX288166	KX288488	KX288776	KX289035	–	–
	CBS 109011		*Angelica sylvestris*	Austria	G. Verkley	KX287029	KX287330	KX287610	KX287888	KX288167	KX288489	KX288777	KX289036	–	KX289244
	CBS 109012		*Angelica sylvestris*	Austria	G. Verkley	KX287030	KX287331	KX287611	KX287889	KX288168	KX288490	KX288778	KX289037	–	KX289245
	CBS 288.49	*M. rubella*	*Angelica sylvestris*	Austria	–	KX287031	AY490767	KX287612	KX287890	KX288169	KX288491	KX288779	KX289038	–	–
R. armoraciae	**CBS 241.90[ET]**		*Armoracia rusticana*	Germany	S. Petzoldt	KX287032	KX287332	KX287613	KX287891	KX288170	KX288492	KX288780	–	–	–
	CBS 253.28		*Armoracia rusticana*	Netherlands	–	KX287033	KX287333	KX287614	KX287892	KX288171	KX288493	KX288781	–	KX289141	KX289246
R. asteris	CBS 131.21; ATCC 44003		*Aster tripolium*	Netherlands	–	KX287034	KX287334	KX287615	KX287893	KX288172	KX288494	KX288782	KX289039	KX289142	–
R. bellunensis	CBS 118417		*Argyranthemum frutescens*	New Zealand	–	KX287035	KX287335	KX287616	KX287894	KX288173	KX348078	KX288783	–	–	–
	CBS 116.43		*Chrysanthemum frutescens*	Netherlands	–	KX287036	KX287336	KX287617	KX287895	KX288174	KX288495	KX288784	–	–	–
R. beticola	CPC 30065		*Beta vulgaris*	Denmark	A.L. Hansen	KX287037	KX287337	KX287618	KX287896	KX288175	KX288496	KX288785	KX289040	–	–
	CBS 141109[ET]; CPC 30066		*Beta vulgaris*	France	A. Champeil	KX287038	KX287338	KX287619	KX287897	KX288176	KX288497	KX288786	KX289041	–	–
	CPC 30067		*Beta vulgaris*	Netherlands	S.I.R. Videira	KX287039	KX287339	KX287620	KX287898	KX288177	KX288498	KX288787	KX289042	–	–
	CPC 30063		*Beta vulgaris*	Netherlands	S.I.R. Videira	KX287040	KX287340	KX287621	KX287899	KX288178	KX288499	KX288788	KX289043	–	–
	CPC 30064		*Beta vulgaris*	Netherlands	–	KX287041	KX287341	KX287622	KX287900	KX288179	KX288500	KX288789	KX289044	–	–
	CBS 341.29	*R. betae*	–	Germany	–	KX287042	KX287342	KX287623	KX287901	KX288180	KX288501	KX288790	KX289045	–	–
	CBS 113540; UPSC 1612		*Beta vulgaris*	Sweden	O. Constantinescu	KX287043	KX287343	KX287624	KX287902	KX288181	KX288502	KX288791	KX289046	–	–
	CBS 151.67		*Beta vulgaris*	Switzerland	–	KX287044	KX287344	KX287625	KX287903	KX288182	KX288503	KX288792	KX289047	–	–
R. bosniaca	CBS 123880; V6024.2	*Ramularia* sp.	*Scabiosa ochroleuca*	Czech Republic	G. Verkley	KX287045	KX287345	KX287626	KX287904	KX288183	KX288504	KX288793	–	KX289143	–
	CBS 123881; V6024.1	*Ramularia* sp.	*Scabiosa ochroleuca*	Czech Republic	G. Verkley	KX287046	KX287346	KX287627	KX287905	KX288184	KX288505	KX288794	–	KX289144	–
R. buniadis	CBS 114301; UPSC 2718		*Bunias orientalis*	Sweden	E. Gunnerbeck	KX287047	KX287347	KX287628	KX287906	KX288185	KX288506	KX288795	KX289048	KX289145	–
R. calcea	CBS 101612		*Symphytum* sp.	Germany	G. Arnold	KP894111	KP894219	KP894326	KP894436	KP894546	KP894657	KP894768	KP894879	KP894966	–
	CBS 101613		*Symphytum* sp.	Germany	G. Arnold	KP894112	KP894220	KP894327	KP894437	KP894547	KP894658	KP894769	–	KP894967	–
	CBS 114442; UPSC 2727	*R. lactea*	*Viola hirta*	Sweden	E. Gunnerbeck	KP894122	KP894229	KP894337	KP894447	KP894557	KP894668	KP894779	KP894884	KP894972	–
R. carneola	CBS 108975		*Scrophularia nodosa*	Netherlands	G. Verkley	KX287048	KX287348	KX287629	KX287907	KX288186	KX288507	KX288796	KX289049	KX289146	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CBS 108976		*Scrophularia nodosa*	Netherlands	G. Verkley	KX287049	KX287349	KX287630	KX287908	KX288187	KX288508	KX288797	KX289050	KX289147	KX289247
	CBS 108977		*Scrophularia nodosa*	Netherlands	G. Verkley	KX287050	KX287350	KX287631	KX287909	KX288188	KX288509	KX288798	KX289051	KX289148	–
	CBS 108978		*Scrophularia nodosa*	Netherlands	G. Verkley	KX287051	KX287351	KX287632	KX287910	KX288189	KX288510	KX288799	KX289052	KX289149	–
	CBS 109847		*Scrophularia nodosa*	Netherlands	G. Verkley	KX287052	KX287352	KX287633	KX287911	KX288190	KX288511	KX288800	KX289053	KX289150	–
R. cerastiicola	**CBS 115913[T]**; CPC 11290	*M. cerastiicola*	*Cerastium semidecandrum*	Netherlands	A. Aptroot	KF251727	KF251224	KX287634	KF253180	KX288191	KX348079	KX288801	–	–	–
R. chamaedryos	CBS 116577; UPSC 2322		*Veronica chamaedrys*	Sweden	E. Gunnerbeck	KX287053	KX287353	KX287635	KX287912	KX288192	KX288512	KX288802	KX289054	–	–
	CBS 113307	*Ramularia* sp.	*Veronica didyma*	South Korea	H.D. Shin	KX287054	KX287354	KX287636	KX287913	KX288193	KX288513	KX288803	–	KX289151	–
	CBS 131773; KACC 42885		*Veronica persica*	South Korea	H.D. Shin & M.J. Park	KX287055	KX287355	KX287637	KX287914	KX288194	KX288514	KX288804	–	KX289152	–
	CBS 118794	*R. veronicae*	*Veronica persica*	New Zealand	–	KX287056	KX287356	KX287638	KX287915	KX288195	KX288515	KX288805	KX289055	–	–
	CBS 114731; UPSC 3243	*R. anagallidis*	*Veronica anagallis-aquatica*	Sweden	E. Gunnerbeck	KX287057	KX287357	KX287639	KX287916	KX288196	KX288516	KX288806	–	–	–
R. chelidonii	CPC 12208		*Hylomecon vernalis*	South Korea	H.D. Shin	KX287058	KX287358	KX287640	KX287917	KX288197	KX288517	KX288807	KX289056	–	–
	CPC 12209		*Hylomecon vernalis*	South Korea	H.D. Shin	KX287059	KX287359	KX287641	KX287918	KX288198	KX288518	KX288808	–	–	–
	CBS 113317	*Ramularia* sp.	*Hylomecon vernalis*	South Korea	H.D. Shin	KX287060	KX287360	KX287642	KX287919	KX288199	KX288519	KX288809	–	–	–
R. coleosporii	CPC 10653	*Ramularia* sp.	*Coleosporium eupatorii* on *Eupatorium japonicum*	South Korea	H.D. Shin	KX287061	KX287361	–	KX287920	–	KX288520	–	–	–	–
	CPC 10669	*Ramularia* sp.	*Coleosporium eupatorii* on *Eupatorium japonicum*	South Korea	H.D. Shin	KX287062	KX287362	KX287643	KX287921	KX288200	KX288521	KX288810	–	KX289153	–
	CPC 10731	*Ramularia* sp.	*Coleosporium clematidis-apiifoliae* on *Clematis apiifolia*	South Korea	H.D. Shin	KX287063	KX287363	KX287644	KX287922	KX288201	KX288522	KX288811	–	KX289154	–
	CPC 10732	*Ramularia* sp.	*Coleosporium clematidis-apiifoliae* on *Clematis apiifolia*	South Korea	H.D. Shin	KX287064	KX287364	KX287645	KX287923	KX288202	KX288523	KX288812	–	KX289155	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CPC 10733	*Ramularia* sp.	*Coleosporium clematidis-apiifoliae* on *Clematis apiifolia*	South Korea	H.D. Shin	KX287065	KX287365	KX287646	KX287924	KX288203	KX288524	KX288813	–	–	–
	CPC 10746	*Ramularia* sp.	*Coleosporium eupatorii* on *Eupatorium lindleyanum*	South Korea	H.D. Shin	KX287066	KX287366	KX287647	KX287925	KX288204	KX288525	KX288814	–	KX289156	–
	CPC 10747	*Ramularia* sp.	*Coleosporium eupatorii* on *Eupatorium lindleyanum*	South Korea	H.D. Shin	KX287067	KX287367	KX287648	KX287926	KX288205	KX288526	KX288815	–	KX289157	–
	CPC 10748	*Ramularia* sp.	*Coleosporium eupatorii* on *Eupatorium lindleyanum*	South Korea	H.D. Shin	KX287068	KX287368	KX287649	KX287927	KX288206	KX288527	KX288816	–	KX289158	–
	CPC 11516		*Coleosporium plectranthi* on *Plectranthus japonicus*	South Korea	H.D. Shin	KX287069	KX287369	KX287650	KX287928	KX288207	KX288528	KX288817	–	KX289159	–
	CBS 131753; KACC 42483		*Coleosporium perillae* on *Perilla frutescens* var. *japonica*	South Korea	H.D. Shin & M.J. Park	KX287070	KX287370	KX287651	KX287929	KX288208	KX288529	KX288818	–	KX289160	–
	CBS 131754; KACC 43177		*Coleosporium asterum on Aster pilosus*	South Korea	H.D. Shin & M.J. Park	KX287071	KX287371	KX287652	KX287930	KX288209	KX288530	KX288819	–	KX289161	–
	CBS 131755; KACC 43977		*Coleosporium asterum* on *Aster pilosus*	South Korea	H.D. Shin & M.J. Park	KX287072	KX287372	KX287653	KX287931	KX288210	–	KX288820	–	KX289162	–
	CBS 131756; KACC 43200		*Coleosporium clematidis-apiifoliae* on *Clematis apiifolia*	South Korea	H.D. Shin & M.J. Park	KX287073	KX287373	KX287654	KX287932	KX288211	KX288531	KX288821	–	KX289163	–
	CBS 131757; KACC 43185		*Coleosporium horianum* on *Codonopsis lanceolata*	South Korea	H.D. Shin & M.J. Park	KX287074	KX287374	KX287655	KX287933	KX288212	KX288532	KX288822	–	–	KX289248
	CBS 131758; KACC 44854		*Coleosporium cacaliae* on *Syneilesis palmata*	South Korea	H.D. Shin & M.J. Park	KX287075	KX287375	KX287656	KX287934	KX288213	KX288533	KX288823	–	–	–
	CBS 131759; KACC 44073		*Coleosporium horianum* on *Codonopsis lanceolata*	South Korea	H.D. Shin & M.J. Park	KX287076	KX287376	KX287657	KX287935	KX288214	KX288534	KX288824	–	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CBS 131760; KACC 44081		*Coleosporium horianum* on *Codonopsis lanceolata*	South Korea	H.D. Shin & M.J. Park	KX287077	KX287377	KX287658	KX287936	KX288215	KX288535	KX288825	–	KX289164	–
	CBS 131761; KACC 44855		*Coleosporium saussureae* on *Saussurea pulchella*	South Korea	H.D. Shin & M.J. Park	KX287078	KX287378	KX287659	KX287937	KX288216	KX288536	KX288826	–	KX289165	–
	CBS 131762; KACC 44860		*Coleosporium* sp. on *Solidago serotina*	South Korea	H.D. Shin & M.J. Park	KX287079	KX287379	KX287660	KX287938	KX288217	KX288537	KX288827	–	KX289166	–
	CBS 131763; KACC 42484		*Coleosporium eupatorii* on *Eupatorium japonicum*	South Korea	H.D. Shin & M.J. Park	KX287080	KX287380	KX287661	KX287939	KX288218	KX288538	KX288828	KX289057	KX289167	KX289249
	CBS 131764; KACC 43182		*Coleosporium eupatorii* on *Eupatorium lindleyanum*	South Korea	H.D. Shin & M.J. Park	KX287081	KX287381	KX287662	KX287940	KX288219	KX288539	KX288829	–	KX289168	–
	CBS 131765; KACC 42635		*Coleosporium asterum* on *Aster pilosus*	South Korea	H.D. Shin & M.J. Park	KX287082	KX287382	KX287663	KX287941	KX288220	KX288540	KX288830	–	KX289169	–
	CBS 131766; KACC 43058		*Coleosporium clerodendri* on *Clerodendron trichotomum*	South Korea	H.D. Shin & M.J. Park	KX287083	KX287383	KX287664	KX287942	KX288221	KX288541	KX288831	–	KX289170	–
	CBS 131767; KACC 44053		*Pileolaria shiraiana* on *Rhus trichocarpa*	South Korea	H.D. Shin & M.J. Park	KX287084	KX287384	KX287665	KX287943	KX288222	KX288542	KX288832	–	KX289171	–
R. collo-cygni	**CBS 101180[NT]**		*Hordeum vulgare*	Austria	Züchtungsfirma Saatbau Linz	KX287085	KX287385	KX287666	KX287944	KX288223	KX288543	KX288833	–	KX289172	–
	CBS 101181		*Hordeum vulgare*	Germany, Bavaria	E. Sachs	KJ504745	KJ504786	KJ504450	KJ504701	KJ504569	KJ504657	KJ504613	KJ504513	KJ504483	–
	CBS 101182		*Hordeum vulgare*	Germany, Bavaria	E. Sachs	KX287086	KX287386	KX287667	KX287945	KX288224	KX288544	KX288834	KX289058	KX289173	–
	CBS 119442; CPC 12688; V22		*Hordeum vulgare*	Norway	S. Salamati	KX287087	KX287387	KX287668	KX287946	KX288225	KX288545	KX288835	–	–	–
	CBS 119441; CPC 12690; V40		*Hordeum vulgare*	Norway	S. Salamati	KX287088	KX287388	KX287669	KX287947	KX288226	KX288546	KX288836	–	–	–
	CBS 119440; CPC 12692; V58		*Hordeum vulgare*	Norway	S. Salamati	KX287089	KX287389	KX287670	KX287948	KX288227	KX288547	KX288837	KX289059	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CBS 119439; CPC 12693; V74		*Hordeum vulgare*	Norway	S. Salamati	KX287090	KX287390	KX287671	KX287949	KX288228	KX288548	KX288838	KX289060	–	–
R. coryli	CBS 117800; CPC 12090	*R. endophylla*	*Corylus avellana*	Netherlands	G. Verkley	KX287091	KX287391	KX287672	KX287950	KX288229	KX288549	KX288839	KX289061	–	KX289250
R. cupulariae	CBS 235.73		*Inula* sp.	former Czechoslovakia	L. Marvanová	KX287092	KX287392	KX287673	KX287951	KX288230	KX288550	KX288840	–	KX289174	–
R. cyclaminicola	CBS 399.51		*Cyclamen persicum*	USA	–	KX287093	KX287393	KX287674	KX287952	KX288231	KX288551	KX288841	–	–	–
R. cynarae	CPC 18427		*Cynara cardunculus*	USA, California	S.T. Koike	KX287094	KX287394	KX287675	KX287953	KX288232	KX288552	KX288842	–	KX289175	–
	CBS 128779; CPC 18725		*Carthamus tinctorius*	USA, California	S.T. Koike	KX287095	HQ728118	KX287676	KX287954	KX288233	KX288553	KX288843	–	KX289176	–
	CBS 128912[ET]; CPC 18426		*Cynara cardunculus*	USA, California	S.T. Koike	KX287096	HQ728117	KX287677	KX287955	KX288234	KX288554	KX288844	–	KX289177	–
	CBS 114728; UPSC 3248	*R. cirsii*	*Cirsium arvense*	Sweden	E. Gunnerbeck	KX287097	KX287395	KX287678	KX287956	KX288235	KX288555	KX288845	–	KX289178	–
	CPC 25896		*Carex acutiformis*	Netherlands	S.I.R. Videira	KX287098	KX287396	KX287679	KX287957	KX288236	KX288556	KX288846	–	–	–
	CPC 25897		*Carduus* sp.	Netherlands	S.I.R. Videira	KX287099	KX287397	KX287680	KX287958	KX288237	KX288557	KX288847	–	KX289179	–
	CBS 114729; UPSC 3338	*R. cardui*	*Carduus crispus*	Sweden	E. Gunnerbeck	KX287100	KX287398	KX287681	KX287959	KX288238	KX288558	KX288848	–	KX289180	–
R. deusta	CBS 473.50; IMI 099672	*R. deusta* f. *latifolia*	*Lathyrus latifolius*	Guadeloupe	–	KX287101	KX287399	KX287682	KX287960	KX288239	KX288559	KX288849	KX289062	KX289181	–
R. didyma var. *didyma*	CBS 114299; UPSC 2746	*R. didyma*	*Ranunculus repens*	Sweden	E. Gunnerbeck	KX287102	KX287400	KX287683	KX287961	KX288240	KX288560	KX288850	–	KX289182	–
	CBS 420.67	*R. didyma*	*Ranunculus repens*	UK, England	–	KX287103	KX287401	KX287684	KX287962	KX288241	KX288561	KX288851	–	KX289183	–
	CBS 431.67*	*R. didyma*	*Ranunculus repens*	Luxembourg	–	KX287104	KX287402	KX287685	KX287963	KX288242	–	KX288852	–	–	–
R. diervillae	CPC 16860	*Ramularia* sp.	*Diervilla lonicera*	Canada	K.A. Seifert	KX287105	KX287403	KX287686	KX287964	KX288243	KX288562	KX288853	–	KX289184	–
	CPC 16864	*Ramularia* sp.	*Diervilla lonicera*	Canada	K.A. Seifert	KX287106	KX287404	KX287687	KX287965	KX288244	KX288563	KX288854	–	KX289185	–
	CPC 16859	*Ramularia* sp.	*Diervilla lonicera*	Canada	K.A. Seifert	KX287107	KX287405	KX287688	KX287966	KX288245	KX288564	–	–	KX289186	–
	CPC 16863	*Ramularia* sp.	*Diervilla lonicera*	Canada	K.A. Seifert	KX287108	KX287406	KX287689	KX287967	KX288246	KX288565	KX288855	–	KX289187	–
R. digitalis-ambiguae	CBS 434.67	*R. variabilis*	*Digitalis purpurea*	Luxembourg	–	KX287109	KX287407	KX287690	KX287968	KX288247	KX288566	KX288856	KX289063	–	–
	CBS 297.37[T]	*R. variabilis*	*Digitalis* sp.	Netherlands	–	KX287110	KX287408	KX287691	KX287969	KX288248	KX288567	KX288857	–	–	–
R. endophylla	CBS 113871		*Quercus robur*	Netherlands	G. Verkley	KP894130	KP894237	KP894345	KP894455	KP894566	KP894677	KP894787	KP894891	KP894977	–
	CBS 113265[ET]		*Quercus robur*	Netherlands	G. Verkley	AY490776	AY490763	KF903461	KF253276	KP894562	KP894673	KP207603	KF253981	KP894975	–
	CBS 101680		*Castanea sativa*	Netherlands	A. Aptroot	KP894126	KP894233	KP894341	KP894451	KP894561	KP894672	KP894783	KP894887	KP894974	–
	CBS 115303		*Quercus robur*	Netherlands	–	KP894133	KP894240	KP894348	KP894458	KP894569	KP894680	KP894790	KP894894	–	–
	CBS 113869		*Quercus robur*	Netherlands	G. Verkley	KP894128	KP894235	KP894343	KP894453	KP894564	KP894675	KP894785	KP894889	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CBS 115302		*Quercus robur*	Netherlands	–	KP894132	KP894239	KP894347	KP894457	KP894568	KP894679	KP894789	KP894893	KP894978	–
R. eucalypti	CBS 120728; CPC 13304		*Eucalyptus* sp.	Australia, Queensland	P.W. Crous	KJ504751	KJ504793	KJ504457	KJ504708	KJ504576	KJ504664	KJ504620	KJ504520	–	–
	CPC 19188	*Ramularia* sp.	*Phragmites* sp.	Netherlands	P.W. Crous	KJ504756	KJ504798	KJ504462	KJ504713	KJ504581	KJ504669	KJ504625	KJ504524	KJ504491	–
	CBS 120726[T]; CPC 13043		*Corymbia grandifolia*	Italy	W. Gams	KF251834	KJ504792	KJ504456	KJ504707	KJ504575	KJ504663	KJ504619	KJ504519	–	KJ504542
R. euonymicola	**CBS 113308[T]**	*Ramularia* sp.	*Euonymus alatus*	South Korea	H.D. Shin	KX287111	KX287409	KX287692	KX287970	KX288249	KX288568	KX288858	–	KX289188	–
R. gaultheriae	**CBS 299.80[T]**	*Ramularia* sp.	*Gaultheria shallon*	Italy	–	KX287112	KX287410	KX287693	KX287971	KX288250	KX288569	KX288859	–	–	–
R. gei	CBS 344.49		*Geum urbanum*	Netherlands	J.A. von Arx	KX287113	KX287411	KX287694	KX287972	KX288251	KX288570	KX288860	KX289064	–	–
	CBS 113977; UPSC 2323		*Geum* sp.	Sweden	E. Gunnerbeck	KX287114	KX287412	KX287695	KX287973	KX288252	KX288571	KX288861	KX289065	KX289189	–
R. geranii	CBS 159.24		*Geranium pyrenaicum*	France	–	KX287115	KX287413	KX287696	KX287974	KX288253	KX288572	KX288862	KX289066	KX289190	KX289251
	CBS 160.24[ET]		*Geranium sylvaticum*	France	C. Killian	KX287116	KX287414	KX287697	KX287975	KX288254	KX288573	KX288863	KX289067	KX289191	–
R. geraniicola	**CPC 25912[T]**		*Geranium* sp.	Netherlands	U. Damm	KX287117	KX287415	KX287698	KX287976	KX288255	KX288574	KX288864	–	–	–
R. glechomatis	CBS 343.49	*R. calcea*	*Glechoma hederacea*	Netherlands	–	KX287118	KX287416	KX287699	KX287977	KX288256	KX288575	KX288865	–	KX289192	–
	CBS 108979		*Glechoma hederacea*	Netherlands	G. Verkley	KJ504757	KJ504799	KJ504463	KJ504714	KJ504582	KJ504670	KJ504626	–	KJ504492	KJ504543
	CBS 108980		*Glechoma hederacea*	Netherlands	G. Verkley	KX287119	KX287417	KX287700	KX287978	KX288257	KX288576	KX288866	–	KX289193	–
R. glennii	**CBS 129441[T]**; det. 11-013M		Human bronchial alveolar lavage	Netherlands	–	KJ504728	KJ504769	KJ504433	KJ504684	KJ504552	KJ504640	KJ504596	KJ504500	–	–
	CBS 122989; CPC 15195		Human skin	Netherlands	–	KJ504727	KJ504768	KJ504432	KJ504683	KJ504551	KJ504639	KJ504595	KJ504499	–	–
	CPC 18468	*R. eucalypti*	Rubber of refrigerator	USA, Athens	A.E. Glenn	KJ504734	KJ504775	KJ504439	KJ504690	KJ504558	KJ504646	KJ504602	KJ504503	–	–
	CBS 120727; CPC 13046		*Corymbia grandifolia*	Italy	W. Gams	KJ504726	KJ504767	KJ504431	KJ504682	–	KJ504638	KJ504594	KJ504498	KJ504474	KJ504530
	CPC 16560	*Ramularia* sp.	*Eucalyptus camaldulensis*	Iraq	A. Saadoon	KJ504731	KJ504772	KJ504436	KJ504687	KJ504555	KJ504643	KJ504599	KJ504501	KJ504475	KJ504532
	CPC 16565	*Ramularia* sp.	*Eucalyptus camaldulensis*	Iraq	A. Saadoon	KJ504733	KJ504774	KJ504438	KJ504689	KJ504557	KJ504645	KJ504601	–	KJ504477	KJ504533
R. grevilleana	CBS 259.36	*M. fragariae*	–	Netherlands	–	KP894114	KP894222	KP894329	KP894439	KP894549	KP894660	KP894771	–	–	–
	CBS 719.84	*M. fragariae*	*Fragaria* × *ananassa* Tioga	New Zealand	–	KP894116	EU167605	KP894331	KP894441	KP894551	KP894662	KP894773	KP894881	–	–
	CBS 298.34	*M. fragariae*	–	Netherlands	–	KP894115	KP894223	KP894330	KP894440	KP894550	KP894661	KP894772	KP894880	KP894969	–
	CBS 114732; UPSC 3244		*Fragaria ananassa*	Sweden	E. Gunnerbeck	KP894113	KP894221	KP894328	KP894438	KP894548	KP894659	KP894770	–	KP894968	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
R. haroldporteri	CPC 16297	*Ramularia* sp.	Unidentified bulb plant	South Africa	P.W. Crous	KX287120	KX287418	KX287701	KX287979	KX288258	KX288577	KX288867	–	–	–
	CBS 137272[T]; CPC 16296		Unidentified bulb plant	South Africa	P.W. Crous	KJ504725	KJ504766	KJ504430	KJ504681	(KJ504549)	KJ504637	KJ504593	KJ504497	–	–
R. heraclei	**CBS 108969**[ET]		*Heracleum sphondylium*	Netherlands	G. Verkley	KX287121	KX287419	KX287702	KX287980	KX288259	KX288578	–	KX289068	–	–
	CBS 108972		*Heracleum sphondylium*	Netherlands	G. Verkley	KX287122	KX287420	KX287703	KX287981	KX288260	KX288579	–	KX289069	–	–
	CBS 108987		*Heracleum* sp.	Austria	G. Verkley	KX287123	KX287421	KX287704	KX287982	KX288261	KX288580	KX288868	–	–	KX289252
	CBS 108988		*Heracleum* sp.	Austria	G. Verkley	KX287124	KX287422	KX287705	KX287983	KX288262	KX288581	KX288869	KX289070	–	–
	CPC 11505	*Ramularia* sp.	*Heracleum moellendorffii*	South Korea	H.D. Shin	KX287125	KX287423	KX287706	KX287984	KX288263	KX288582	KX288870	KX289071	–	KX289253
	CPC 11506	*Ramularia* sp.	*Heracleum moellendorffii*	South Korea	H.D. Shin	KX287126	KX287424	KX287707	KX287985	KX288264	KX288583	KX288871	KX289072	–	–
	CPC 11507	*Ramularia* sp.	*Heracleum moellendorffii*	South Korea	H.D. Shin	KX287127	KX287425	KX287708	KX287986	KX288265	KX288584	KX288872	KX289073	–	–
	CBS 113976; UPSC 2344		*Heracleum sphondylium*	Sweden	E. Gunnerbeck	KX287128	KX287426	KX287709	KX287987	KX288266	KX288585	KX288873	KX289074	–	–
	CBS 194.25		*Pastinaca sativa*	–	–	KX287129	KX287427	KX287710	KX287988	KX288267	KX288586	KX288874	KX289075	–	–
R. hieracii-umbellati	CPC 10690	*R. inaequalis*	*Hieracium umbellatum*	South Korea	H.D. Shin	KX287130	KX287428	KX287711	KX287989	KX288268	KX288587	KX288875	–	–	–
	CPC 10691	*R. inaequalis*	*Hieracium umbellatum*	South Korea	H.D. Shin	KX287131	KX287429	KX287712	KX287990	KX288269	KX288588	KX288876	–	–	–
	CPC 10692	*R. inaequalis*	*Hieracium umbellatum*	South Korea	H.D. Shin	KX287132	KX287430	KX287713	KX287991	KX288270	KX288589	KX288877	–	–	–
	CPC 10788	*R. inaequalis*	*Hieracium umbellatum*	South Korea	H.D. Shin	KX287133	KX287431	KX287714	KX287992	KX288271	KX288590	KX288878	–	–	–
	CPC 10789	*R. inaequalis*	*Hieracium umbellatum*	South Korea	H.D. Shin	KX287134	KX287432	KX287715	KX287993	KX288272	KX288591	KX288879	KX289076	–	–
R. hydrangeae-macrophyllae	**CBS 122273**[T]; 2007/2068		*Hydrangea macrophylla*	New Zealand	C.F. Hill	KX287135	KX287433	KX287716	KX287994	KX288273	KX288592	KX288880	KX289077	–	–
	CPC 25908		*Laurus* sp.	Netherlands	W. Quaedvlieg	KX287136	KX287434	KX287717	KX287995	KX288274	KX288593	KX288881	–	–	–
	CBS 118410	*Ramularia* sp.	*Ligularia clivorum*	New Zealand	–	KX287137	KX287435	KX287718	KX287996	KX288275	KX288594	KX288882	KX289078	KX289194	–
	CPC 25905		*Carex* sp.	Netherlands	W. Quaedvlieg	KX287138	KX287436	KX287719	KX287997	KX288276	KX288595	KX288883	–	–	–
	CBS 122625; CPC 14811; 2007/3485-B	*R. rollandii*	*Iris* × *hollandica* hybrid	New Zealand	C.F. Hill	KX287139	KX287437	KX287720	KX287998	KX288277	KX288596	KX288884	KX289079	KX289195	–
	CBS 122272; 2007/2973	*Ramularia* sp.	*Iris* sp.	New Zealand	C.F. Hill	KX287140	KX287438	KX287721	KX287999	KX288278	KX288597	KX288885	KX289080	KX289196	–
	CPC 25902		*Aesculus hippocastanum*	Netherlands	S.I.R. Videira	KX287141	KX287439	KX287722	KX288000	KX288279	KX288598	KX288886	KX289081	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CPC 25906		*Carex* sp.	Netherlands	W. Quaedvlieg	KX287142	KX287440	KX287723	KX288001	KX288280	KX288599	KX288887	–	–	–
	CPC 19854	*Ramularia* sp.	*Feijoa sellowiana*	Italy	G. Polizzi	KX287143	KX287441	KX287724	KX288002	KX288281	KX288600	KX288888	KX289082	–	–
	CPC 19026	*Ramularia* sp.	*Phragmites* sp.	Netherlands	P.W. Crous	KX287144	KX287442	KX287725	KX288003	KX288282	KX288601	KX288889	–	–	–
	CPC 19027	*Ramularia* sp.	*Phragmites* sp.	Netherlands	P.W. Crous	KX287145	KX287443	KX287726	KX288004	KX288283	KX288602	KX288890	KX289083	–	–
	CBS 341.49	*R. archangelicae*	*Angelica sylvestris*	Netherlands	–	KX287146	KX287444	KX287727	KX288005	KX288284	KX288603	KX288891	KX289084	KX289197	–
	CPC 25907		*Juncus* sp.	Netherlands	U. Damm	KX287147	KX287445	KX287728	KX288006	KX288285	KX288604	KX288892	–	–	–
	CPC 20406	*Ramularia* sp.	*Eucalyptus caesia*	USA, California	P.W. Crous	KX287148	KX287446	KX287729	KX288007	KX288286	KX288605	KX288893	–	–	–
	CPC 20484	*Ramularia* sp.	*Iris foetidissima*	Netherlands	–	KX287149	KX287447	KX287730	KX288008	KX288287	KX288606	KX288894	–	–	–
	CPC 25901		*Platanus* sp.	Netherlands	S.I.R. Videira	KX287150	KX287448	KX287731	KX288009	KX288288	KX288607	KX288895	KX289085	–	KX289254
	CBS 766.84	*R. deusta* var. *alba*	*Ulex europaeus*	UK, England	–	KX287151	KX287449	KX287732	KX288010	KX288289	KX288608	KX288896	–	KX289198	–
	CBS 159.82	*R. sparganii*	*Sparganium ramosum*	Netherlands	W. Gams	KX287152	KX287450	KX287733	KX288011	KX288290	KX288609	KX288897	KX289086	KX289199	–
	CPC 19030	*Ramularia* sp.	*Iris* sp.	UK	P.W. Crous	KX287153	KX287451	KX287734	KX288012	KX288291	KX288610	KX288898	KX289087	KX289200	–
	CBS 114117; UPSC 2662	*R. butomi*	*Filipendula vulgaris*	Sweden	E. Gunnerbeck	KX287154	KX287452	KX287735	KX288013	KX288292	KX288611	KX288899	KX289088	KX289201	–
	CPC 25904		*Potentilla* sp.	Netherlands	U. Damm	KX287155	KX287453	KX287736	KX288014	KX288293	KX288612	KX288900	–	–	–
	CBS 113614	*Ramularia* sp.	*Sparganium ramosum*	Netherlands	–	KX287156	KX287454	KX287737	KX288015	KX288294	KX288613	KX288901	KX289089	–	–
	CPC 25903		*Typha* sp.	Netherlands	S.I.R. Videira	KX287157	KX287455	KX287738	KX288016	KX288295	KX288614	KX288902	KX289090	KX289202	–
	CBS 118408	*R. hellebori*	*Helleborus niger*	New Zealand	C.F. Hill	KX287158	KX287456	KX287739	KX288017	KX288296	KX288615	KX288903	KX289091	–	–
R. inaequalis	CPC 15815	Cercosporoid sp.	*Taraxacum* sp.	Mexico	M. de Jesús Yáñez-Morales	KX287159	KX287457	KX287740	KX288018	KX288297	KX288616	KX288904	KX289092	KX289203	–
	CBS 250.96	*R. inaequalis*	*Taraxacum officinale*	Canada, Nova Scotia	S. Green	KP894117	KP894224	KP894332	KP894442	KP894552	KP894663	KP894774	KP894882	KP894970	–
	CPC 15752	*Ramularia* sp.	*Taraxacum* sp.	Mexico	M. de Jesús Yáñez-Morales	KP894118	KP894225	KP894333	KP894443	KP894553	KP894664	KP894775	–	–	–
	CPC 15753	*Ramularia* sp.	*Taraxacum* sp.	Mexico	M. de Jesús Yáñez-Morales	KP894119	KP894226	KP894334	KP894444	KP894554	KP894665	KP894776	KP894883	KP894971	–
	CBS 141111[ET]; CPC 25741		*Taraxacum officinale*	Netherlands	U. Damm	KP894120	KP894227	KP894335	KP894445	KP894555	KP894666	KP894777	–	–	–
	CPC 25742; X40		*Corylus avellana*	Netherlands	S.I.R. Videira	KP894121	KP894228	KP894336	KP894446	KP894556	KP894667	KP894778	–	–	–
R. interstitialis	CBS 120.68	*R. primulae*	*Primula variabilis*	UK	S.A.J. Tarr	KX287160	KX287458	–	–	–	–	–	–	–	–
R. kriegeriana	CPC 10825		*Plantago asiatica*	South Korea	H.D. Shin	KX287161	KX287459	KX287741	KX288019	KX288298	KX288617	KX288905	–	KX289204	KX289255
	CPC 10826		*Plantago asiatica*	South Korea	H.D. Shin	KX287162	KX287460	KX287742	KX288020	KX288299	KX288618	KX288906	–	KX289205	KX289256
	CPC 10827		*Plantago asiatica*	South Korea	H.D. Shin	KX287163	KX287461	KX287743	KX288021	KX288300	KX288619	KX288907	–	KX289206	KX289257

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
R. lamii var. *lamii*	**CBS 108970[ET]**		*Lamium album*	Netherlands	G. Verkley	KX287164	KX287462	KX287744	KX288022	KX288301	KX288620	KX288908	KX289093	–	KX289258
	CBS 108971		*Lamium album*	Netherlands	G. Verkley	KX287165	KX287463	KX287745	KX288023	KX288302	KX288621	KX288909	KX289094	–	–
R. leonuri	CPC 11312	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KF251835	KF251331	KF253636	KF253178	KX288303	KX348080	KX288910	KF253983	KF252711	–
	CPC 11313	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KX287166	KX287464	KX287746	KX288024	KX288304	KX288622	KX288911	–	KX289207	–
	CPC 11314	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KX287167	KX287465	KX287747	KX288025	KX288305	KX288623	KX288912	KX289095	KX289208	–
	CPC 11411	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KX287168	KX287466	KX287748	KX288026	KX288306	KX288624	KX288913	KX289096	KX289209	–
	CPC 11412	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KX287169	KX287467	KX287749	KX288027	KX288307	KX288625	KX288914	–	KX289210	–
	CPC 11413	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KX287170	KX287468	KX287750	KX288028	KX288308	KX288626	KX288915	–	KX289211	–
	CBS 141112; CPC 14570	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KX287171	KX287469	KX287751	KX288029	KX288309	KX288627	KX288916	–	KX289212	–
	CPC 14571	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KX287172	KX287470	KX287752	KX288030	KX288310	KX288628	KX288917	–	KX289213	–
	CPC 14572	*R. lamii* var. *lamii*	*Leonurus sibiricus*	South Korea	H.D. Shin	KX287173	KX287471	KX287753	KX288031	KX288311	KX288629	KX288918	–	KX289214	–
R. lethalis	CBS 141113; CPC 25910		*Acer pseudoplatanus*	Netherlands	S.I.R. Videira	KX287174	KX287472	KX287754	KX288032	KX288312	KX288630	KX288919	KX289097	–	–
R. ligustrina	CBS 379.52		*Ligustrum vulgare*	Italy	–	KX287175	KX287473	KX287755	KX288033	KX288313	KX288631	KX288920	KX289098	–	–
R. macrospora	CBS 109015		–	–	–	KX287176	KX287474	–	–	–	KX288632	KX288921	–	–	–
R. major	CBS 141114; CPC 12542		*Petasites japonicus*	South Korea	H.D. Shin	KX287177	KX287475	KX287756	KX288034	KX288314	KX288633	KX288922	–	KX289215	–
	CPC 12543		*Petasites japonicus*	South Korea	H.D. Shin	KJ504758	KJ504800	KJ504464	KJ504715	KJ504583	KJ504671	KJ504627	–	KJ504493	–
	CPC 12544		*Petasites japonicus*	South Korea	H.D. Shin	KX287178	KX287476	KX287757	KX288035	KX288315	KX288634	KX288923	–	KX289216	–
R. mali	**CBS 129581[T]**		*Apple in cold storage*	Italy	–	KJ504737	KJ504778	KJ504442	KJ504693	KJ504561	KJ504649	KJ504605	KJ504506	KJ504478	KJ504534
R. malicola	**CBS 119227[T]**; P5	*Ramularia* sp.	*Malus* sp.	USA, Missouri	J. Batzer	AY598910	AY598873	KX287758	KX288036	KX288316	KX288635	KX288924	KX289099	KX289217	–
R. miae	**CBS 120121[T]**; CPC 12736		*Wachendorfia thyrsifolia*	South Africa	M.K. & P.W. Crous	DQ885902	KJ504801	KJ504465	KJ504716	KJ504584	KJ504672	KJ504628	KJ504525	–	KJ504544
	CPC 21692	*Ramularia* sp.	*Wachendorfia thyrsifolia*	South Africa	M.J. Wingfield	KX287179	KX287477	KX287759	KX288037	KX288317	KX288636	KX288925	–	–	–
	CPC 19770	*Teratosphaeria* sp.	*Leonotis leonurus*	South Africa	P.W. Crous	KJ504762	KJ504805	KJ504469	KJ504720	KJ504588	KJ504676	KJ504632	KJ504528	–	–
	CPC 19835	*Ramularia* sp.	*Gazania rigens* var. *uniflora*	South Africa	P.W. Crous	KJ504761	KJ504804	KJ504468	KJ504719	KJ504587	KJ504675	KJ504631	KJ504527	–	–
R. neodeusta	CPC 13568	*R. deusta* var. *alba*	*Lathyrus odoratus*	New Zealand	C.F. Hill	KX287180	KX287478	KX287760	KX288038	KX288318	KX288637	KX288926	KX289100	–	–
	CBS 141115[T]; CPC 13567	*Ramularia* sp.	*Vicia faba*	New Zealand	C.F. Hill	KX287181	KX287479	KX287761	KX288039	KX288319	KX288638	KX288927	KX289101	–	–
R. helminthiae	CPC 11502	*R. inaequalis*	*Picris hieracioides* var. *glabrensis*	South Korea	H.D. Shin	KX287182	KX287480	KX287762	KX288040	KX288320	KX288639	KX288928	KX289102	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CPC 11504	*R. inaequalis*	*Picris hieracioides* var. *glabrensis*	South Korea	H.D. Shin	KX287183	KX287481	KX287763	KX288041	KX288321	KX288640	KX288929	KX289103	–	–
	CBS 118418	*R. inaequalis*	*Picris echioides*	New Zealand	–	KX287184	KX287482	KX287764	KX288042	KX288322	KX288641	KX288930	KX289104	KX289218	–
R. nyssicola	**CBS 127665[ET]**; AR 4656; DM 2		*Nyssa ogeche* × *sylvatica* hybrid	USA, Maryland	R. Olsen	KJ504724	KJ504765	KJ504429	KJ504680	KJ504548	KJ504636	KJ504592	KJ504496	KJ504473	–
	CBS 127664; AR 4629	*M. nyssicola*	*Nyssa ogeche* × *sylvatica* hybrid	USA, Maryland	R. Olsen	KP894124	KP894231	KP894339	KP894449	KP894559	KP894670	KP894781	KP894885	–	–
R. osterici	**CBS 141116[T]; CPC 10750**	*R. archangelicae*	*Ostericum koreanum*	South Korea	H.D. Shin	KX287185	KX287483	KX287765	KX288043	KX288323	KX288642	KX288931	KX289105	–	–
	CPC 10751	*R. archangelicae*	*Ostericum koreanum*	South Korea	H.D. Shin	KX287186	KX287484	KX287766	KX288044	KX288324	KX288643	KX288932	KX289106	–	–
	CPC 10752	*R. archangelicae*	*Ostericum koreanum*	South Korea	H.D. Shin	KX287187	KX287485	KX287767	KX288045	KX288325	KX288644	KX288933	KX289107	–	–
R. parietariae	CBS 123730; V6019.1		*Parietaria officinalis*	Czech Republic	G. Verkley	KX287188	KX287486	KX287768	KX288046	KX288326	KX288645	KX288934	KX289108	–	–
	CBS 123731; V6019.2		*Parietaria officinalis*	Czech Republic	G. Verkley	KX287189	KX287487	KX287769	KX288047	KX288327	KX288646	KX288935	KX289109	–	–
R. phacae-frigidae	**CBS 234.55[T]**	*M. phacae-frigidae*	*Phaca frigida*	Switzerland	E. Müller	KP894125	KP894232	KP894340	KP894450	KP894560	KP894671	KP894782	KP894886	–	–
R. plurivora	**CBS 118743[T]**; CPC 12207		Human bone marrow	Netherlands	–	KJ504739	KJ504780	KJ504444	KJ504695	KJ504563	KJ504651	KJ504607	KJ504508	KJ504479	KJ504536
	CPC 16123	Cladosporium-like sp.	Melon in storage	Netherlands	J.H. Houbraken	KJ504741	KJ504782	KJ504446	KJ504697	KJ504565	KJ504653	KJ504609	KJ504510	–	KJ504538
	CBS 118693; CPC 12206		Human skin	Netherlands	–	KJ504738	KJ504779	KJ504443	KJ504694	KJ504562	KJ504650	KJ504606	KJ504507	–	–
	CPC 16124	Cladosporium-like sp.	Melon in storage	Netherlands	J.H. Houbraken	KJ504742	KJ504783	KJ504447	KJ504698	KJ504566	KJ504654	KJ504610	KJ504511	–	–
R. pratensis var. *pratensis*	CBS 122105; RoKi 3045	*R. pratensis*	*Rumex* sp.	Taiwan	R. Kirschner & C.-J. Chen	KX287190	KX287488	KX287770	KX288048	KX288328	KX288647	KX288936	KX289110	–	–
	CPC 16868	*Ramularia* sp.	*Verbascum* sp.	Canada	K.A. Seifert	KX287191	KX287489	KX287771	KX288049	KX288329	KX288648	KX288937	–	–	KX289259
	CPC 19448	*Ramularia* sp.	*Prunus domestica*	–	–	KX287192	KX287490	KX287772	KX288050	KX288330	KX288649	KX288938	–	KX289219	–
R. proteae	**CBS 112161[T]**; CPC 3075		*Protea longifolia*	Australia, Tasmania	A. Macfadyen	EU707899	EU707899	–	–	–	KX288650	KX288939	–	–	–
R. pusilla	**CBS 124973[ET]**; RoKi 3143		*Poa annua*	Germany	R. Kirschner	KP894141	KP894248	KP894356	KP894466	–	KP894687	KP894798	KP894901	–	–
R. rhabdospora	CBS 312.92		–	Germany	S. Petzoldt	KX287193	KX287491	KX287773	KX288051	KX288331	KX288651	KX288940	–	KX289220	–
	CBS 118415		*Plantago lanceolata*	New Zealand	–	KX287194	KX287492	KX287774	KX288052	KX288332	KX288652	KX288941	–	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
R. rubella	CPC 15748	*Ramularia* sp.	*Rumex* sp.	Mexico	M. de Jesús Yáñez-Morales	KX287195	KX287493	KX287775	KX288053	KX288333	KX288653	KX288942	–	–	–
	CPC 15749	*Ramularia* sp.	*Rumex* sp.	Mexico	M. de Jesús Yáñez-Morales	KX287196	KX287494	KX287776	KX288054	KX288334	KX288654	KX288943	–	KX289221	–
	CPC 15750	*Ramularia* sp.	*Rumex* sp.	Mexico	M. de Jesús Yáñez-Morales	KX287197	KX287495	KX287777	KX288055	KX288335	KX288655	KX288944	–	KX289222	–
	CBS 120161		*Rumex obtusifolius*	New Zealand	–	KX287198	KX287496	KX287778	KX288056	KX288336	KX288656	KX288945	KX289111	–	–
	CBS 114440; UPSC 2857		*Rumex longifolius*	Sweden	E. Gunnerbeck	KX287199	KX287497	KX287779	KX288057	KX288337	KX288657	KX288946	KX289112	–	KX289260
	CPC 19471	*Cercosporella* sp.	*Prunus* sp.	Netherlands	W. Quaedvlieg	KX287200	KX287498	KX287780	KX288058	KX288338	KX288658	KX288947	KX289113	–	–
	CPC 19472	*Cercosporella* sp.	*Prunus* sp.	Netherlands	W. Quaedvlieg	KX287201	KX287499	KX287781	KX288059	KX288339	KX288659	KX288948	–	–	–
	CPC 15821	*Ramularia* sp.	*Rumex* sp.	Mexico	M. de Jesús Yáñez-Morales	KX287202	KX287500	KX287782	KX288060	KX288340	KX288660	KX288949	KX289114	KX289223	–
	CBS 141117[NT]; CPC 25911		*Rumex* sp.	Netherlands	U. Damm	KX287203	KX287501	KX287783	KX288061	KX288341	KX288661	KX288950	–	–	–
R. rufibasis	CBS 114567; UPSC 3339	*Ph. rufibasis*	*Myrica gale*	Sweden	E. Gunnerbeck	KX287204	KX287502	KX287784	KX288062	KX288342	KX288662	KX288951	–	KX289224	–
R. rumicicola	**CBS 141118[T]**; CPC 11294	*R. pratensis* var. *pratensis*	*Rumex crispus*	South Korea	H.D. Shin	KF902111	KF901756	KF903599	KX288063	KX288343	KX348081	KX288952	–	(KF902946)	–
	CPC 11295	*R. pratensis* var. *pratensis*	*Rumex crispus*	South Korea	H.D. Shin	KX287205	KX287503	KX287785	KX288064	KX288344	KX288663	KX288953	KX289115	–	KX289261
	CPC 11296	*R. pratensis* var. *pratensis*	*Rumex crispus*	South Korea	H.D. Shin	KX287206	KX287504	KX287786	KX288065	KX288345	KX288664	KX288954	–	–	–
R. rumicis	CBS 114300; UPSC 2724	*R. decipiens*	*Rumex aquaticus*	Sweden	E. Gunnerbeck	KJ504746	KJ504787	KJ504451	KJ504702	KJ504570	KJ504658	KJ504614	KJ504514	–	KJ504539
Ramularia sp. A	CBS 114566; UPSC 3340		*Geranium pusillum*	Sweden	E. Gunnerbeck	KX287207	KX287505	KX287787	KX288066	KX288346	KX288665	KX288955	KX289116	–	–
Ramularia sp. B	CBS 114568; UPSC 3246	*Ramularia* sp.	*Epilobium hirsutum*	Sweden	E. Gunnerbeck	KJ504747	KJ504788	KJ504452	KJ504703	KJ504571	KJ504659	KJ504615	KJ504515	–	KJ504540
Ramularia sp. C	CBS 299.49		*Symphytum officinale*	Netherlands	–	KX287208	KX287506	KX287788	KX288067	KX288347	KX288666	KX288956	–	–	–
Ramularia sp. D	CBS 135.23	*R. lactea*	*Viola odorata*	–	–	KP894123	KP894230	KP894338	KP894448	KP894558	KP894669	KP894780	–	KP894973	–
Ramularia sp. E	CPC 14767	*Ramularia* sp.	*Hydrangea serrata*	South Korea	H.D. Shin	KX287209	KX287507	KX287789	KX288068	KX288348	KX288667	KX288957	–	–	–
	CPC 14768	*Ramularia* sp.	*Hydrangea serrata*	South Korea	H.D. Shin	KX287210	KX287508	KX287790	KX288069	KX288349	KX288668	KX288958	–	–	–
	CPC 14769	*Ramularia* sp.	*Hydrangea serrata*	South Korea	H.D. Shin	KX287211	KX287509	KX287791	KX288070	KX288350	KX288669	KX288959	–	–	–
	CPC 14832	*Ramularia* sp.	*Hydrangea serrata*	South Korea	H.D. Shin	KX287212	KX287510	KX287792	KX288071	KX288351	KX288670	KX288960	–	–	–
	CPC 14833	*Ramularia* sp.	*Hydrangea serrata*	South Korea	H.D. Shin	KX287213	KX287511	KX287793	KX288072	KX288352	KX288671	KX288961	–	–	–
	CPC 14834	*Ramularia* sp.	*Hydrangea serrata*	South Korea	H.D. Shin	KX287214	KX287512	KX287794	KX288073	KX288353	KX288672	KX288962	–	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
R. sphaeroidea	CBS 112891; CPC 5242		*Vicia villosa* subsp. *varia*	USA, California	S.T. Koike	KX287215	AY352584	KX287795	KX288074	KX288354	KX288673	KX288963	KX289117	–	–
R. stellariicola	CPC 11298	*Cercosporella* sp.	*Stellaria aquatica*	South Korea	H.D. Shin	KX287216	KX287513	KX287796	KX288075	KX288355	KX288674	KX288964	–	–	–
	CBS 130592[T]; CPC 11297; KACC 42363	*P. stellariicola*	*Stellaria aquatica*	South Korea	H.D. Shin & M.J. Park	GU214693	GU214693	KX287797	KX288076	KX288356	KX288675	KX288965	KX289118	–	–
R. stellenboschensis	**CBS 130600[T]**; CPC 18294		*Protea* sp., with *Vizella interupta*	South Africa	P.W. Crous	JN712566	JN712499	KX287798	–	KX288357	KX288676	KX288966	–	–	–
R. tovarae	**CBS 113305[ET]**	*Ramularia* sp.	*Polygonum filiforme*	South Korea	H.D. Shin	KJ504764	KJ504807	KJ504471	KJ504722	KJ504590	KJ504678	KJ504634	KJ504529	KJ504494	–
R. tricherae	CBS 108973		*Knautia arvensis*	Netherlands	G. Verkley	KP894142	KP894249	KP894357	KP894467	KP894577	KP894688	KP894799	KP894902	KP894985	–
	CBS 108974		*Knautia arvensis*	Netherlands	G. Verkley	KX287217	KX287514	KX287799	KX288077	KX288358	KX288677	KX288967	KX289119	KX289225	KX289262
	CBS 108994		*Knautia arvensis*	Netherlands	G. Verkley	KP894145	KP894252	KP894360	KP894470	KP894580	KP894691	KP894802	KP894905	KP894987	–
	CBS 108995		*Knautia arvensis*	Netherlands	G. Verkley	KX287218	KX287515	KX287800	KX288078	KX288359	KX288678	KX288968	KX289120	KX289226	–
	CBS 108989		*Knautia dipsacifolia*	Austria	G. Verkley	KP894143	KP894250	KP894358	KP894468	KP894578	KP894689	KP894800	KP894903	KP894986	–
	CBS 108990		*Knautia dipsacifolia*	Austria	G. Verkley	KP894144	KP894251	KP894359	KP894469	KP894579	KP894690	KP894801	KP894904	–	–
	CBS 236.73; CCM F-369		*Knautia drymeia*	former Czechoslovakia	–	KP894146	KP894253	KP894361	KP894471	KP894581	KP894692	KP894803	KP894906	–	–
R. trigonotidis	**CBS 141119[T]**; CPC 14764	*Ramularia* sp.	*Trigonotis nakaii*	South Korea	H.D. Shin	KX287219	KX287516	KX287801	KX288079	KX288360	KX288679	KX288969	–	–	–
	CPC 14765	*Ramularia* sp.	*Trigonotis nakaii*	South Korea	H.D. Shin	KX287220	KX287517	KX287802	KX288080	KX288361	KX288680	KX288970	–	–	–
	CPC 14766	*Ramularia* sp.	*Trigonotis nakaii*	South Korea	H.D. Shin	KX287221	KX287518	KX287803	KX288081	KX288362	KX288681	KX288971	–	–	–
R. trollii	CBS 109118	*P. trollii*	*Trollius europaeus*	Austria	G. Verkley	KX287222	KX287519	KX287804	KX288082	KX288363	KX288682	KX288972	–	KX289227	–
	CBS 109119	*P. trollii*	*Trollius europaeus*	Austria	G. Verkley	KX287223	KX287520	KX287805	KX288083	KX288364	KX288683	KX288973	–	–	–
R. unterseheri	CBS 124846	*R. endophylla*	*Fagus sylvatica*	Germany	M. Unterseher	KP894160	KP894267	KP894375	KP894485	KP894595	KP894706	KP894817	KP894920	KP894999	–
	CBS 124838; li-26.4	*R. endophylla*	*Fagus sylvatica*	Germany	M. Unterseher	KP894158	KP894265	KP894373	KP894483	KP894593	KP894704	KP894815	KP894918	–	–
	CBS 130721	*R. endophylla*	Room inside a castle	Germany	–	KP894164	KP894271	KP894379	KP894489	KP894599	KP894710	KP894821	KP894924	–	–
	CBS 117879; CPC 11207	*R. endophylla*	*Acer pseudoplatanus*	Netherlands	G. Verkley	KP894150	KP894257	KP894365	KP894475	KP894585	KP894696	KP894807	KP894910	–	–
	CBS 124884[T]	*R. endophylla*	*Fagus sylvatica*	Germany	M. Unterseher	KP894163	KP894270	KP894378	KP894488	KP894598	KP894709	KP894820	KP894923	KP895002	–
R. uredinicola	**CBS 141120[T]**; CPC 11852		*Melampsora* sp. on *Salix babylonia*	Iran	S.A. Khodaparast	KX287224	KX287521	KX287806	KX288084	KX288365	KX288684	KX288974	–	KX289228	–
	CBS 179.68	*R. uredinis*	*Melampsora* sp. on *Populus* sp.	Italy	–	KX287225	KX287522	KX287807	KX288085	KX288366	KX288685	KX288975	–	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CPC 12491	*Ramularia* sp.	*Melampsora* sp. on *Salix* sp.	South Korea	H.D. Shin	KX287226	KX287523	KX287808	KX288086	KX288367	KX288686	KX288976	–	KX289229	–
	CPC 12492	*Ramularia* sp.	*Melampsora* sp. on *Salix* sp.	South Korea	H.D. Shin	KX287227	KX287524	KX287809	KX288087	KX288368	KX288687	KX288977	–	KX289230	–
	CPC 12493	*Ramularia* sp.	*Melampsora* sp. on *Salix* sp.	South Korea	H.D. Shin	KX287228	KX287525	KX287810	KX288088	KX288369	KX288688	KX288978	–	KX289231	–
	CPC 11481	*Ramularia* sp.	*Melampsora* sp. on *Salix* sp.	South Korea	H.D. Shin	KX287229	KX287526	KX287811	KX288089	KX288370	KX288689	KX288979	–	KX289232	–
	CPC 11482	*Ramularia* sp.	*Melampsora* sp. on *Salix* sp.	South Korea	H.D. Shin	KX287230	KX287527	KX287812	KX288090	KX288371	KX288690	KX288980	–	KX289233	–
	CBS 131769; KACC 42535		*Melampsora* sp. on *Salix gracilistyla*	South Korea	H.D. Shin & M.J. Park	KX287231	KX287528	KX287813	KX288091	KX288372	KX288691	KX288981	–	KX289234	–
	CBS 131770; KACC 44864		*Melampsora* sp. on *Populus alba* × *glandulosa*	South Korea	H.D. Shin & M.J. Park	KX287232	KX287529	KX287814	KX288092	KX288373	KX288692	KX288982	–	KX289235	–
	CBS 131771; KACC 44215		*Melampsora* sp. on *Salix koreensis*	South Korea	H.D. Shin & M.J. Park	KX287233	KX287530	KX287815	KX288093	KX288374	KX288693	KX288983	–	KX289236	–
	CBS 131772; KACC 44218		*Melampsora* sp. on *Salix matsudana* for. *tortuosa*	South Korea	H.D. Shin & M.J. Park	KX287234	KX287531	KX287816	KX288094	KX288375	–	KX288984	–	KX289237	–
R. urticae	CBS 105.26	*An. pulmonalis*	–	–	–	KP894169	KP894276	KP894384	KP894494	KP894604	KP894715	KP894826	–	–	–
	CBS 113974; UPSC 2359		*Urtica dioica*	Sweden	E. Gunnerbeck	KP894168	KP894275	KP894383	KP894493	KP894603	KP894714	KP894825	KP894926	KP895005	–
	CBS 162.91	*Ramulariopsis* sp.	*Urtica dioica*	Germany, Thüringen	G. Arnold	KP894170	KP894277	KP894385	KP894495	KP894605	KP894716	KP894827	–	KP895006	–
	CPC 14807	*Ramularia* sp.	*Aconitum pseudo-laeve* var.*erectum*	South Korea	H.D. Shin	KX287235	KX287532	KX287817	KX288095	KX288376	KX288694	KX288985	–	–	–
R. valerianae var. *valerianae*	CBS 109122		*Valeriana* sp.	Austria	G. Verkley	KX287237	KX287534	KX287818	KX288096	–	KX288696	KX288986	–	–	–
	CBS 109123		*Valeriana* sp.	Austria	G. Verkley	KX287238	KX287535	KX287819	KX288097	KX288377	KX288697	KX288987	–	KX289238	–
R. vallisumbrosae	CBS 271.38		*Narcissus* cv. Victoria	UK, England	–	KX287239	KX287536	KX287820	KX288098	KX288378	KX288698	KX288988	KX289121	KX289239	–
	CBS 272.38[ET]		*Narcissus* cv. Golden Spur	UK, England	–	KX287240	KX287537	KX287821	KX288099	KX288379	KX288699	KX288989	KX289122	KX289240	–
R. variabilis	CPC 16865	*Ramularia* sp.	*Verbascum* sp.	Canada	K.A. Seifert	KP894171	KP894278	KP894386	KP894496	KP894606	KP894717	KP894828	–	KP895007	–
	CPC 16866	*Ramularia* sp.	*Verbascum* sp.	Canada	K.A. Seifert	KP894172	KP894279	KP894387	KP894497	KP894607	KP894718	KP894829	–	KP895008	–
	CBS 141121[ET]; CPC 25967		*Verbascum* sp.	Germany	C. Scheuer	KP894173	KP894280	KP894388	KP894498	KP894608	KP894719	KP894830	–	–	–
R. veronicicola	CBS 113981; UPSC 2320	*Ph. veronicae*	*Veronica spicata*	Sweden	E. Gunnerbeck	KX287241	KX287538	KX287822	KX288100	KX288380	KX288700	KX288990	–	KX289241	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
R. vizellae	**CBS 130601[T]**; CPC 18283		*Protea* sp., in association with *Vizella interupta*	South Africa	P.W. Crous	JN712567	KJ504808	KJ504472	KJ504723	KJ504591	KJ504679	KJ504635	–	KJ504495	–
	CBS 117798; CPC 12088	*R. endophylla*	*Carpinus betulus*	Netherlands	G. Verkley	KP894182	KP894289	KP894397	KP894507	KP894617	KP894728	KP894839	–	–	–
	CBS 115981	*R. endophylla*	*Malus* dead leaf litter	Netherlands	–	KP894176	KP894283	KP894391	KP894501	KP894611	KP894722	KP894833	KP894928	KP895010	–
	CBS 115982	*R. endophylla*	*Malus* dead leaf litter	Netherlands	–	KP894177	KP894284	KP894392	KP894502	KP894612	KP894723	KP894834	KP894929	KP895011	–
	CBS 117871; CPC 11194	*R. endophylla*	*Quercus rubra*	Netherlands	G. Verkley	KP894188	KP894295	KP894403	KP894513	KP894623	KP894734	KP894845	KP894939	KP895021	–
	CBS 117872; CPC 11197	*R. endophylla*	*Amelanchier lamarckii*	Netherlands	G. Verkley	KP894189	KP894296	KP894404	KP894514	KP894624	KP894735	KP894846	KP894940	KP895022	–
R. weberiana	**CBS 136.23[T]**	*R. pratensis*	–	–	–	KJ504763	KJ504806	KJ504470	KJ504721	KJ504589	KJ504677	KJ504633	–	–	KJ504547
R. weigelae	CBS 113309	*Phaeoramularia weigecola*	*Weigela subsessilis*	South Korea	H.D. Shin	KX287242	KX287539	–	KX288101	–	KX288701	–	–	–	–
Ramulariopsis gossypii	**CBS 141099[ET]**; CPC 25909		*Gossypium* sp.	Brazil	–	KX287243	KX287540	KX287823	KX288102	KX288381	KX288702	KX288991	–	–	–
Rp. pseudoglycines	CPC 20036	*Rp. gossypii*	*Gossypium barbadense*	Togo	M. Piatek	KX287244	KX287541	KX287824	KX288103	–	KX288703	KX288992	KX289123	–	–
	CPC 18241	*Rp. gossypii*	*Gossypium* sp.	Brazil	–	KX287245	KX287542	KX287825	KX288104	–	KX288704	KX288993	KX289124	–	–
	CBS 141100[T]; CPC 18242	*Rp. gossypii*	*Gossypium* sp.	Brazil	–	KX287246	KX287543	KX287826	KX288105	–	KX288705	KX288994	–	–	–
Readeriella angustia	CBS 124998; CPC 13618		*Eucalyptus delegatensis*	Australia, Tasmania	B.A. Summerell	KF902113	KF901758	(KF903567)	(KF903245)	–	KX348082	–	(KF902668)	(KF902949)	–
Re. eucalyptigena	**CBS 124999[T]**; CPC 13026		*Eucalyptus dives*	Australia, New South Wales	B.A. Summerell	KF901868	KF901546	(KF903568)	(KF903254)	–	KX348083	–	(KF902676)	(KF902957)	–
Re. menaiensis	**CBS 125003[T]**; CPC 14447		*Eucalyptus oblonga*	Australia, New South Wales	B.A. Summerell	KF901870	KF901548	(KF903572)	(KF903256)	–	KX348084	–	(KF902678)	(KF902959)	–
Re. pseudocallista	**CBS 125001[T]**; CPC 13599		*Eucalyptus prominula*	Australia, New South Wales	B.A. Summerell	KF901861	KF901539	(KF903570)	(KF903239)	–	KX348085	–	(KF902664)	(KF902943)	–
Re. tasmanica	**CBS 125002[T]**; CPC 13631		*Eucalyptus delegatensis*	Australia, Tasmania	B.A. Summerell	KF902116	KF901761	(KF903656)	(KF903264)	–	KX348086	–	(KF902687)	(KF902967)	–
Septoria cerastii	CBS 132028; CPC 12343		*Cerastium holosteoides* var. *hallaisanense*	South Korea	H.D. Shin	GU253869	KF251366	(KF253670)	(KF253313)	–	KX348087	–	(KF254018)	(KF252838)	–
S. dysentericae	CBS 131892; CPC 12328		*Inula britannica* var. *chinensis*	South Korea	H.D. Shin	GU253866	KF251406	(KF253710)	(KF253353)	–	KX348088	–	(KF254058)	(KF252877)	–
S. lamiicola	CBS 123882; V6020.2		*Lamium* sp.	Czech Republic	G. Verkley	KF251951	KF251447	(KF253751)	(KF253395)	–	KX348089	–	(KF254099)	(KF252919)	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
S. leucanthemi	CBS 353.58; BBA 8504; IMI 091322		*Chrysanthemum maximum*	Germany, Hamburg	R. Schneider	KF251962	KF251458	(KF253762)	(KF253406)	–	KX348090	–	(KF254110)	(KF252930)	–
S. lycopersici	CBS 128654; KACC 42519; SMKC 22002		*Lycopersicum esculentum*	South Korea	–	KF251966	KF251462	(KF253766)	(KF253410)	–	KX348091	–	(KF254114)	(KF252934)	–
S. paridis	CBS 109110		*Paris quadrifolia*	Austria	G. Verkley	KF251995	KF251490	(KF253794)	(KF253439)	–	KX348092	–	(KF254143)	(KF252960)	–
Sphaerulina chaenomelis	CBS 131897; CPC 14795	*P. chaenomellis*	*Chaenomeles speciosa*	South Korea	H.D. Shin	GU253834	GU269817	(GU320520)	(GU384530)	–	KX288706	–	–	–	–
Sp. berberidis	CBS 324.52	*M. berberidis*	*Berberis vulgaris*	Switzerland	E. Müller	KF252106	KF251601	(KF253903)	(KF253548)	–	KX348093	–	(KF254253)	(KF253067)	–
Sp. betulae	CBS 128597; KACC 43119; SMKC 23059		*Betula schmidtii*	South Korea	–	KF252109	KF251604	(KF253906)	(KF253551)	–	KX348094	–	(KF254256)	(KF253070)	–
Sp. Gei	CBS 128632; KACC 44051; SMKC 23686		*Geum japonicum*	South Korea	–	KF252120	KF251615	(KF253917)	(KF253562)	–	KX348095	–	(KF254267)	(KF253081)	–
Sp. koreana	**CBS 135462[T]**; CPC 11414	*P. koreana*	*Vicia amurensis*	South Korea	H.D. Shin	GU214683	GU269852	(GU320556)	(GU384564)	–	KX288707	–	–	–	–
	CBS 131898; CPC 11415	*Sp. viciae*	*Vicia amurensis*	South Korea	H.D. Shin	KF252144	KF251639	(KF253940)	(KF253586)	–	KX348096	–	(KF254291)	(KF253101)	–
Sphaerulina sp.	CPC 13566		*Haloragis erecta*	New Zealand	C.F. Hill	KX287247	–	–	–	–	KX288708	–	–	–	–
Sp. tirolensis	**CBS 109018[T]**		*Rubus idaeus*	Austria	G. Verkley	KF252143	KF251638	(KF253939)	(KF253585)	–	KX348097	–	(KF254290)	(KF253100)	–
Stromatoseptoria castaneicola	CBS 102322		*Castanea sativa*	Netherlands	G. Verkley	KF251774	KF251271	–	(KF253219)	–	KX348098	–	–	(KF252752)	–
	CBS 102377		*Castanea sativa*	Netherlands	G. Verkley	KF251775	KF251272	–	(KF253220)	–	KX348099	–	–	(KF252753)	–
Teratoramularia infinita	CBS 120815	*Cercosporella* sp.	*Thladiantha punctata*	Taiwan	R. Kirschner & C.-J. Chen	KX287248	KX287544	KX287827	KX288106	KX288382	KX288709	KX288995	–	–	–
	CBS 141104[T]; CPC 19488	*Cercosporella* sp.	*Conyza canadensis*	Brazil	–	KX287249	KX287545	KX287828	KX288107	KX288383	KX288710	–	KX289125	–	–
Tr. persicariae	CPC 11408	*Ramularia* sp.	*Persicaria nepalensis*	South Korea	H.D. Shin	KX287250	KX287546	KX287829	KX288108	KX288384	KX288711	KX288996	–	–	–
	CPC 11409	*Ramularia* sp.	*Persicaria nepalensis*	South Korea	H.D. Shin	KX287251	KX287547	KX287830	KX288109	KX288385	KX288712	KX288997	–	–	–
	CBS 141105[T]; CPC 11410	*Ramularia* sp.	*Persicaria nepalensis*	South Korea	H.D. Shin	KX287252	KX287548	KX287831	KX288110	KX288386	KX288713	KX288998	–	–	–
	CBS 195.27	*R. anomala*	*Fagopyrum esculentum*	–	–	KX287253	–	–	KX288111	KX288387	KX288714	KX288999	–	–	–
Tr. rumicicola	CPC 14652	*R. pratensis* var. *pratensis*	*Rumex crispus*	South Korea	H.D. Shin	KX287254	KX287549	–	KX288112	KX288388	KX288715	KX289000	–	–	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
	CBS 141106[T]; CPC 14653	*R. pratensis* var. *pratensis*	*Rumex crispus*	South Korea	H.D. Shin	KX287255	KX287550	–	KX288113	KX288389	KX288716	KX289001	–	–	–
	CPC 14654	*R. pratensis* var. *pratensis*	*Rumex crispus*	South Korea	H.D. Shin	KX287256	KX287551	–	KX288114	KX288390	KX288717	KX289002	–	–	–
Tr. kirschneriana	**CBS 113093[T]**; RoKi 1144	*Ph. paspali*	*Setaria palmifolia*	Taiwan	R. Kirschner & C.-J. Chen	GQ852627	GU214669	KX287832	KX288115	KX288391	KX288718	KX289003	–	–	–
Tr. biformis	**CBS 124578[T]**; MUCC 693		*Eucalyptus globulus*	Australia, Queensland	G. Whyte	KF901887	KF901564	(KF903551)	(KF903287)	–	KX348100	–	(KF902703)	(KF902987)	–
Tr. cryptica	CBS 111663; CPC 1558		–	–	–	KF901823	KF901506	(KF903449)	(KF903300)	–	KX348101	–	(KF902715)	(KF902999)	–
Tr. eucalypti	CPC 12552	*Phaeophleospora eucalypti*	*Eucalyptus nitens*	Australia	C. Mohammed	KF901900	KF901576	(KF903619)	(KF903303)	–	KX348102	–	(KF902718)	(KF903002)	–
Tr. gauchensis	CBS 119465; CMW 17545		*Eucalyptus grandis*	Uruguay	M.J. Wingfield	KF902145	KF901787	(KF903509)	(KF903312)	–	KX348103	–	(KF902726)	(KF903010)	–
Tr. molleriana	CBS 118359; CMW 11560		*Eucalyptus globulus*	Australia, Tasmania	–	KF902120	KF901764	(KF903490)	(KF903327)	–	KX348104	–	(KF902740)	(KF903024)	–
Uwebraunia australiensis	CBS 120729; CPC 13282	*U. australiensis*	*Eucalyptus platyphylla*	Australia, Queensland	P.W. Crous	KF442553	EF394854	–	(JQ622129)	–	KX348105	–	–	(KF442475)	–
U. commune	CPC 12397	*M. lateralis*	*Eucalyptus globulus*	Australia	I. Smith	KF251740	KF251237	–	(KF253190)	–	KX348106	–	–	(KF252724)	–
U. musae	**CBS 122453[T]**; X1021		*Musa acuminata* cv. Nendran	India	I. Buddenhagen	JQ739816	EU514225	(EU514296)	–	–	KX348107	(EU514349)	–	–	–
	CBS 122454; X1022		*Musa acuminata* cv. Grande Naine	Indonesia	I. Buddenhagen	KX287257	EU514226	(EU514297)	–	–	KX288719	(EU514350)	–	–	–
Xenoramularia arxii	**CBS 342.49[T]**	*R. aromatica*	*Acorus calamus*	Netherlands	J.A. von Arx	KX287258	KX287552	KX287833	KX288116	KX288392	KX288720	KX289004	–	–	–
X. neerlandica	CBS 113615	*Pseudocercosporella* sp.	*Sparganium ramosum*	Netherlands	–	KX287259	KX287553	KX287834	KX288117	KX288393	KX288721	KX289005	–	–	–
	CBS 141101[T]; CPC 18377	*Pseudocercosporella* sp.	*Iris pseudacorus*	Netherlands	P.W. Crous	KX287260	KX287554	KX287835	KX288118	KX288394	KX288722	KX289006	–	–	–
	CPC 18378	*Pseudocercosporella* sp.	*Iris pseudacorus*	Netherlands	P.W. Crous	KX287261	–	KX287836	KX288119	KX288395	KX348108	KX289007	–	–	–
X. polygonicola	**CBS 141102[T]**; CPC 10852	*Ramularia* sp.	*Polygonum* sp.	South Korea	H.D. Shin	GU214695	GU214695	KX287837	KX288120	KX288396	KX288723	KX289008	–	–	–
	CPC 10853	*Ramularia* sp.	*Polygonum* sp.	South Korea	H.D. Shin	KX287262	KX287555	–	KX288121	KX288397	KX288724	KX289009	–	–	–
	CPC 10854	*Ramularia* sp.	*Polygonum* sp.	South Korea	H.D. Shin	KX287263	KX287556	–	KX288122	KX288398	KX288725	KX289010	–	–	–
Z. brevis	**CBS 128853[T]**; CPC 18106; no. 8S		*Phalaris minor*	Iran	M. Razavi	JQ739833	JF700867	(JF701036)	(JQ739777)	–	KX348109	–	(JF701104)	(JF700968)	–

Table 1. (Continued).

Species[4]	Culture number[1,2]	Previous name[4]	Host	Country	Collector	LSU	ITS	*actA*	*tef1*-α	*gapdh*	*rpb2*	*his3*	*cmdA*	*tub2*	*chs-1*
Z. halophila	**CBS 128854[T]**; CPC 18105; IRAN1483C; GLS1		*Hordeum glaucum*	Iran	M. Razavi	KF252150	KF251645	(KF253946)	(KF253592)	–	KX348110	–	(KF254297)	(JF700977)	–
Z. passerinii	**CBS 120382[ET]**; P 83		*Hordeum vulgare*	USA, North Dakota	S. Goodwin	JQ739843	JF700877	(JF701046)	(JQ739787)	(KP894652)	KP894763	(KP894874)	(JF701114)	(JF700978)	–
Z. tritici	CPC 18116	*Septoria* sp.	*Avena* sp.	Iran	Amir	KX287264	JF700884	(JF701053)	–	–	KX348111	–	(JF701121)	(JF700985)	–
	CBS 115943[ET]; IPO 323	*M. graminicola*	*Triticum aestivum*	Netherlands	R. Daamen	GU214436	AF181692	(JF701061)	–	–	KX348112	–	(JF701129)	(JF700993)	–
Z. verkleyi	**CBS 133618[T]**		*Poa annua*	Netherlands	S.I.R. Videira	KF442686	KC005781	–	–	–	KX348113	–	–	–	–
	CBS 136761		*Poa annua*	Netherlands	U. Damm	KX287265	KX287557	–	–	–	KX288726	–	–	–	–

* Strains not included in the phylogenetic analyses for lack of complete dataset. Species identification is based on the available data.

[1] AR: Personal culture collection of Amy Rossman; ATCC: American Type Culture Collection, Virginia, USA; BRIP: Plant Pathology Herbarium, Department of Primary Industries, Queensland, Australia; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CCM: Czech Collection of Microorganisms, Masaryk University, Brno, Czech Republic; CMW: Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI) of the University of Pretoria, Pretoria, South Africa; CPC: Personal culture collection of Pedro Crous, housed at CBS; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, United Kingdom; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; JCM: Japan Collection of Microorganism, RIKEN BioResource Center, Japan; JT: Personal number of J.E. Taylor; KACC: Korean Agricultural Culture Collection, National Institute of Agricultural Biotechnology, Rural Development Administration, Suwon, Republic of Korea; MUCL: Universit e Catholique de Louvain, Louvain-la-Neuve, Belgium; QM: Quartermaster Research and Development Center, U.S. Army, Massachusetts, USA; RoKI: Personal culture collection of Roland Kirschner; UPSC: Uppsala University Culture Collection of Fungi, Botanical Museum University of Uppsala, Uppsala, Sweden.

[2] Status of the strains: (**T**) ex-type, (**ET**) ex-epitype, (**NT**) ex-neotype.

[3] LSU: large subunit (28S) of the nrRNA gene operon; ITS: internal transcribed spacers and intervening 5.8S nrDNA; *actA*: partial actin gene; *tef1-α*: partial translation elongation factor 1-alpha gene; *gapdh*: partial glyceraldehyde-3-phosphate dehydrogenase (GAPDH) gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *his3*: partial histone H3 gene; *cmdA*: partial calmodulin gene; *tub2*: partial beta-tubulin gene; *chs-1*: partial chitin synthase-1 gene; "–" represents missing data.

[4] *A. = Acrodontium; An. = Antennaria; C. = Cercosporella; Ca. = Caryophylloseptoria; Ce. = Cercospora; D. = Dothistroma; N. = Neopseudocercosporella; M. = Mycosphaerella; P. = Pseudocercosporella; Pa. = Passalora; Pal. = Pallidocercospora; Ph. = Phacellium; Pp. = Parapenidiella; Ps. = Pseudocercospora; R. = Ramularia; Re. = Readeriella; Rp. = Ramulariopsis; S. = Septoria; Sp. = Sphaerulina; T. = Teratosphaeria; Tr. = Teratoramularia; U. = Uwebraunia; X. = Xenoramularia; Z. = Zymoseptoria.*

Table 2. Details of primers used and/or developed for this study for the PCR amplification and sequencing of different loci.

Locus[1]	Primer Name	Sequence 5'→3'	Annealing temperature (°C)	Orientation	Reference
actA	ACT-2Rd	ARR TCR CGD CCR GCC ATG TC	55	Reverse	Groenewald *et al*. (2013)
	ACT-512F	ATG TGC AAG GCC GGT TTC GC	55	Forward	Carbone & Kohn (1999)
	ACT-783R	TAC GAG TCC TTC TGG CCC AT	55	Reverse	Carbone & Kohn (1999)
chs-1	CHS-354R	TGG AAG AAC CAT CTG TGA GAG TTG	52	Reverse	Carbone & Kohn (1999)
	CHS-79F	TGG GGC AAG GAT GCT TGG AAG AAG	52	Forward	Carbone & Kohn (1999)
cmdA	CAL-228F	GAG TTC AAG GAG GCC TTC TCC C	58	Forward	Carbone & Kohn (1999)
	CAL-737R	CAT CTT TCT GGC CAT CAT GG	58	Reverse	Carbone & Kohn (1999)
	Cal2Rd	TGR TCN GCC TCD CGG ATC ATC TC	58	Reverse	Groenewald *et al*. (2013)
gapdh	Gapdh-F1	ATY GTC TTC CGC AAY GCGT	56	Forward	This study
	gpd1	CAA CGG CTT CGG TCG CAT TG	58	Forward	Berbee *et al*. (1999)
	gpd2	GCC AAG CAG TTG GTT GTG C	58	Reverse	Berbee *et al*. (1999)
his3	CylH3F	AGG TCC ACT GGT GGC AAG	52	Forward	Crous *et al*. (2004d)
	CylH3R	AGC TGG ATG TCC TTG GAC TG	52	Reverse	Crous *et al*. (2004d)
ITS	ITS4	TCC TCC GCT TAT TGA TAT GC	52	Reverse	White *et al*. (1990)
	V9G	TTA CGT CCC TGC CCT TTG TA	52	Forward	Hoog & Gerrits van den Ende (1998)
LSU	LR5	TCC TGA GGG AAA CTT CG	52	Reverse	Vilgalys & Hester (1990)
	LSU1Fd	GRA TCA GGT AGG RAT ACC CG	52	Forward	Crous *et al*. (2009c)
mcm7	Mcm7-1348rev	GAY TTD GCI ACI CCI GGR TCW CCC AT	56	Reverse	Schmitt *et al*. (2009)
	Mcm7-709for	ACI MGI GTI TCV GAY GTH AAR CC	56	Forward	Schmitt *et al*. (2009)
rpb2	RPB2-5f2	GGG GWG AYC AGA AGA AGG C	60→58→54	Forward	Sung *et al*. (2007)
	RPB2-7cR	CCC ATR GCT TGY TTR CCC AT	60→58→54	Reverse	Liu *et al*. (1999)
	Rpb2-F1	GGTGTCAGTCARGTGYTGAA	60→58→54	Forward	This study
	Rpb2-F4	GAY YTB GCI GGI CCI YTI ATG GC	60→58→54	Forward	This study
	RPB2-f5f	GAY GAY MGW GAT CAY TTY GG	60→58→54	Forward	Liu *et al*. (1999)
	Rpb2-R1	TCC TCN GGV GTC ATG ATR ATC AT	60→58→54	Reverse	This study
tef1-α	EF-2	GGA RGT ACC AGT SAT CAT GTT	54	Reverse	O'Donnell *et al*. (1998)
	EF1-728F	CAT CGA GAA GTT CGA GAA GG	54	Forward	Carbone & Kohn (1999)
	TEF-1R	CTT GAT GAA ATC ACG GTG ACC	54	Reverse	Videira *et al*. (2015a)
tub2	Bt-2a	GGT AAC CAA ATC GGT GCT GCT TTC	52	Forward	Glass & Donaldson (1995)
	Bt-2b	ACC CTC AGT GTA GTG ACC CTT GGC	52	Reverse	Glass & Donaldson (1995)

Table 2. Details of primers used and/or developed for this study for the PCR amplification and sequencing of different loci.

Locus[1]	Primer Name	Sequence 5'→3'	Annealing temperature (°C)	Orientation	Reference
	T1	AAC ATG CGT GAG ATT GTA AGT	52	Forward	O'Donnell & Cigelnik (1997)
	β-Sandy-R	GCR CGN GGV ACR TAC TTG TT	52	Reverse	Stukenbrock *et al*. (2012)

[1] *actA*: partial actin gene; *chs-1*: partial chitin synthase-1 gene; *cmdA*: partial calmodulin gene; *gapdh*: partial glyceraldehyde-3-phosphate dehydrogenase gene; *his3*: partial histone H3 gene; ITS: internal transcribed spacer regions and intervening 5.8S nrRNA gene of the nrDNA operon; LSU: partial 28S nrRNA gene; *mcm7*: partial gene encoding a minichromosome maintenance protein gene; *rpb2*: partial RNA polymerase II second largest subunit gene; *tef1-α*: partial translation elongation factor 1-α gene; *tub2*: partial β-tubulin gene.

(Stamatakis 2014) and a Bayesian analysis performed with MrBayes v. 3.2 (Ronquist *et al.* 2011). The Neighbour-Joining analysis using the HKY85 substitution model was applied to each gene partition individually in order to manually check the congruency among the genes (data not shown, trees deposited in TreeBASE S19315). Alignment gaps were treated as missing data and all characters were unordered and of equal weight. Any ties were broken randomly when encountered. For parsimony analysis, alignment gaps were treated as fifth character state and all characters were unordered and of unequal weight. Maximum parsimony analysis was performed in PAUP using the heuristic search option with 100 random taxon additions and tree bisection and reconnection (TBR) as the branch-swapping algorithm. Branches of zero length were collapsed and all multiple, equally most parsimonious trees were saved. The robustness of the trees obtained was evaluated by 1 000 bootstrap replications (Hillis & Bull 1993). Other measures calculated included tree length (TL), consistency index (CI), retention index (RI) and rescaled consistency index (RC). MrModeltest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model settings for each data partition in order to perform a model-optimised Bayesian phylogenetic reconstruction. The Markov Chain Monte Carlo (MCMC) analysis of four chains started in parallel from a random tree topology, the heat parameter was set at 0.1 and trees were saved every 100 (overview phylogeny) or 1 000 (*Ramularia* species phylogeny) generations until the average standard deviation of split frequencies reached 0.01 (stop value). Burn-in was set to 25 % after which the likelihood values were considered to be stationary. The Maximum-Likelihood analysis used the GTRGAMMA model and included 1 000 bootstrap replicates. All resulting trees were printed with Geneious v. 7.0.6 (Kearse *et al.* 2012). All new sequences generated in this study were deposited in NCBI's GenBank nucleotide database (www.ncbi.nlm.nih.gov) and the accession numbers are listed in Table 1. The alignments and respective phylogenetic trees were deposited in TreeBASE S19315 (www.TreeBASE.org).

Kimura-2-parameter values

To evaluate the ability of each gene for species resolution, inter- and intra-specific distance matrixes were calculated based on each gene's individual alignment using MEGA v. 5 (Tamura *et al.* 2011). Single strain species were excluded from the analyses. The matrixes were generated using the Kimura-2-parameter model, with substitutions including transitions and transversions, using uniform rates among sites and treating gaps as complete deletion. The obtained distance values were sorted into frequency distribution bins using Microsoft Excel 2007. The frequency distribution mean was calculated according to the formula $x = \Sigma(f.b) / \Sigma(f)$, in which the "f" is the frequency and "b" is the bin. The distance between the mean of the inter- and intraspecific distance distributions represents the barcoding gap (Hebert *et al.* 2003).

Taxonomy

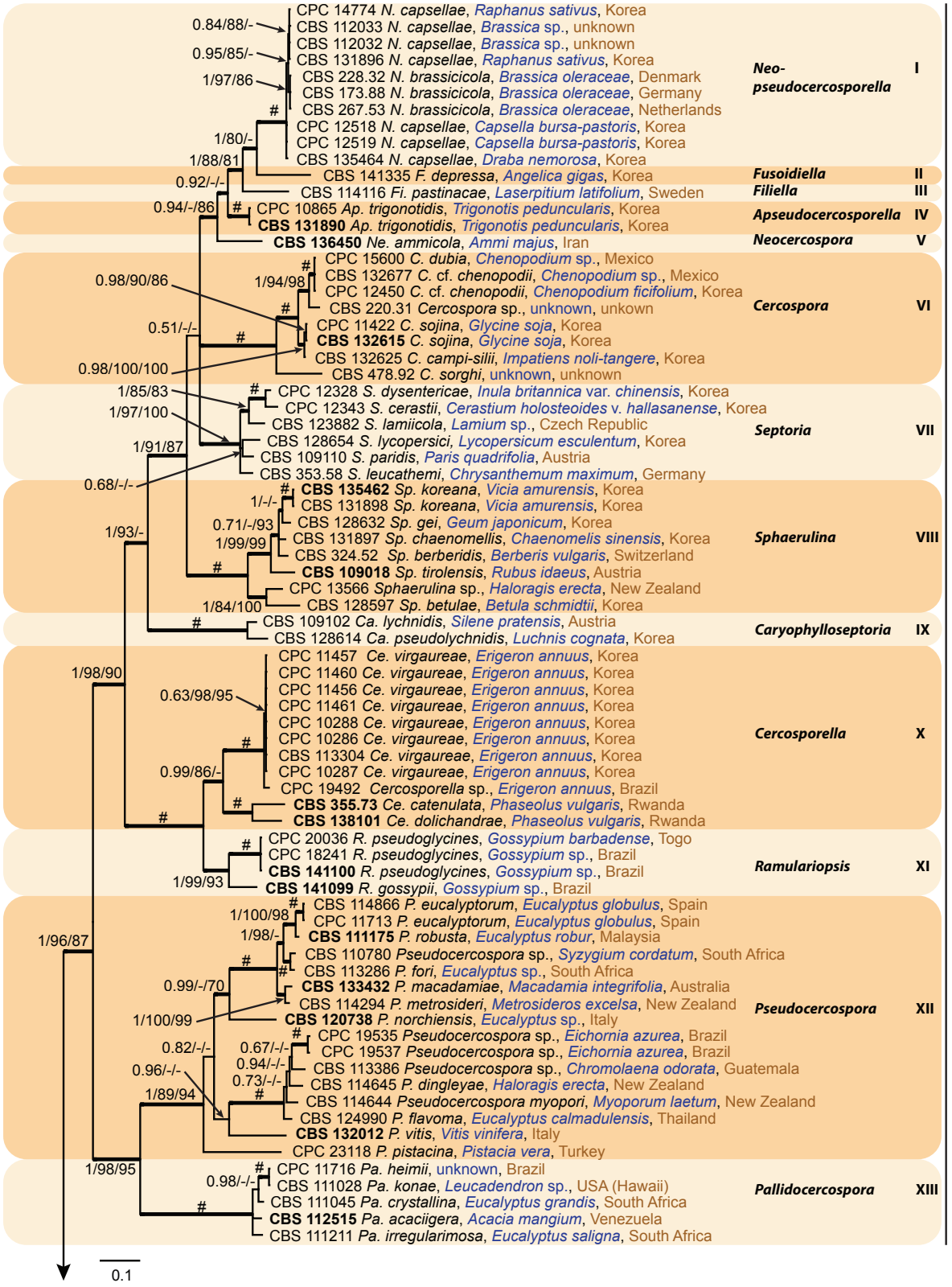
Isolates were cultivated for 7–15 d at 21 °C in a regular day/night regime. Morphological observations of reproductive structures were determined using a Nikon Eclipse 80i compound microscope with differential interference contrast (DIC) illumination. Slides were prepared using the inclined coverslip method (Kawato & Shinobu 1959, revised in Nugent *et al.* 2006) and also transparent adhesive tape (Titan Ultra Clear Tape, Conglom Inc., Toronto, Canada) (Bensch *et al.* 2012). Clear lactic acid was used as mounting medium for microscopic observations of structures *in vivo* while Shear's solution was used for structures from herbarium material. The

morphological structure terminology followed those used for *Ramularia* species by Crous *et al.* (2011c). The observed isolates were cultivated on synthetic nutrient-poor agar (SNA) for the observation and measurement of conidiogenous structures (recipes according to Crous *et al.* 2009f). The recorded measurements represent the minimum value followed by the 95 % confidence interval of 30 individual measurements and the maximum value, for both length and width. For culture characterisation the isolates were inoculated on 2 % potato dextrose agar (PDA), oatmeal agar (OA) and 2 % malt extract agar (MEA) (recipes according to Crous *et al.* 2009f), and incubated in the dark at 25 °C. After 14 d, the colony diameter was measured and the colony colour described according to the mycological colour charts of Rayner (1970). Nomenclatural novelties and descriptions were deposited in MycoBank (Crous *et al.* 2004a).

RESULTS

The PCR amplification and sequencing of *actA*, *gapdh*, *his3*, ITS, LSU, *rpb2* and *tef1*-α was successful for most of the isolates included in this study. The amplification of *cmdA* and *tub2* often resulted in multiple bands, despite the attempts of protocol optimisation, and were therefore excluded from the phylogenetic analysis. The amplification of the partial genes *chs-1* and *mcm7* was unsuccessful for most of the strains tested and were therefore not targeted for the complete dataset. The amplification of *gapdh* and *his3* of a few isolates resulted in double bands from which the band with the correct size was subsequently purified from the agarose gel and re-amplified using the same primers to obtain a single band. All the obtained sequences were deposited in GenBank (Table 1). The individual gene trees based on Neighbour-Joining analysis using the HKY85 substitution model (data not shown, available in TreeBASE S19315) showed that: 1) ITS was able to discriminate several clades but some species could not be distinguished; 2) *actA*, *gapdh*, *rpb2* and *tef1*-α each supported the same general species clades and were suitable to use in a multigene analysis, and 3) the *his3* phylogenetic tree was not congruent with the other genes trees and these sequences were therefore not used in the multigene analysis. Based on the *his3* gene, clades were split apart and closely related species based on the other gene trees were positioned far apart (e.g. Fig. 2, clades 19–20, 21, 23–25).

Fig. 1. Phylogenetic tree resulting from a Bayesian analysis on the combined alignment of LSU and *rpb2*. Bayesian posterior probabilities (≤1; BPP), maximum likelihood bootstrap support values (≥80 %; MLBS) and parsimony bootstrap support values (≥80 %; PBS) are indicated at the nodes (BPP/MLBS/PBS). Values of BPP/MLBS/PBS equal to 1/100/100 were replaced with a hash (#). The scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Species names are written in black text, host names in green and country of origin in brown. In the species names, in descending order on the tree, the genus is abbreviated as: *N.* = *Neopseudocercosporella*; *F.* = *Fusoidiella*; *Fi.* = *Filiella*; *A.* = *Apseudocercosporella*; *Ne.* = *Neocercospora*; *C.* = *Cercospora*; *S.* = *Septoria*; *Sp.* = *Sphaerulina*; *Ca.* = *Caryophylloseptoria*; *Ce.* = *Cercosporella*; *R.* = *Ramulariopsis*; *P.* = *Pseudocercospora*; *Pa.* = *Pallidocercospora*; *Ra.* = *Ramularia*; *X.* = *Xenoramularia*; *Z.* = *Zymoseptoria*; *D.* = *Dothistroma*; *St.* = *Stromatoseptoria*; *Ps.* = *Pseudocercosporella*; *M.* = *Microcyclosporella*; *My.* = *Mycosphaerelloides*; *E.* = *Epicoleosporium*; *U.* = *Uwebrawnia*; *Di.* = *Dissoconium*; *Ram.* = *Ramichloridium*; *Ac.* = *Acrodontium*; *Par.* = *Parapenidiella*; *T.* = *Teratosphaeria*; *R.* = *Readeriella*; *Te.* = *Teratoramularia*. Genus clades are delimited in coloured blocks, with genus names and clade numbers indicated to the right of the tree together with the family they belong to. Type strains are represented in bold. The tree was rooted to *Cladosporium cladosporioides* (CBS 112388).


CPC 14774 N. capsellae, Raphanus sativus, Korea
CBS 112033 N. capsellae, Brassica sp., unknown
CBS 112032 N. capsellae, Brassica sp., unknown
CBS 131896 N. capsellae, Raphanus sativus, Korea
CBS 228.32 N. brassicicola, Brassica oleraceae, Denmark
CBS 173.88 N. brassicicola, Brassica oleraceae, Germany
CBS 267.53 N. brassicicola, Brassica oleraceae, Netherlands
CPC 12518 N. capsellae, Capsella bursa-pastoris, Korea
CPC 12519 N. capsellae, Capsella bursa-pastoris, Korea
CBS 135464 N. capsellae, Draba nemorosa, Korea
Neo-pseudocercosporella
I
CBS 141335 F. depressa, Angelica gigas, Korea
Fusoidiella
II
CBS 114116 Fi. pastinacae, Laserpitium latifolium, Sweden
Filiella
III
CPC 10865 Ap. trigonotidis, Trigonotis peduncularis, Korea
CBS 131890 Ap. trigonotidis, Trigonotis peduncularis, Korea
Apseudocercosporella
IV
CBS 136450 Ne. ammicola, Ammi majus, Iran
Neocercospora
V
CPC 15600 C. dubia, Chenopodium sp., Mexico
CBS 132677 C. cf. chenopodii, Chenopodium sp., Mexico
CPC 12450 C. cf. chenopodii, Chenopodium ficifolium, Korea
CBS 220.31 Cercospora sp., unknown, unkown
CPC 11422 C. sojina, Glycine soja, Korea
CBS 132615 C. sojina, Glycine soja, Korea
CBS 132625 C. campi-silii, Impatiens noli-tangere, Korea
CBS 478.92 C. sorghi, unknown, unknown
Cercospora
VI
CPC 12328 S. dysentericae, Inula britannica var. chinensis, Korea
CPC 12343 S. cerastii, Cerastium holosteoides v. hallasanense, Korea
CBS 123882 S. lamiicola, Lamium sp., Czech Republic
CBS 128654 S. lycopersici, Lycopersicum esculentum, Korea
CBS 109110 S. paridis, Paris quadrifolia, Austria
CBS 353.58 S. leucathemi, Chrysanthemum maximum, Germany
Septoria
VII
CBS 135462 Sp. koreana, Vicia amurensis, Korea
CBS 131898 Sp. koreana, Vicia amurensis, Korea
CBS 128632 Sp. gei, Geum japonicum, Korea
CBS 131897 Sp. chaenomellis, Chaenomelis sinensis, Korea
CBS 324.52 Sp. berberidis, Berberis vulgaris, Switzerland
CBS 109018 Sp. tirolensis, Rubus idaeus, Austria
CPC 13566 Sphaerulina sp., Haloragis erecta, New Zealand
CBS 128597 Sp. betulae, Betula schmidtii, Korea
Sphaerulina
VIII
CBS 109102 Ca. lychnidis, Silene pratensis, Austria
CBS 128614 Ca. pseudolychnidis, Luchnis cognata, Korea
Caryophylloseptoria
IX
CPC 11457 Ce. virgaureae, Erigeron annuus, Korea
CPC 11460 Ce. virgaureae, Erigeron annuus, Korea
CPC 11456 Ce. virgaureae, Erigeron annuus, Korea
CPC 11461 Ce. virgaureae, Erigeron annuus, Korea
CPC 10288 Ce. virgaureae, Erigeron annuus, Korea
CPC 10286 Ce. virgaureae, Erigeron annuus, Korea
CBS 113304 Ce. virgaureae, Erigeron annuus, Korea
CPC 10287 Ce. virgaureae, Erigeron annuus, Korea
CPC 19492 Cercosporella sp., Erigeron annuus, Brazil
CBS 355.73 Ce. catenulata, Phaseolus vulgaris, Rwanda
CBS 138101 Ce. dolichandrae, Phaseolus vulgaris, Rwanda
Cercosporella
X
CPC 20036 R. pseudoglycines, Gossypium barbadense, Togo
CPC 18241 R. pseudoglycines, Gossypium sp., Brazil
CBS 141100 R. pseudoglycines, Gossypium sp., Brazil
CBS 141099 R. gossypii, Gossypium sp., Brazil
Ramulariopsis
XI
CBS 114866 P. eucalyptorum, Eucalyptus globulus, Spain
CPC 11713 P. eucalyptorum, Eucalyptus globulus, Spain
CBS 111175 P. robusta, Eucalyptus robur, Malaysia
CBS 110780 Pseudocercospora sp., Syzygium cordatum, South Africa
CBS 113286 P. fori, Eucalyptus sp., South Africa
CBS 133432 P. macadamiae, Macadamia integrifolia, Australia
CBS 114294 P. metrosideri, Metrosideros excelsa, New Zealand
CBS 120738 P. norchiensis, Eucalyptus sp., Italy
CPC 19535 Pseudocercospora sp., Eichornia azurea, Brazil
CPC 19537 Pseudocercospora sp., Eichornia azurea, Brazil
CBS 113386 Pseudocercospora sp., Chromolaena odorata, Guatemala
CBS 114645 P. dingleyae, Haloragis erecta, New Zealand
CBS 114644 Pseudocercospora myoporI, Myoporum laetum, New Zealand
CBS 124990 P. flavoma, Eucalyptus calmadulensis, Thailand
CBS 132012 P. vitis, Vitis vinifera, Italy
CPC 23118 P. pistacina, Pistacia vera, Turkey
Pseudocercospora
XII
CPC 11716 Pa. heimii, unknown, Brazil
CBS 111028 Pa. konae, Leucadendron sp., USA (Hawaii)
CBS 111045 Pa. crystallina, Eucalyptus grandis, South Africa
CBS 112515 Pa. acaciigera, Acacia mangium, Venezuela
CBS 111211 Pa. irregularimosa, Eucalyptus saligna, South Africa
Pallidocercospora
XIII
Mycosphaerellaceae
0.84/88/-
0.95/85/-
1/97/86
1/80/-
1/88/81
0.92/-/-
0.94/-/86
0.98/90/86
1/94/98
0.51/-/-
0.98/100/100
1/85/83
1/97/100
1/91/87
0.68/-/-
1/-/-
0.71/-/93
1/93/-
1/99/99
1/84/100
1/98/90
0.63/98/95
0.99/86/-
1/99/93
1/96/87
1/100/98
1/98/-
0.99/-/70
1/100/99
0.82/-/-
0.67/-/-
0.96/-/-
0.94/-/-
0.73/-/-
1/89/94
1/98/95
0.98/-/-
0.1

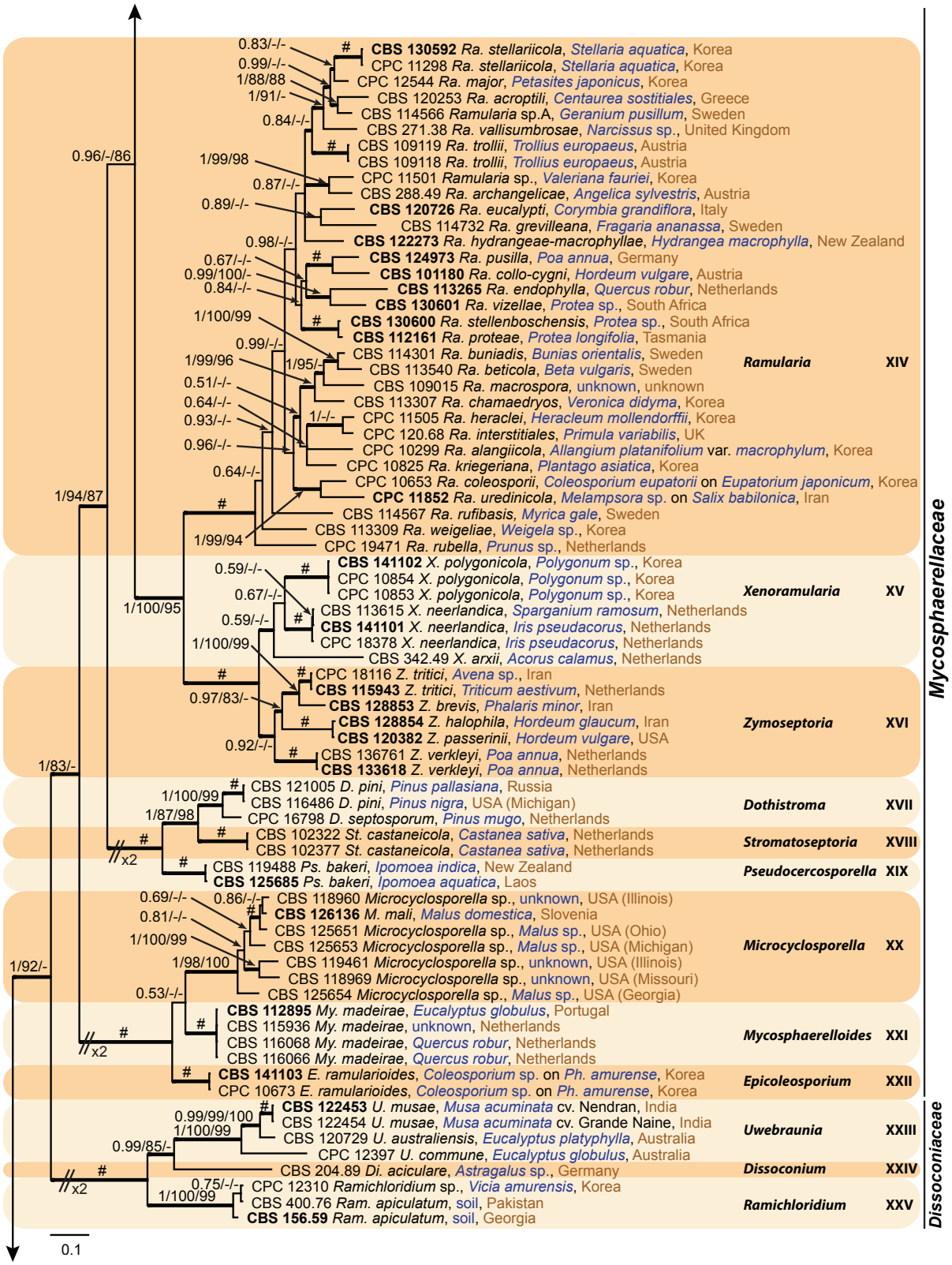


Fig. 1. (Continued).

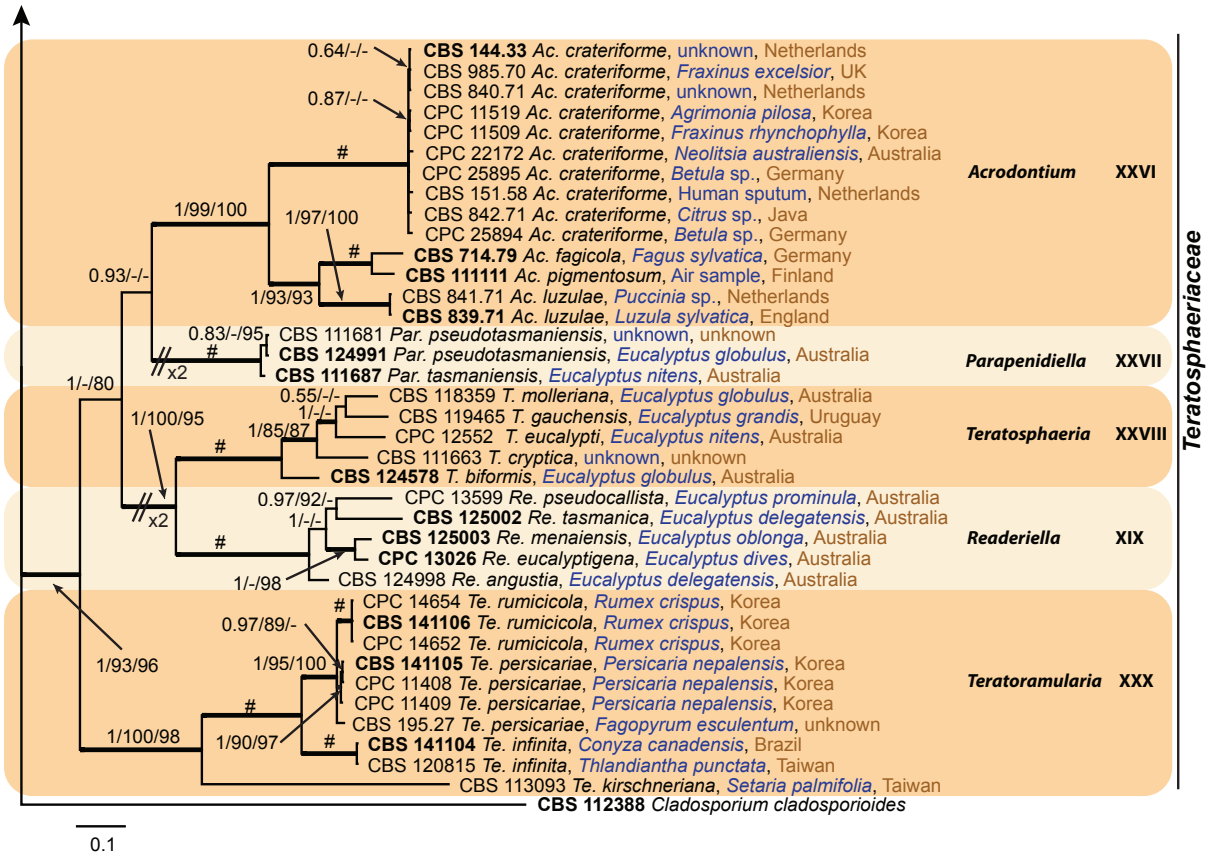


Fig. 1. (Continued).

LSU & *rpb2* phylogeny: The concatenated alignment of two loci (LSU and *rpb2*) was used to build a phylogeny that resolved the phylogenetic position of *Ramularia* and allied genera known from culture within the *Dissoconiaceae*, *Mycosphaerellaceae* and *Teratosphaeriaceae*. A strain of *Cladosporium cladosporioides* (CBS 112388) was used as outgroup. Based on the results of MrModelTest the Bayesian (BA) analysis was performed with the GTR+I+G substitution model, with inverse gamma rates and with dirichlet base frequencies for both genes (LSU and *rpb2*). The alignment contained a total of 625 unique site patterns: 200 (LSU) and 425 (*rpb2*). The analysis generated 9 222 trees from which 6 918 were sampled and 2 304 were discarded (25 % burnin) and the consensus tree is depicted in Fig. 1. The Maximum-Likelihood (ML) analysis detected 625 distinct patterns and reached a final ML optimisation likelihood of −31995.929951. The bootstrap support values from the best-scoring tree were mapped on the Bayesian tree as the second value in the tree nodes (Fig. 1; bootstrap values ≥80 %). The Parsimony (PA) analysis generated the maximum of 1 000 equally most parsimonious trees. From the total of 1 367 characters analysed, 745 were constant, 62 were variable and parsimony-uninformative and 560 were parsimony-informative. The robustness of the trees obtained was evaluated by 1 000 bootstrap replications. The bootstrap support values were mapped on the Bayesian tree as the third value in the tree nodes (Fig. 1, bootstrap values ≥80 %). A parsimony strict consensus tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 1). The additional parameters calculated were TL = 7149, CI = 0.167, RI = 0.793, RC = 0.132.

The phylogenetic trees generated using the three phylogenetic methods separated the strains into the same genus clades (Fig. 1). Clades I to XXII belong to *Mycosphaerellaceae*, clades XXIII to XXV to *Dissoconiaceae* and clades XXVI to XXX to *Teratosphaeriaceae*. Within these families we observed well-known and highly supported clades (Bayesian posterior probability/Maximum Likelihood bootstrap support/Parsimony bootstrap support) such as *Cercospora* (clade VI, 1/100/100), *Septoria* (clade VII, 1/97/100), *Sphaerulina* (clade VIII, 1/100/ 100), *Caryophylloseptoria* (clade IX, 1/100/100), *Cercosporella* (clade X, 0.99/86/-), *Ramulariopsis* (clade XI, 1/99/93), *Pseudocercospora* (clade XII, 1/89/94), *Pallidocercospora* (clade XIII, 1/100/100), *Ramularia* (clade XIV, 1/100/100), *Zymoseptoria* (clade XVI, 0.92/–/–), *Dothistroma* (clade XVII, 1/100/99), *Stromatoseptoria* (clade XVIII, 1/100/100), *Pseudocercosporella* (clade XIX, 1/100/100), *Microcyclosporella* (clade XX, 1/98/100), *Uwebraunia* (clade XXIII, 1/100/99), *Ramichloridium* (clade XXV, 1/100/99), *Acrodontium* (clade XXVI, 1/99/100), *Parapenidiella* (clade XXVII, 1/100/100), *Teratosphaeria* (clade XXVIII, 1/100/100) and *Readeriella* (clade XXIX, 1/100/100). In this phylogeny, the genera *Neocercospora* (clade V) and *Dissoconium* (clade

XXIV) are represented as single lineages (Fig. 1). Additional distinct clades with high support values were observed and are described as new genera in the Taxonomy section below, namely, *Neopseudocercosporella* (clade I, 1/100/100), *Apseudocercosporella* (clade IV, 1/100/100), *Xenoramularia* (clade XV, 0.57/–), *Mycosphaerelloides* (clade XXI, 1/100/100), *Epicoleosporium* (clade XXII, 1/100/100) and *Teratoramularia* (clade XXX, 1/100/98). The genera *Fusoidiella* (clade II) and *Filiella* (clade III) are represented as single lineages and are described as new genera based on both molecular and morphological differences.

Multigene phylogeny of *Ramularia s. str.*: The concatenated alignment of five loci was used to build a phylogeny that revealed the species diversity within the genus *Ramularia* for species known from culture. A strain of *Zymoseptoria halophila* (CBS 128854) was used as outgroup. The final alignment included 300 taxa and contained 2 689 characters (including alignment gaps) divided into five partitions: 664 (*rpb2*), 529 (ITS), 263 (*actA*), 633 (*gapdh*) and 580 (*tef1*-α) characters respectively. The five characters artificially introduced as spacers between partitions were excluded from the phylogenetic analysis (see alignment in TreeBASE S19315). The following characters were also excluded as ambiguously aligned regions: 1 053–1 059 (ITS), 1 391–1 400 (*actA*), 1 545–1 560 and 1 686–1 720 (*gapdh*), 2 255–2 276, 2 369–2 376 and 2 426–2 506 (*tef1*-α). Based on the results of MrModelTest the **Bayesian** analysis was performed with the GTR+I+G substitution model, with inverse gamma rates and with dirichlet base frequencies for *actA*, *gapdh* and *rpb2*. The ITS partition was analysed with a SYM+I+G substitution model with fixed frequencies and with inverse gamma rates while the *tef1*-α partition was analysed with the HKY+I+G substitution model with inverse gamma rates and with dirichlet base frequencies. The alignment contained a total of 1 476 unique site patterns: 374 (*rpb2*), 178 (ITS), 191 (*actA*), 354 (*gapdh*), and 379 (*tef1*-α). The analysis generated 17 232 trees from which 12 924 were sampled and 4 308 were discarded (25 % burnin) and the final tree is depicted in Fig. 2. The **Maximum Likelihood** analysis using the GTRGAMMA model detected 1 415 distinct patterns and reached a final ML optimisation likelihood of -62205.001171. The bootstrap support values from the best-scoring tree were mapped on the Bayesian tree as the second value in the tree nodes (Fig. 2; bootstrap values ≥80 %). The **parsimony** analysis generated the maximum of 1 000 equally most parsimonious trees. From the 2 499 characters analysed, 1 068 were constant, 182 were variable and parsimony-

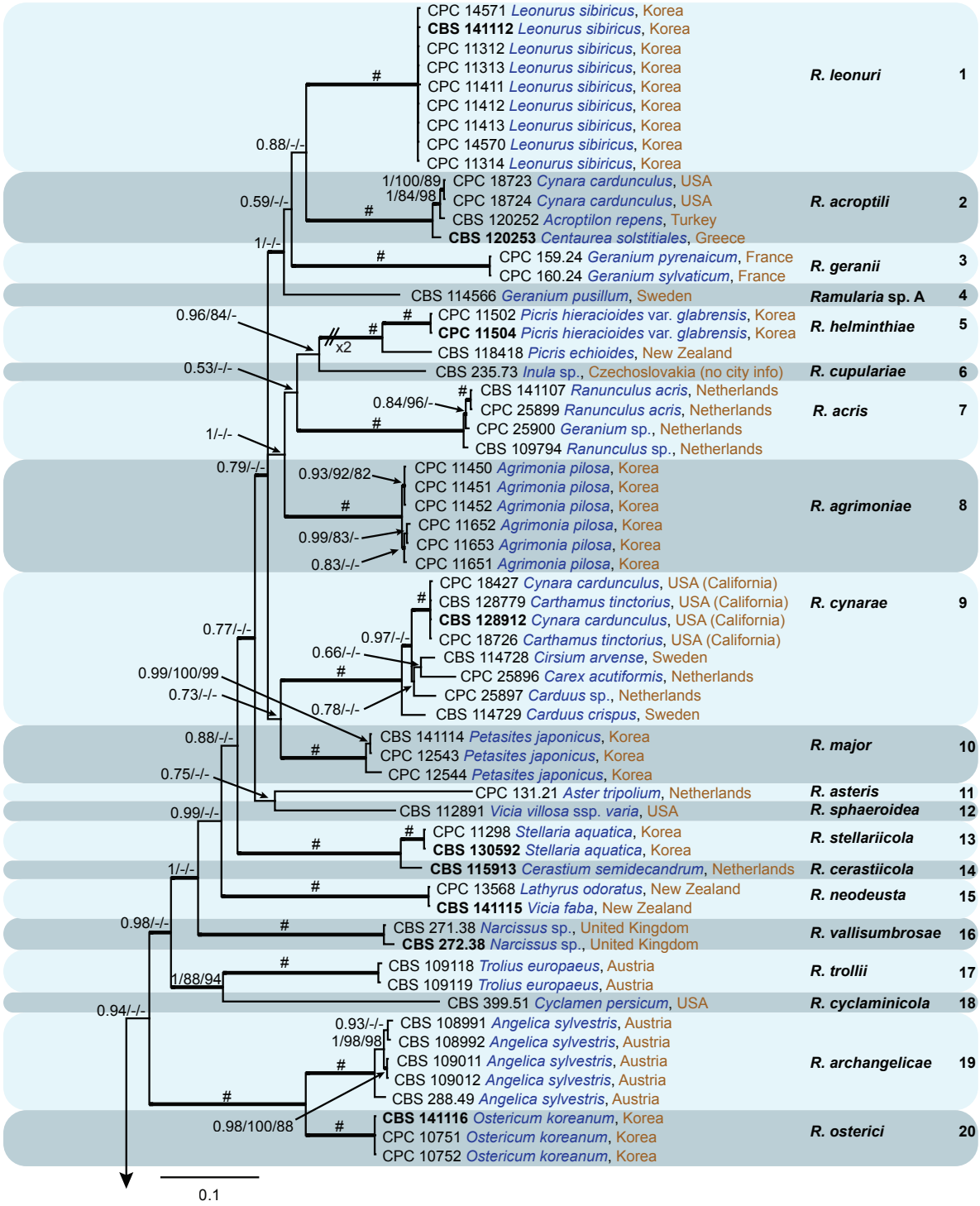


Fig. 2. Phylogenetic tree resulting from a Bayesian analysis on the combined alignment of five genes (*rpb2*, ITS, *actA*, *gapdh*, *tef1*-α). Bayesian posterior probabilities (≤1 BPP), maximum likelihood bootstrap support values (≥80 %; MLBS) and parsimony bootstrap support values (≥80 %; PBS) are indicated at the nodes (BPP/MLBS/PBS). Values of BPP/MLBS/PBS equal to 1/100/100 were replaced with a hash (#). The scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Species clades are delimited in coloured blocks, where strain numbers are written in black, host names in blue and country of origin in brown. The current species name and clade number are indicated to the right of the tree. Type strains are represented in bold. The tree was rooted to *Zymoseptoria halophila* (CBS 128854).

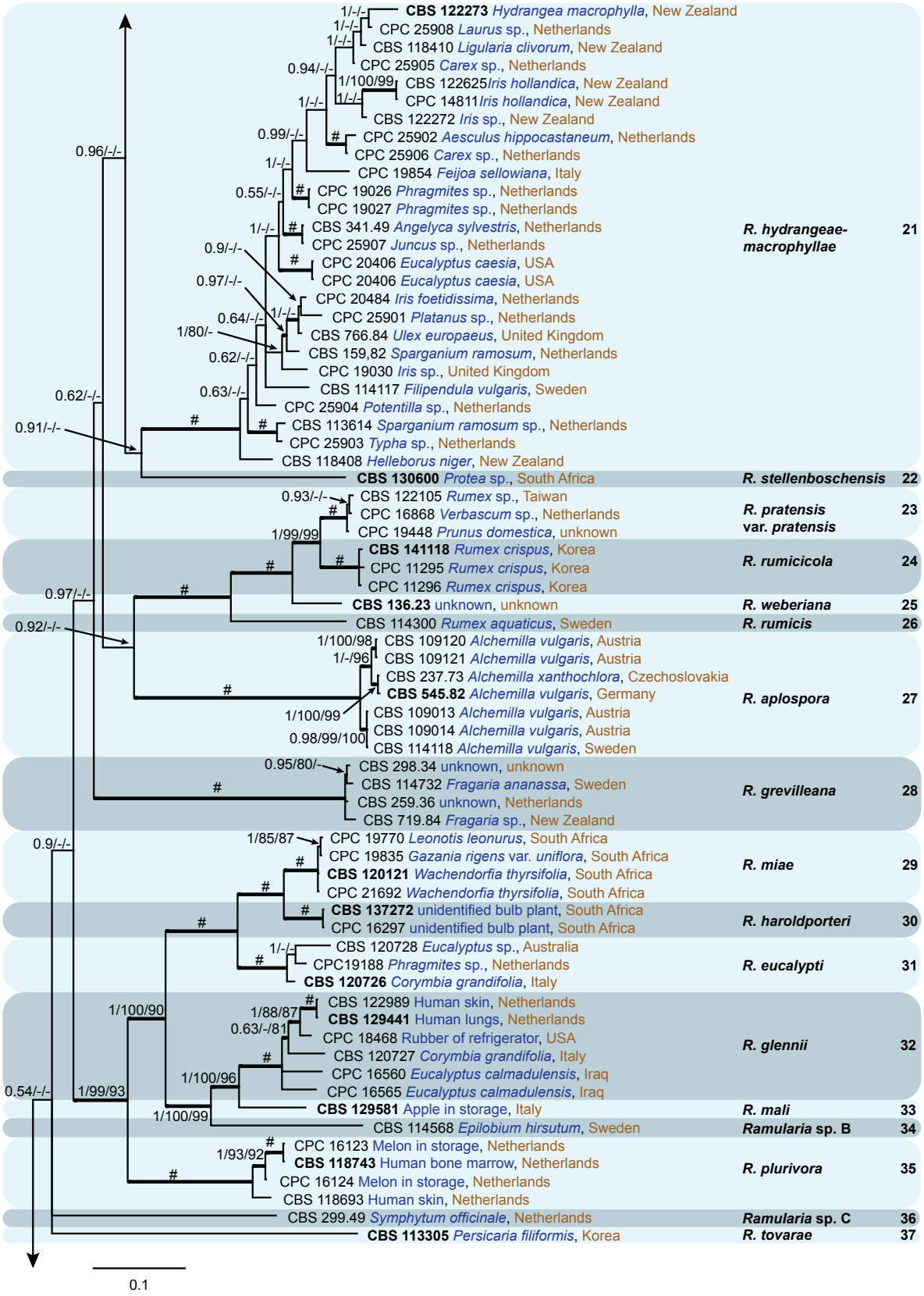


Fig. 2. (Continued).

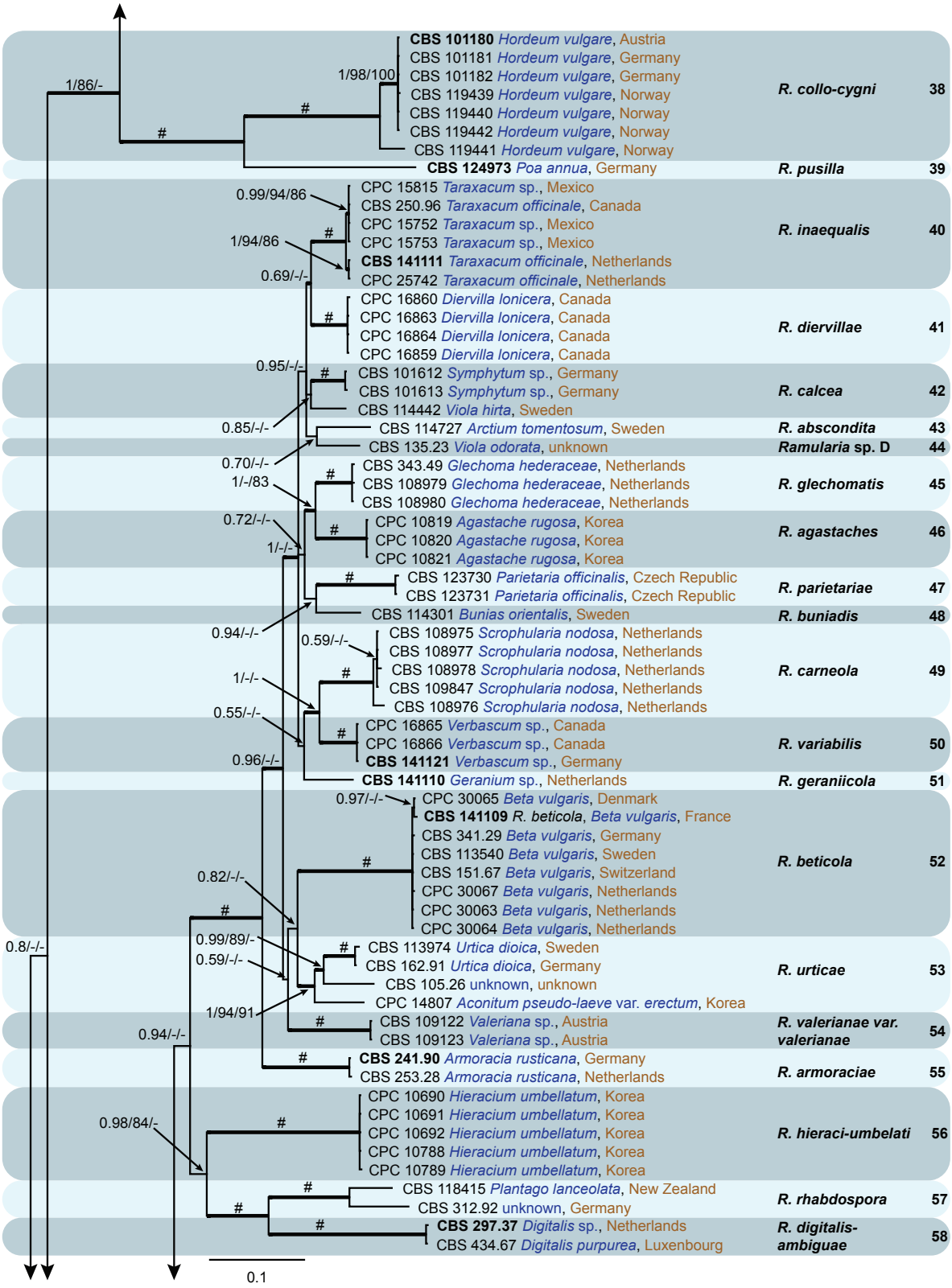


Fig. 2. (Continued).

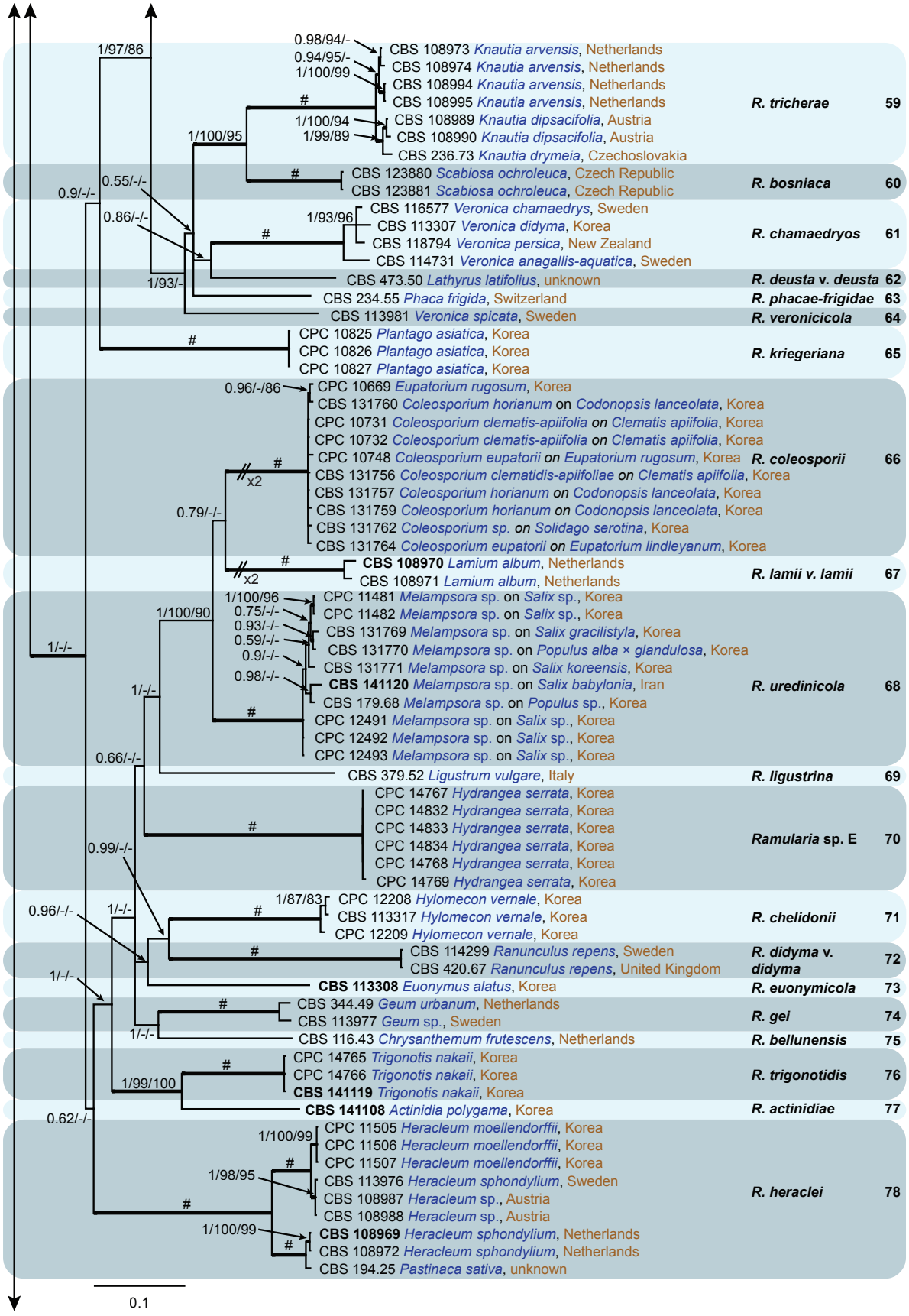


Fig. 2. (Continued).

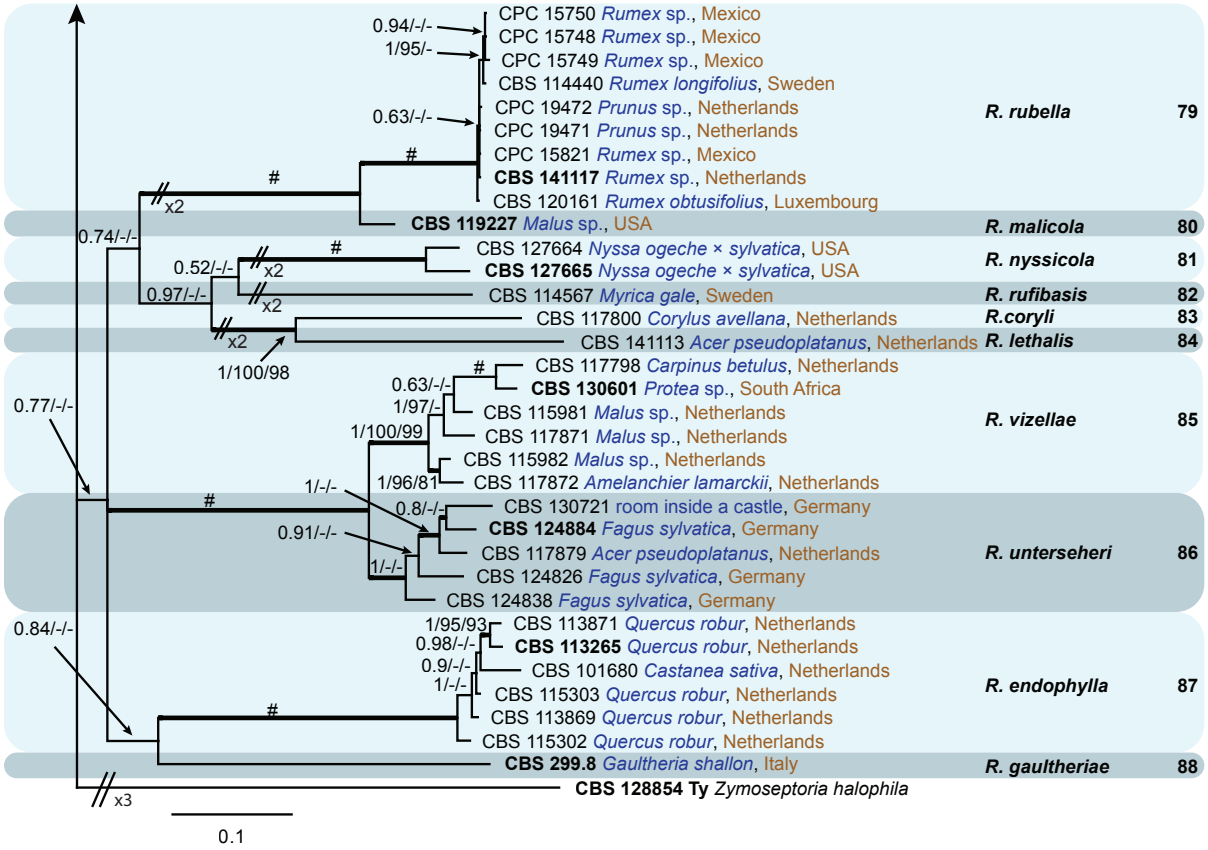


Fig. 2. (Continued).

uninformative and 1 249 were parsimony-informative. The robustness of the trees obtained was evaluated by 1000 bootstrap replications. The bootstrap support values were mapped on the Bayesian tree as the third value in the tree nodes (Fig. 2, bootstrap values ≥80 %). A consensus parsimony tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 2). The additional parameters calculated were TL = 14589, CI = 0.213, RI = 0.827 and RC = 0.176.

The phylogenetic trees based on the multigene dataset (Fig. 2) that were generated with BA, ML and PA separated the strains into similar species clades. The phylogeny distributed the species into three main clades, and the position of single species clades varied with each gene and each phylogenetic method. The tree depicted a total of 86 clades, of which 30 are single lineages (clades 4, 6, 11, 12, 14, 18, 22, 25, 26, 33, 34, 36, 37,39, 43, 44, 48, 51, 62–64, 69, 73, 75, 77, 80, 82–84, 88), 20clades represent new species (clades 1, 5, 7, 15, 20, 24, 25, 44, 51, 56, 58, 70, 76, 77, 80, 83, 84, 88), and 12 clades contained good candidates for epitypification for existing species (clades 3, 16, 27, 38–40, 48, 50, 52, 67, 78, 79). These are discussed in further detail in the Taxonomy section below.

Kimura-2-parameter values: The individual loci showed varying degrees of effectiveness in their ability to separate species (Fig. 3). In these datasets, *rpb2* and *gapdh* showed the best barcode gap distances between the inter- and intraspecific distances, followed by *actA*, *tef1*-α and *his3*. The ITS lacked a significant barcode gap, which indicates that this gene performs

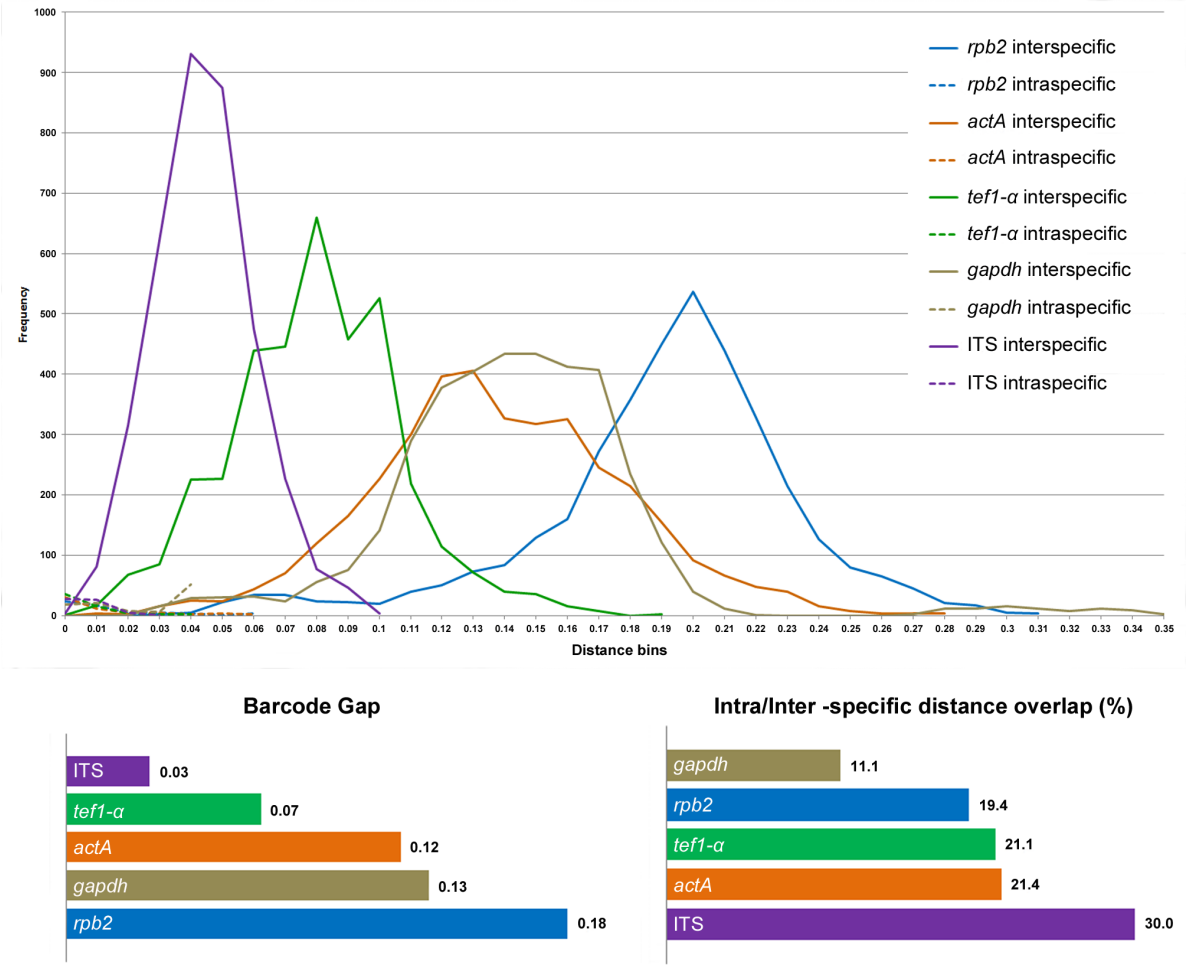


Fig. 3. Frequency distribution graph of the Kimura-2-parameter distance test for the five individual gene loci (*actaA*; *gapdh*; ITS; *rpb2*; *tef1*-α). Barcoding gap calculated based on the frequency distributions. Percentage of overlap between the inter- and intra-specific distances based on the frequency distributions.

poorly for species resolution in the genus *Ramularia*. The *gapdh* and *rpb2* also showed the lowest overlap between the intra- and interspecific distances, followed by *tef1*-α, *actA* and ITS, respectively. A good barcode should be easily amplifiable by PCR, have a large barcode gap and a small overlap between intra- and interspecific distances (Schoch *et al.* 2012, Stielow *et al.* 2015). Based on these characteristics, both *rpb2* and *actA* make good secondary barcode loci for *Ramularia* species.

Taxonomy

In this study we applied the Consolidated Species Concept (Quaedvlieg *et al.* 2014), a polyphasic approach combining the concordance of multiple gene genealogies with morphological and ecological information to improve fungal species delimitation. The genera mapped in Fig. 1 are discussed by clade order followed by a section describing and illustrating the allied genera of *Ramularia* for which only herbarium specimens were available. The species of *Ramularia* resolved in Fig. 2 are discussed in alphabetical order in a third section to which a few important species not known from culture but of phytopathological importance were added.

Clade I: ***Neopseudocercosporella*** Videira & Crous, **gen. nov.** MycoBank MB816820.

Etymology: Named after the similarity with *Pseudocercosporella*.

Phytopathogenic, causing leaf spots. *Mycelium* internal, hyaline, septate, branched, stromata almost absent to well-developed. *Ascomata* pseudothecial, mycosphaerelloid, single to aggregated, black, immersed, becoming erumpent, globose, with an apical ostiole; wall of medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid to narrowly ellipsoid. *Ascospores*, straight to fusoid-ellipsoid, hyaline, guttulate, thin-walled, with subobtuse ends, medianly 1-septate. *Conidiophores* solitary or grouped, erumpent through the cuticle or emerging through stomata, hyaline, sometimes faintly pigmented, smooth, simple, straight, slightly curved or geniculate-sinuous, usually aseptate, i.e. reduced to conidiogenous cells, thin-walled, smooth. *Conidiogenous cells* hyaline, subcylindrical to geniculate-sinuous, with inconspicuous conidiogenous loci, unthickened, neither darkened nor refractive, mostly truncate. *Conidia* solitary, hyaline or rarely slightly pigmented, thin-walled, smooth, straight to flexuous, subcylindrical to obclavate, with apex obtuse to subacute and base truncate, sometimes somewhat obconically, one- to multiseptate, hilum not thickened or darkened.

Type species: *Neopseudocercosporella capsellae* (Ellis & Everh.) Videira & Crous.

Notes: This genus currently accommodates two species, *Neopseudocercosporella capsellae* (syn. *Pseudocercosporella capsellae*/*Mycosphaerella capsellae*) and *Neopseudocercosporella brassicae* (syn. *Mycosphaerella brassicicola*) (Fig. 1, clade I; Fig. 4) which are not congeneric with the type species of *Pseudocercosporella*. Both are considered as important pathogens of *Brassica* species, especially in the *Brassica oleraceae* group that includes broccoli, cauliflower and Brussel sprouts, and have been reported worldwide. *Neopseudocercosporella capsellae* is the causative agent of White Leaf Spot disease while *Neopseudocercosporella brassicae* causes Ringspot disease. In literature, these pathogens are usually distinguished based on their disease symptoms, morphology of their ascospores, and culture characteristics (Inman *et al.* 1991). Both pathogens cause symptoms on leaves, stems and pods. The lesions caused by *N. capsellae* are round to angular and tan to light grey while the lesions caused by *N. brassicae* expand in a pattern of concentric rings with shades of grey. The ascomata, asci and ascospores of *N. capsellae* and *N. brassicae* are very similar in size and shape. The ascospores in both species are 1-septate and not constricted at the septa but the ascospores of *N. brassicae* typically have one cell that is broader than the other while in *N. capsellae* they are of similar size and shape. In culture, *N. capsellae* isolates produced spermogonia and conidia and also secreted a pink pigment into the media, while *N. brassicae* isolates produced no spermogonia, conidia or pigment. The similarity between these two diseases is high and White Leaf Spot disease was previously misdiagnosed as Ringspot in Canada, since both diseases produce slate grey lesions with spermogonia and pseudothecia on stems and pods (Rimmer *et al.* 2007). The character used to distinguish these two species that is most emphasised in literature is their ascospore morphology (Inman *et al.* 1991, Rimmer *et al.* 2007). The production of pigment into the media should be considered a poor character to distinguish these species since it has been observed that, among a large number of isolates of *N. capsellae*, only a small percentage could produce pigment and this ability was highly dependant on the media used (Gunasinghe *et al.* 2016). Although these are economically important fungi, only a few isolates are available in culture collections and mostly of *N. capsellae*. The sequences of five gene regions of strains deposited in the culture collection as *N. capsellae* and *N. brassicae* used in

this study showed only 6–8 unique nucleotide differences in a concatenated alignment containing about 3 000 nucleotides. None of these are from ex-type cultures or specimens and only *N. capsellae* ITS and LSU sequences were available on GenBank for comparison. Based on molecular data there is a distinct possibility that these two species might be synonymous but for now we prefer to keep them separate pending the recollection of fresh material. *Neopseudocercosporella capsellae* has a predominantly asexual life cycle and the sexual morph is produced at the end of the season to enable survival. *Neopseudocercosporella brassicae* has no recorded asexual morph other than spermatogonia *in vivo*. Ascomata can be produced all year round and the fungus is homothallic, meaning ascomata can be produced without the need for two complementary mating types (Rimmer *et al.* 2007).

Neopseudocercosporella brassicae (Chevall.) Videira & Crous, **comb. nov.** MycoBank MB817145.
Basionym: *Asteroma brassicae* Chevall., *Fl. g,en. env.* (Paris) 1:
449. 1826.
≡ *Asteromella brassicae* (Chevall.) Boerema & Kesteren, Persoonia 3: 18. 1964.
= *Sphaeria brassicicola* Duby, as "*brassicaecola*", Bot. gall., Edn 2 (Paris) 2: 712. 1830.
≡ *Depazea brassicicola* (Duby) Klotzsch, in Klotzsch, Herb. Viv. Mycol.: no. 1142. 1848.
≡ *Mycosphaerella brassicicola* (Duby) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 1(1): 424. 1897.
≡ *Sphaerella brassicicola* (Duby) Ces. & De Not., Comment. Soc. Crittog. Ital. 1(4): 238. 1863.
= *Dothidea brassicae* Desm., Ann. Sci. Nat., Bot., ser. 2 17: 113. 1842.
= *Phyllosticta brassicicola* Grove, J. Roy. Hort. Soc. 40: 76. 1914.

Specimens examined: **Denmark**, on *Brassica oleraceae*, date and collector unknown, isol. and dep. by C.A. Jörgensen, Feb. 1932, culture CBS 228.32. **Netherlands**, Berlikum, on *Brassica oleraceae* var. *acephala* subvar. *sabelica*, date and collector unknown, isol. and dep. by F. Quak, Nov. 1953, culture CBS 267.53. **Germany**, Schleswig-Holstein, Marne, on *Brassica oleracea*, date and collector unknown, isol. by W. Zornbach, Aug. 1986, dep. by W. Zornbach, Mar.1988, culture CBS 173.88.

Substrate and distribution: On various *Brassica oleraceae* subspecies and varieties (Brussels sprouts, broccoli, cauliflower and cabbage) and other cruciferous species such as oilseedrape, rutabanga and kale.

Notes: Boerema & van Kesteren (1964) addressed the nomenclatural history of *Mycosphaerella brassicicola. Mycosphaerella brassicicola* (1897) is based on *Sphaeria brassicicola* (1830) from *Brassica oleraceae* from France, Germany, Italy and Belgium. It is hereby transferred to the genus *Neopseudocercosporella.* Although the isolates used in this study match this host and localities, they were unfortunately sterile in culture (Fig. 1, clade I). Fresh cultures need to be collected from plants exhibiting typical disease symptoms and included in a molecular phylogeny.

Neopseudocercosporella capsellae (Ellis & Everh.) Videira & Crous, **comb. nov.** MycoBank MB817119. Fig. 4.
Basionym: *Cylindrosporium capsellae* Ellis & Everh., J. Mycol. 3(11): 130. 1887.
≡ *Cercoseptoria capsellae* (Ellis & Everh.) H.C. Greene, Trans. Wisconsin Acad. Sci. 47: 127. 1959.

Fig. 4. *Neopseudocercosporella capsellae* (A–D. CPC 14774; E–I. CPC 12518; J–N. CPC 11677). A, E. Leaf spot symptoms on hosts. B–D, F. Conidiogenous cell and conidia from herbarium material. G, H, J, K, L. Conidiogenous cells and conidia from culture. I, M, N. Conidia from culture. Scale bars = 10 µm.

≡ *Pseudocercosporella capsellae* (Ellis & Everh.) Deighton, Mycol. Pap. 133: 42. 1973.
≡ *Cercoseptoria capsellae* (Ellis & Everh.) Arx, Proc. Kon. Ned. Akad. Wetensch. C 86(1): 35. 1983.
= *Mycosphaerella capsellae* A.J. Inman & Sivan., Mycol. Res. 95: 1339. 1991.
For additional synonyms see Braun (1995) or MycoBank.

Description in vivo: See Braun (1995).

Specimens examined: **South Korea**, Hongcheon, on *Capsella bursa-pastoris*, 4 Nov. 2005, H.D. Shin, culture CPC 12519; on *Draba nemorosa*, 30 Oct. 2004, H.D. Shin, culture CBS 135464 = CPC 11677; Inje, on *Trigonotis peduncularis*, 14 Sep. 2003, H.D. Shin, culture CPC 10865; Namyangju, on *Raphanus sativus*, 22 Oct. 2007, H.D. Shin, culture CBS 131896 = CPC 14773. **New Zealand**, Auckland, Mt. Albert, on *Brassica* sp., unknown date and collector, isol. C.F. Hill, Jul. 2005, culture CBS 118412. **Unknown country**, on *Brassica* sp., unknown date and collector, isol. R. Evans, 28 Aug. 2002, cultures CBS 112032, CBS 112033. **USA**, Columbia,

Missouri, Boone Co., on *Capsella bursa-pastoris*, May 1887, Galloway 253 (holotype NY 883641, isotype BPI 399944).

Substrate and distribution: Various cruciferous species (*Brassicaceae*), circumglobal (host list and detailed distribution see Braun 1995).

Notes: *Pseudocercosporella capsellae* (1973) is based on *Cylindrosporium capsellae* (1887) from *Capsella bursa-pastoris* from the USA (Columbia, Missouri). It is hereby combined in the new genus *Neopseudocercosporella*. *Neopseudocercosporella capsellae* causes White Leaf Spot disease, an important disease of cruciferous species worldwide (Fig. 1, Clade I; Fig. 4). The strains CPC 12518 and CPS 12519 were isolated from this host but originated from South Korea. *Mycosphaerella capsellae* (1991) is described from *Brassica napus* in the UK and linked to *Pseudocercosporella capsellae*. The isolates CBS 112032 and 112033 are listed from the UK but with *Brassica* sp. as host and were deposited by R. Evans who also at approximately the same time deposited IMI 389562, which is listed in the IMI database as being from *Brassica napus*. Based on ITS and partial LSU, an isolate from ATCC (38562 from *Brassica rapa*, USA, California; GenBank JX499036) which is listed in ATCC as *Pseudocercosporella capsellae*, also belongs to this clade. Unfortunately no other sequences were available for this isolate. Fresh cultures need to be collected from plants exhibiting typical disease symptoms and included in a molecular phylogeny.

Clade II: *Fusoidiella* Videira & Crous, **gen. nov.** MycoBank MB816818.

Etymology: Named after the fusiform-shaped conidia of the type species.

Phytopathogenic, causing small yellow to olivaceous green spots on leaves. *Mycelium* internal. *Conidiophores* aggregated in dense fascicles, arising through stomata, aseptate, i.e. usually reduced to conidiogenous cells, smooth, brown, subcylindrical to clavate, straight to curved due to thickening of the wall on one side, not geniculate, one to multiple conidiogenous loci located laterally or apically, loci conspicuous, thickened and broad, areolate, darkened and refractive. *Conidia* solitary, smooth, light brown, thin-walled, fusiform to obclavate-fusiform, straight to somewhat curved, septate, not constricted at the septa, apex obtuse and base truncate, hilum flattened, thickened, darkened and refractive.

Type species: *Fusoidiella depressa* (Berk. & Broome) Videira & Crous.

Notes: The morphology of the type species is quite unique and different from the closest phylogenetic species, *Neopseudocercosporella capsellae*. *Fusoidiella depressa* forms a single lineage in the phylogenetic analysis (Fig. 1, clade II).

Fusoidiella depressa (Berk. & Broome) Videira & Crous, **comb. nov.** MycoBank MB817146. Fig. 5.
Basionym: *Cladosporium depressum* Berk. & Broome, Ann. Mag. Nat. Hist. 7: 99, t. 5: 8. 1851.
≡ *Passalora depressa* (Berk. & Broome) Sacc., Nuovo Giorn. Bot. Ital. 8(2): 187. 1876.
≡ *Fusicladium depressum* (Berk. & Broome) Roum., Fungi Sel. Gall. Exs.: No. 86. 1879.
≡ *Cercospora depressa* (Berk. & Broome) Vassiljevsky, Fungi imperfecti Parasitici. I. Hyphomycetes: 385. 1937.

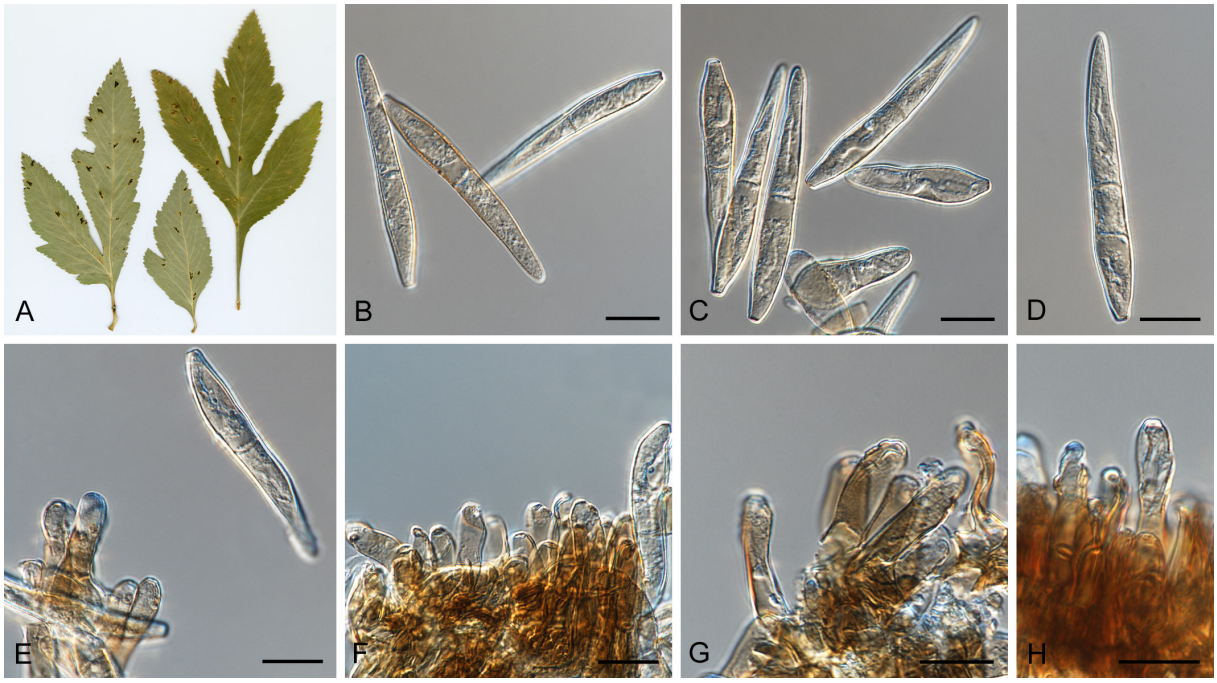


Fig. 5. *Fusoidiella depressa* (CBS 141335). A–H. Observations from herbarium material. A. Leaf spot symptoms on the host. B–D. Conidia. E. Conidia and conidiophores. F–H. Conidiophores. Scale bars = 10 µm.

≡ *Cercosporidium depressum* (Berk. & Broome) Deighton, Mycol. Pap. 112: 37. 1967.
For additional synonyms see Deighton (1967), Crous & Braun (2003) and MycoBank.

Specimen examined: **South Korea**, Bonghwa, on *Angelica gigas*, 18 Oct. 2007, H.D. Shin, KUS-F23064 = CBS H-22632, culture CBS 141335 = CPC 14915.

Notes: The specimen studied here (KUS-F23064) was initially identified as *Passalora depressa* and both the symptoms on the host and morphological characters (Fig. 5) are similar to those described from the authentic specimen (herb. K(M) 29181, on *Angelica sylvestris*, Great Britain; Deighton 1967). The conidiophores of the herbarium specimen observed are slightly smaller [(10.5–)20–23(–29) × (3–)4–5(–6) µm] than those described for the type [20–70(–120) × 4–8 µm]. Similarly, the observed conidia were also slightly smaller [(17.5–)32–38(–47) × (4.5–)5–6(–8) µm] than those described for the type [20–78 × 6.5–11 µm]. This species forms a single lineage in the phylogenetic analysis (Fig. 1, clade II). Fresh collections of *Passalora depressa* on *Angelica sylvestris* from the UK are required to facilitate an epitypification, and to fix the application of the name.

Clade III: *Filiella* Videira & Crous, **gen. nov.** MycoBank MB816823.

Etymology: Named after the filiform-shaped conidia of the type species.

Phytopathogenic. Mycelium internal, hyaline, septate, branched, forming well-developed stromata composed of swollen hyphae. *Conidiophores* emerging in dense fascicles, through the cuticle or through stomata, subcylindrical, straight to flexuous, geniculate-sinuous, aseptate, i.e. usually reduced to conidiogenous cells, rarely 1-septate near the base, hyaline to pale yellow

at the base, thin-walled, smooth, with inconspicuous conidiogenous loci, unthickened, neither darkened nor refractive. *Conidia* solitary, acicular, subcylindrical, filiform, narrowly obclavate, hyaline, discretely septate, thin-walled, smooth, apex subacute, base truncate, hila unthickened, not darkened (adapted from Braun 1993).

Type species: *Filiella pastinacae* (P. Karst.) Videira & Crous.

Notes: This monotypic genus (Fig. 1, Clade III) was established to accommodate *Pseudocercosporella pastinacae*, since it is not congeneric with *Pseudocercosporella s. str*. based on *P. bakeri* (Fig. 1, clade XIX). This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade III). It is closely related to *Neopseudocercosporella* and *Fusoidiella*, but can be distinguished by the acicular-filiform conidia instead of the subcylindrical conidia of *N. capsellae*, or pigmented, fusiform conidia of *F. depressa*.

Filiella pastinacae (P. Karst.) Videira & Crous, **comb. nov.** MycoBank MB817147.
Basionym: *Cercosporella pastinacae* P. Karst., Hedwigia 23: 63. 1884.
≡ *Ramularia pastinacae* (P. Karst.) Lindr. & Vestergr., Acta Soc. Fauna Fl. Fenn. 22(1): 8. 1902.
≡ *Pseudocercosporella pastinacae* (P. Karst.) U. Braun, Nova Hedwigia 56(3–4): 444. 1993.
= *Phyllosticta umbellatarum* Rabenh., Fungi Eur. Exs., Cent. XII: no. 1262. 1869.
= *Phloeospora laserpitii* Bres., Fungi trident. 2(8–10): 45. 1892.
= *Cylindrosporium septatum* Romell, Syll. Fung. 10: 503. 1892.
For additional synonyms see Braun (1995) and MycoBank.

Specimens examined: **Germany**, Dresden, on *Pastinaca sativa*, 1866, Rabenh., Fungi Eur. Exs. 1262 (neotype, designated in Braun 1995, HAL). **Sweden**, Uppland, Uppsala Näs, Vreta, on *Laserpitium latifolium*, 2 Jun. 1988, K. & L. Holm, culture CBS 114116.

Substrate and distribution: On *Angelica*, *Apium*, *Archangelica*, *Astrantia*, *Eremodaucus*, *Heracleum*, *Laserpitium*, *Libanotis*, *Pastinaca*, and other hosts (*Apiaceae*); Caucasus, Central Asia, Europe, N. America and S. Africa (see Braun 1995).

Notes: *Cercosporella pastinacae* was transferred to *Pseudocercosporella* by Braun (1993). It was originally described on *Pastinaca sativa* from Finland. The type material was not preserved and a neotype specimen on *Pastinaca sativa* from Germany was selected (Braun 1995; neotype in HAL). This species is known for causing cercosporoid leaf blight of parsnip that is characterised by the formation of yellow-brown spots on leaves and petioles that later become necrotic and lead to plant defoliation. *Filiella pastinacae* (= *P. pastinacae*) is often found in mixed infections with *R. heraclei* (= *R. pastinacae-sativa*) and they have been often confused. *Filiela pastinacae* also infects celery, and *Angelica* species and seeds contaminated with this pathogen must be discarded. The disease has been reported from Europe and Central Asia (Braun 1995) and is susceptible to various fungicides (Davis & Raid 2002). This species is represented by a single lineage in the phylogenetic analyses (Fig. 1, clade III).

Clade IV: ***Apseudocercosporella*** Videira & Crous, **gen. nov.** MycoBank MB816816.

Etymology: Named after the similarity with the genus *Pseudocercosporella*.

Phytopathogenic. *Mycelium* composed of hyaline, septate, branched, thin-walled, smooth hyphae. *Conidiophores* arising from hyphae, simple, and occasionally branched, straight and subcylindrical to flexuous, geniculate-sinuous, septate or aseptate, hyaline, thin-walled, smooth. *Conidiogenous cells* integrated, terminal or conidiophores often reduced to conidiogenous cells, subcylindrical to geniculate-sinuous, conidiogenous loci slightly thickened and darkened. *Conidia* formed singly, filiform, or subcylindrical, hyaline, thin-walled, smooth, septate or aseptate, base more or less truncate, hilum slightly thickened and darkened.

Type species: *Apseudocercosporella trigonotidis* Videira, H.D. Shin & Crous.

Notes: This monotypic genus (Fig. 1, Clade IV) was established to accommodate a pseudocercosporella-like species, since it is not congeneric with *Pseudocercosporella s. str*. based on *P. bakeri* (Fig. 1, clade XIX). This genus clade is highly supported in the phylogenetic analysis (Fig. 1, clade IV, 1/100/100). It is closely related to *Filiella* and *Neopseudocercosporella*, but can be distinguished by the conidial hila and conidiogenous loci that are slightly thickened and darkened instead of inconspicuous.

Apseudocercosporella trigonotidis Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816845. Fig. 6.

Etymology: Named after the host on which it was observed, *Trigonotis*.

Mycelium composed of hyaline, septate, branched, hyphae, 1–2 µm diam. *Conidiophores* arising from hyphae, simple, occasionally branched, straight and subcylindrical to flexuous, geniculate-sinuous, (5.5–)11–16(–32) × 1–1.5 µm, aseptate to 1(–2)-septate, hyaline, thin-walled, smooth. *Conidiogenous cells* integrated, terminal or conidiophores often reduced to conidiogenous cells, subcylindrical to geniculate-sinuous, (4–)6.5–8(–13) × 1–2 µm; conidiogenous loci slightly thickened and darkened, 1–2 µm diam. *Conidia* formed singly, filiform, or subcylindrical, (11–)19–22(–30) × 1 µm, hyaline, thin-walled, smooth, aseptate or 1–4-septate, apex obtuse, base more or less truncate, 1 µm diam, hilum slightly thickened and darkened.

Culture characteristics: On MEA, 32 mm diam, surface low convex, smooth, white with a greyish tinge, with margins undulate, colony reverse ochraceous; on OA, 20 mm diam, surface flat, white, sparse aerial mycelium in the colony centre, fluffy, with margins crenate, colony reverse buff; on PDA, 29 mm diam, surface low convex, white, sparse aerial mycelium in the colony centre, fluffy, with margins entire, colony reverse buff.

Specimen examined: **South Korea**, Jeju, on *Trigonotis peduncularis*, 12 Nov. 2003, H.D. Shin (holotype KUS-F20054, isotype CBS H-22515, culture ex-type CBS 131890 = CPC 10864); *idem*. CPC 10865.

Notes: *Apseudocercosporella* is the first cercosporoid species isolated from *Trigonotis*. It differs from the closest species in the phylogenetic tree (Fig. 1) by the slightly darkened conidiogenous loci and hila (Fig. 6). The clade is highly supported by BA and ML phylogenetic analysis (Fig. 1, clade IV, 1/100/100).

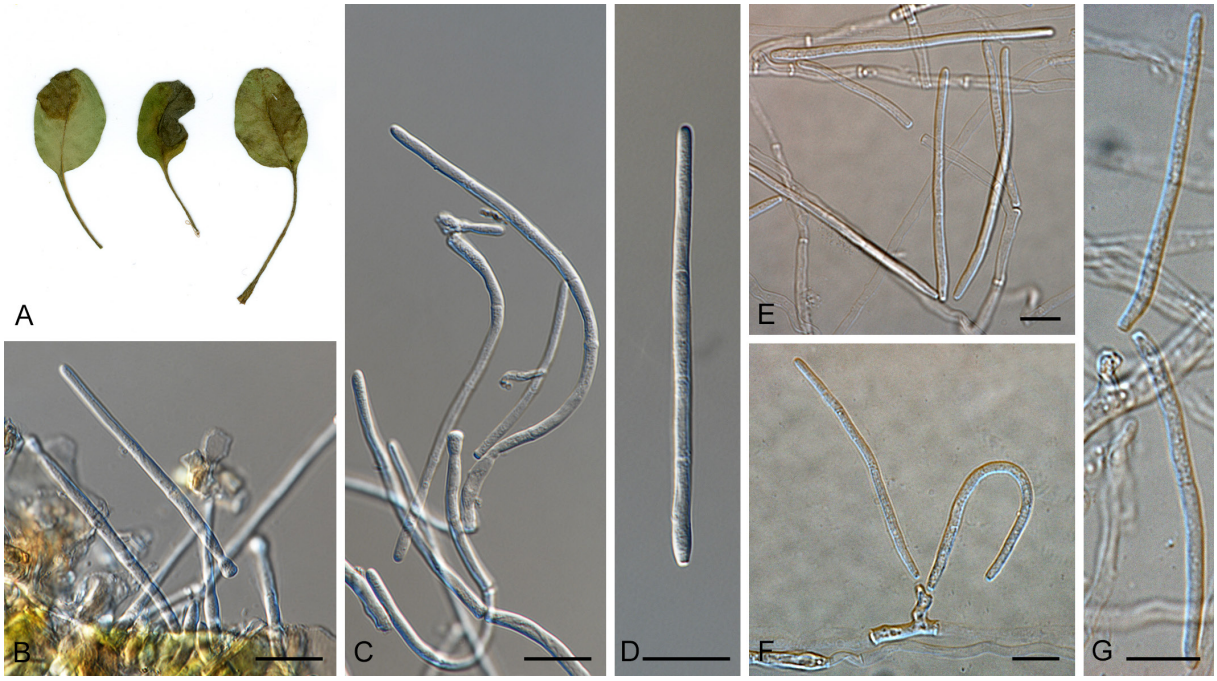


Fig. 6. *Apseudocercosporella trigonotidis* (CPC 10865). A–D. Observations from herbarium material. E–G. Structures formed in culture. A. Leaf spot symptoms on the host. B, C, E–G. Conidiophores, conidiogenous cells and conidia. D. Conidium. Scale bars = 10 µm.

Clade V: ***Neocercospora*** M. Bakhhshi *et al.*, Phytotaxa 213: 28. 2015.

Note: See Bakhshi *et al.* (2015a).

Clade VI: ***Cercospora*** Fresen. ex Fuckel, Fungi Rhen. Exs., Fasc. II: no. 117, 1863.

Note: See Groenewald *et al.* (2013), Bakhshi *et al.* (2015b) and Braun *et al.* (2015b).

Clade VII: ***Septoria*** Sacc., Syll. Fung. 3: 474. 1884.

Note: See Verkley *et al.* (2013) and Quaedvlieg *et al.* (2013).

Clade VIII: ***Sphaerulina*** Sacc., Michelia 1(4): 399. 1878.

Note: See Quaedvlieg *et al.* (2013).

Sphaerulina chaenomelis (Y. Suto) Videira, U. Braun, H.D. Shin & Crous, **comb. nov.** MycoBank MB817148.
Basionym: *Cercosporella chaenomelis* Y. Suto, Mycoscience 40: 513. 1999.
≡ *Pseudocercosporella chaenomelis* (Y. Suto) C. Nakash. *et al.*, Stud. Mycol. 75: 70. 2013.

Specimens examined: **Japan**, Mie Pref., Tsu, on leaves of *Chaenomeles sinensis*, 29 Oct. 2011, C. Nakashima (epitype TFM: FPH-8101, culture ex-epitype CBS 132131 = MUCC 1510). **South Korea**, Kimhae, on *Chaenomeles speciosa*, 14 Nov. 2007, H.D. Shin, CBS H-20844 = KUS-F23225, culture CBS 131897 = CPC 14795.

Notes: *Chaenomeles sinensis* is a deciduous tree native to China that is planted as ornamental in Japan. It is susceptible to a leaf spot disease commonly called frosty mildew caused by *Cercosporella chaenomelis* (Horie & Kobayashi 1982). Disease symptoms include large coalescing leaf spots, the development of white tufts of conidiophores on the lower surfaces, and tree defoliation. This species has been linked to the sexual morph *Mycosphaerella chaenomelis* (Suto 1999) that forms ascomata on fallen overwintered leaves providing inoculum for new infections. Crous *et al.* (2013a) considered that the fungus would be better placed in *Pseudocercosporella* due to the hyaline conidia with unthickened conidial hila and proposed a new combination in that genus. Based on DNA sequence data from the ITS and *actA* gene regions, strains from Japan and South Korea are identical (Crous *et al.* 2013a, unpubl. data). *Pseudocercosporella chaenomelis* is morphologically comparable only with *Pseudocercosporella gei*, known on *Geum* spp. in North America and the Far East of Russia (Braun 1995). In this study, based on LSU and *rpb2*, this species falls in the *Sphaerulina* clade (Fig. 1, clade VIII), and a new combination is therefore proposed. In the genus *Sphaerulina*, there is also *Sphaerulina gei*, on *Geum japonicum* from South Korea, and one could speculate that *Pseudocercosporella gei* may be a synonym of the latter, but no molecular data are presently available for this species, which could of course also be a different fungus.

Sphaerulina koreana (Crous *et al.*) Videira, H.D. Shin & Crous, **comb. nov.** MycoBank MB817149.
Basionym: *Pseudocercosporella koreana* Crous *et al.*, Stud. Mycol. 75: 71. 2013 (2012).
= *Sphaerulina viciae* Quaedvl. *et al.*, Stud. Mycol. 75: 348. 2013.

Specimen examined: **South Korea**, Hoengseong, on *Vicia amurensis*, 4 Aug. 2004, H.D. Shin (holotype CBS H-20845, isotypes HAL 1850 F, KUS-F20554, culture ex-type CBS 135462 = CPC 11414; CPC 11415).

Notes: This isolate was described as a new species in two different papers in the same journal volume (Studies in Mycology 75). The name *Pseudocercosporella koreana* (Crous *et al.* 2013a) was published online earlier than the name *Sphaerulina viciae* (Quaedvlieg *et al.* 2013). Therefore, the name *Pseudocercosporella koreana* is retained as basionym with *Sphaerulina viciae* as later synonym.

Clade IX: *Caryophylloseptoria* Verkley *et al.*, Stud. Mycol. 75: 233. 2013.

Note: See Verkley *et al.* (2013) and Quaedvlieg *et al.* (2013).

Clade X: *Cercosporella* Sacc., Michelia 2(6): 20. 1880.

Phytopathogenic, mostly causing leaf spots. *Hyphae* restricted to intercellular spaces and forming cup- or bowl-shaped appresoria, 7–17 µm diam that attach to walls of mesophyll cells. *Conidiophores* emerging through stomata or erumpent through the cuticle, straight, subcylindrical to geniculate-sinuous, hyaline, sometimes lightly pigmented near the base, more or less thin-walled and smooth. *Conidiogenous cells* integrated, terminal, polyblastic, sympodial, mostly conspicuously geniculate, conidiogenous loci conspicuous, hyaline but refractive, thickened and raised in the shape of a truncated cone (ultrastructure). *Conidia* formed singly, hyaline, subcylindrical to obclavate, sometimes fusiform, 1- to multi-septate, usually thin-walled and

smooth, apex obtuse, base often rounded to truncate or obconically truncate, hilum thickened, not darkened but refractive. Description adapted from Braun (1995) and Kirschner (2009).

Type species: *Cercosporella virgaureae* (Thüm.) Allesch. [= *Cercosporella cana* (Sacc.) Sacc. (designated by Deighton 1973)].

Notes: *Cercosporella* species are phytopathogenic and mostly cause leaf spots. The genus was first described by Saccardo (1880a) on *Solidago virgaurea*, Austria, and was later redescribed by Deighton (1973). Species with consistently internal mycelium *in vivo* are allocated to *Cercosporella* subgen. *Cercosporella* (type species *C. virgaureae*) and species with superficial mycelium *in vivo* to *Cercosporella* subgen. *Pseudovellosiella* (type species *C. crataevae*) (Braun 1995). Morphologically, *Cercosporella* differs from *Ramularia* by producing cup-shaped appressoria and by having flat conidial loci in the shape of a truncated cone (Kirschner 2009). Conidiogenous loci of *Ramularia* spp. have a raised rim with a central dome that is cladosporium-like and does not produce appressoria. A representative of the type species of the genus, *C. virgaureae*, was recently recollected but unfortunately not deposited in a culture collection (Kirschner 2009). A LSU sequence retrieved from the *Cercosporella* strain clustered in a sister clade to *Ramularia* (Kirschner 2009, this study). The LSU sequence of this isolate (GenBank EU710894) is 100 % identical to the LSU sequence of the South Korean isolates used in this study (Fig. 1, clade X). The recently described species *C. dolichandrae* belongs to *Cercosporella* as currently circumscribed (Crous *et al.* 2014a). A first report of the leaf spot disease caused by *Cercosporella pfaffiae* on Brazilian Ginseng was published, with the closest match on LSU data (GenBank JQ990330) being *Cercosporella virgaureae* (CBS 113304; GenBank GU214658) (Machado *et al.* 2012), but due to the lack of an *rpb2* sequence it was not included in the phylogeny created in this study. There are a total of 50 species described in the genus *Cercosporella* (Braun 1995, Seifert *et al.* 2011) but very few are available as cultures, and many are not congeneric with *Cercosporella s. str*. (e.g. Fig. 1, clades XII, XIV, XXX). A particularly important species cited in literature is *Cercosporella rubi* (G. Winter) Plakidas (≡ *Fusisporium rubi* G. Winter), the causal agent of the Blackberry rosette disease, a major disease of blackberries in the Southeastern USA. It infects the axillary buds and induces them to germinate as leafy bunches called rosettes. The disease causes reduced yield, poor quality fruit and in severe cases, cane death (Ellis & Converse 1991). Braun (1995) re-examined type material of this species and described and discussed this fungus under "Excluded, doubtful and insufficiently known species". Unfortunately no cultures of this species were available for study.

Cercosporella catenulata Videira & Crous, **sp. nov.** MycoBank MB816846. Fig. 7.

Etymology: Named after the unusual production of short conidial chains.

Mycelium composed of hyaline, septate, branched hyphae, 1–2 µm diam. *Conidiophores* arising from hyphae, simple or branched, straight and subcylindrical to flexuous or geniculate-sinuous, (8.5–)37–50(–77) × (1–)1.5–2 µm, 2–6-septate, hyaline, thin-walled, smooth. *Conidiogenous cells* integrated, terminal or lateral, subcylindrical to geniculate-sinuous, (4–)8.5–10.5(–15) × (1–)1.5(–2) µm, with a single to multiple conidiogenous loci, conspicuous, thickened but not darkened. *Conidia* hyaline, smooth, formed singly or in very short chains, aseptate but rarely 1-septate, with *hila* thickened but not darkened, 1 µm diam. *Ramoconidia* fusoid, (5–)9–11(–15)

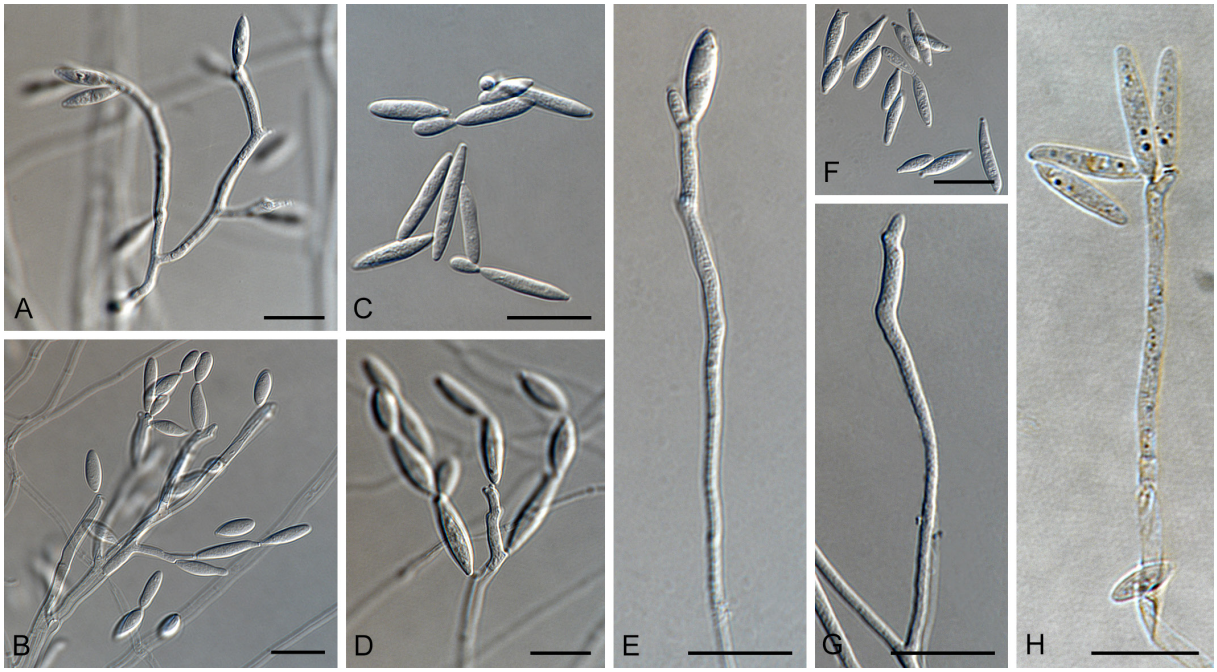


Fig. 7. *Cercosporella catenulata* (CBS 355.73). A–H. Structures observed in culture. A, B, D, E, H. Conidiophores, conidiogenous cells and conidia. C, F. Conidia. G. Conidiophore. Scale bars = 10 µm.

× 2–2.5(–3) µm, with two apical hila. *Intercalary conidia* fusoid, (7–)9.5–11(–14) × 2–2.5(–3) µm, in branched chains of up to two conidia. *Terminal conidia* fusoid to obovoid, (3.5–)6–7.5(–12) × 2–2.5(–3) µm.

Culture characteristics: On MEA, 5 mm diam, surface raised, erumpent aerial mycelium, buff, with margins undulate, colony reverse hazel; on OA, 5 mm diam, surface low convex, erumpent aerial mycelium, buff, with margins crenate, feathery, colony reverse hazel; on PDA, 11 mm diam, surface convex, erumpent aerial mycelium, rosy buff, with margins entire and with sparse mycelium, colony reverse honey in the centre and buff at the margin.

Specimen examined: **Rwanda**, Rubona, on leaves of *Phaseolus vulgaris*, 10 Jan. 1973, D. Froment (holotype CBS H-17715, culture ex-type CBS 355.73).

Substrate and distribution: Only known from the type host and location.

Notes: *Cercosporella catenulata* is an unusual member of the genus, since it produces catenate conidia (Fig. 7). This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade X).

Cercosporella virgaureae (Thüm.) Allesch., Hedwigia 34: 286. 1895. Fig. 8.
Basionym: *Ramularia virgaureae* Thüm., Fungi Austr. Exs., Cent. 11: no. 1072. 1874.
≡ *Ovularia virgaureae* (Thüm.) Sacc., Syll. Fung. 4: 142. 1886.
≡ *Cylindrosporium virgaureae* (Thüm.) J. Schröt., Krypt.-Fl. Schlesien 3–2(10): 489. 1897.
≡ *Cercospora virgaureae* (Thüm.) Oudem., Ned. Kruidk. Arch. 2: 315. 1901.
For additional synonyms see Braun (1995) or MycoBank.

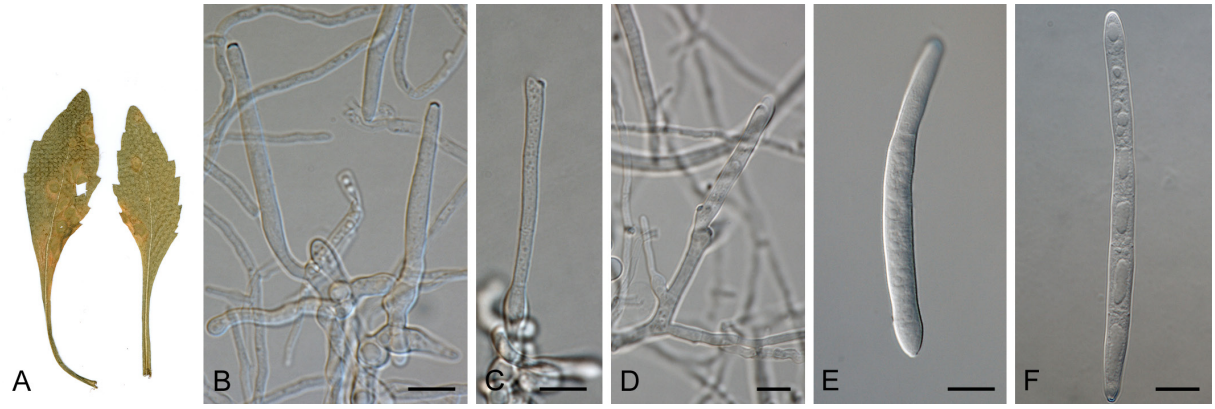


Fig. 8. *Cercosporella virgaureae* (CPC 11461). A. Leaf spot symptoms on the host in herbarium material. B–F. Structures observed in culture. B–D. Conidiophores and conidiogenous cells. E, F. Conidia. Scale bars = 10 µm.

Description in vivo: See Braun (1995).

Specimens examined: **Austria**, Krems, on *Solidago virgaurea*, 1871 [Thüm., Fungi Austr. Exs. 1072] (lectotype K). Brazil, Guimarania, Minas Gerais, on *Conyza canadensis*, unknown date, B.S. Vieira, culture CPC 19492. **South Korea**, Jinju, on *Erigeron annuus*, 1 Jul. 2004, H.D. Shin, cultures CPC 11456, CPC 11457, CPC 11460, CPC 11461; Namyangju, on *Erigeron annuus*, 9 Oct. 2002, H.D. Shin, cultures CPC 10286–10288; Chuncheon, on *Erigeron annuus*, 21 May 2003, H.D. Shin, culture CBS 113304.

Notes: *Cercosporella virgaureae* has a nearly circumglobal distribution and has been isolated from several hosts in the *Asteraceae* (Braun 1995), although it was originally described on *Solidago virgaurea*, Austria. Deighton (1973) reduced numerous *Cercosporella* species to synonymy with *C. virgaureae*. Kirschner (2009) collected representative strains of the type species of *Ramularia* (*R. pusilla*) and *Cercosporella* (*C. virgaureae*) and compared them based on LSU sequences, light microscopy and scanning electron microscopy, confirming them to represent two separate genera. The phylogenetic analysis in this study also supports the separation of *Cercosporella* (Fig. 1, clade X) from *Ramularia* (Fig. 1, clade XIV).

Clade XI: *Ramulariopsis* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 20(13): 421 [ser. 3, 13]. 1910. Fig. 9.

Phytopathogenic on vascular plants and usually forming leaf spots. *Mycelium* internal. *Conidiophores* fasciculate, arising through stomata or erumpent, hyaline, septate, thin-walled, smooth, simple or often branched. *Conidiogenous cells* integrated, terminal, intercalary as well as pleurogenous (as short nodulose protuberances or subcylindrical branchlets), polyblastic, sympodial, with thickened and darkened conidiogenous loci. *Conidia* catenate, in simple as well as branched chains, ellipsoid-ovoid, subcylindrical-fusiform, 0–1- to multi-euseptate, thin-walled, hyaline, with thickened and darkened hila; conidialsecession schizolytic. Description adapted from Braun (1998).

Type species: *Ramulariopsis cnidoscoli* Speg.

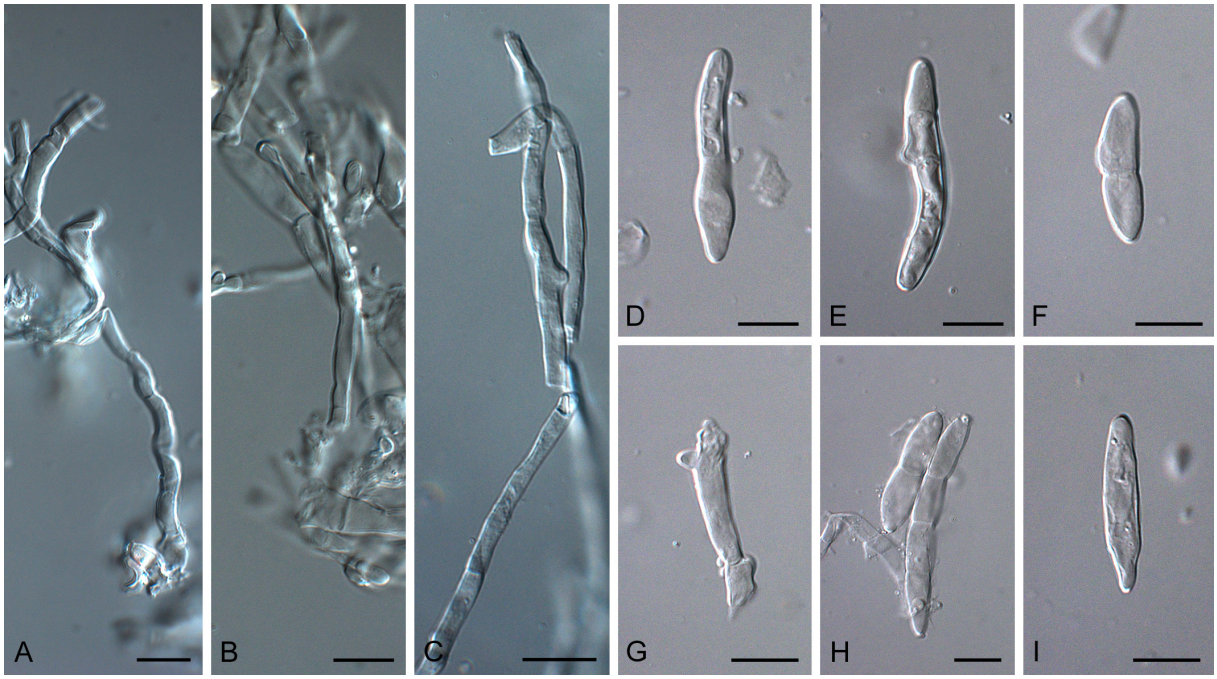


Fig. 9. *Ramulariopsis cnidoscoli* (LPS herbarium No12.850, type specimen). A–C. Conidiophores. D–F, H, I. Conidia. G. Conidiogenous cell. Scale bars = 10 µm.

Specimen examined: **Argentina**, Salta, Or'an, on *Cnidoscolus vitifolius* var. *cnicodendron* (= *C. cnicodendron*), Apr. 1905, C. Spegazzini (lectotype, designated by Deighton 1972, LPS 12.850) (Fig. 9).

Notes: *Ramulariopsis* species have frequently branched conidiophores with integrated, terminal, intercalary and pleurogenous conidiogenous cells with thickened and darkened conidiogenous loci. The conidia are catenate in simple or branched chains. *Ramularia* is very similar to the present genus, but differs in having simple conidiophores with consistently terminal conidiogenous cells. *Ramulariopsis* was described by Spegazzini (1910) and emended by Deighton (1972). The type species, *R. cnidoscoli*, was collected on *Cnidoscolus vitifolius* in Argentina, and is only known from herbarium material (Fig. 9). This genus currently accommodates four species (Seifert *et al.* 2011) that are phytopathogenic, and usually cause leaf spots (Braun 1998). The most widespread and economically important species is *R. gossypii*, known to be the causal agent of areolate mildew of cotton.

Ramulariopsis gossypii (Speg.) U. Braun, Nova Hedwigia 56: 432. 1993. Fig. 10.
Basionym: *Cercosporella gossypii* Speg., Anales Soc. Ci. Argent. 22(4): 208. 1886.
≡ *Ramularia gossypii* (Speg.) Cif., Quad. Lab. Crittog. Ist. Bot. Univ. Pavia 19: 124. 1962.
≡ *Septocylindrium gossypii* (Speg.) Subram., Hyphomycetes (New Delhi): 309. 1971.
= *Ramularia areola* G.F. Atk., Bot. Gaz. 15: 168. 1890.
= *Mycosphaerella areola* Ehrlich & F.A. Wolf, Phytopathology 22: 238. 1932.

Description in vivo: See Braun (1998: 314).

Mycelium composed of hyaline, septate, branched hyphae, 1–3 µm diam. *Conidiophores* hyaline, thin-walled, smooth, erect, subcylindrical to geniculate-sinuous, simple or sometimes

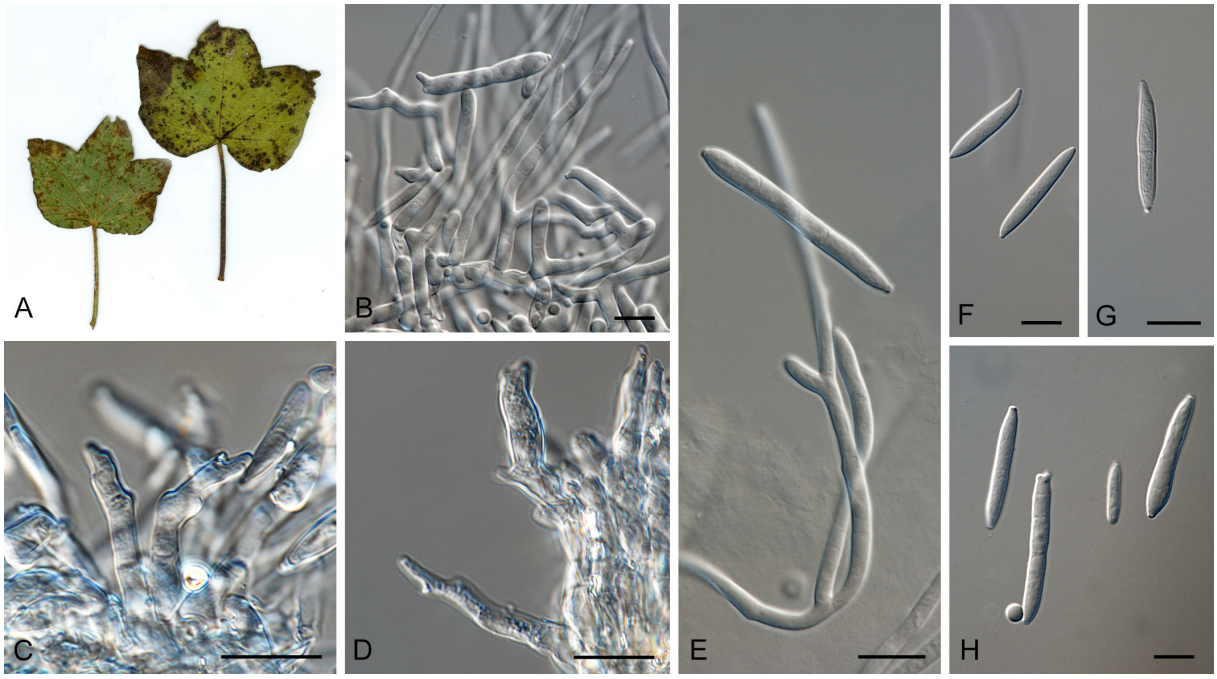


Fig. 10. *Ramulariopsis gossypii* (CBS 141099). A, C, D. Observations from herbarium material. B, E–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, E. Conidiophores and conidia. C, D. Conidiophores. F–H. Conidia. Scale bars = 10 µm.

branching from the base to the apex, septate, (18–)27–35(–46) × (1.5–)2–3 µm. *Conidiogenous cells* hyaline, smooth, integrated, terminal or pleurogenous, formed as short lateral branchlets, subcylindrical to geniculate-sinuous, (15–)17–19(–20) × (2–)2.5–3 µm, with conidiogenous loci slightly thickened and darkened. *Ramoconidia* hyaline, thin-walled, smooth, subcylindrical-fusiform, 0–3-septate, (12–)16–19(–23) × (1.5–)2–3(–4) µm. *Intercalary conidia* hyaline, smooth, fusiform, 0–3-septate, (7.5–)11.5–13(–17) × (1.5–)2–3 µm. *Terminal conidia* hyaline, smooth, catenate, 0–1-septate, fusiform, obovoid, (3–)9–11(–16) × (1–)2–3(–4) µm, hila slightly thickened and darkened.

Culture characteristics: On MEA, 8 mm diam, surface raised, lumpy, hairy, iron-grey and olivaceous grey, with margins crenate, convex, colony reverse iron-grey and olivaceous grey; on OA, 8 mm diam, surface irregular, patches with pale olivaceous grey erumpent mycelium and others naked and iron-grey, with margins undulate, with sparse mycelium and hazel, colony reverse olivaceous grey; on PDA, 8 mm diam, surface raised, lumpy, hairy in the centre with iron-grey and pale olivaceous grey patches, with margins crenate and convex, colony reverse olivaceous grey.

Specimens examined: **Brazil**, Paraguari, on *Gossypium* sp., May 1883, Balansa 3856 (lectotype, designated in Braun (1998), LPS). **Brazil**, on *Gossypium* sp., Oct. 2000, collector unknown (epitype designated here CBS H-22535, MBT204824, culture ex-epitype CBS 141099 = CPC 25909).

Notes: *Ramulariopsis gossypii* is the causal agent of a major disease of cotton known as cotton areolate mildew. In countries like Madagascar and India, yield losses due to the disease can

reach up to 60 % of the crop (Kirkpatrick & Rothrock 2001). In Brazil it was considered a minor disease but the expansion of the cultivated area on cotton and the introduction of susceptible varieties increased the disease incidence and yield losses now reach 30 % of crop production (Lima *et al.* 2010). *Ramulariopsis gossypii* was originally described on *Gossypium* sp. from Brazil (lectotype in LPS) but the species has a worldwide distribution wherever cotton is cultivated (Braun 1998). Therefore, strain CPC 25909, which is from the same host and country and conforms to the morphological description of this species (Fig. 10), is herewith designated as epitype. This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade XI).

Ramulariopsis pseudoglycines Videira, Crous & Braun, **sp. nov.** MycoBank MB816926. Fig. 11.

Etymology: Named after its morphological similarity to the species *Ramulariopsis glycines*.

Mycelium composed of hyaline, septate, branched, hyphae, 1.5–3 µm diam. *Conidiophores* hyaline, thin-walled, smooth, erect, subcylindrical to geniculate-sinuous, simple or sometimes branching from the base to the apex, septate, (67–)121–175(–226) × 2 µm. *Conidiogenous cells* hyaline, smooth, terminal or formed as short lateral branchlets, subcylindrical to geniculate-sinuous, sometimes integrated in the mycelium, pleurogenous, (14–)21–25(–33) × (1.5–)2(–3) µm, with conidiogenous loci slightly thickened and darkened. *Ramoconidia* hyaline, smooth, 0–3-septate, (9–)14–17(–21) × (2–)2.5–3 µm. *Intercalary conidia* hyaline, smooth, fusiform, 0–2-septate, (7–)12–15(–23) × (1.5–)2–3(–3.5) µm. *Terminal conidia* hyaline, smooth, catenate, aseptate, fusiform to obovoid, (4.5–)6.5–8(–12) × (2–)2.5–3 µm; hila slightly thickened and darkened.

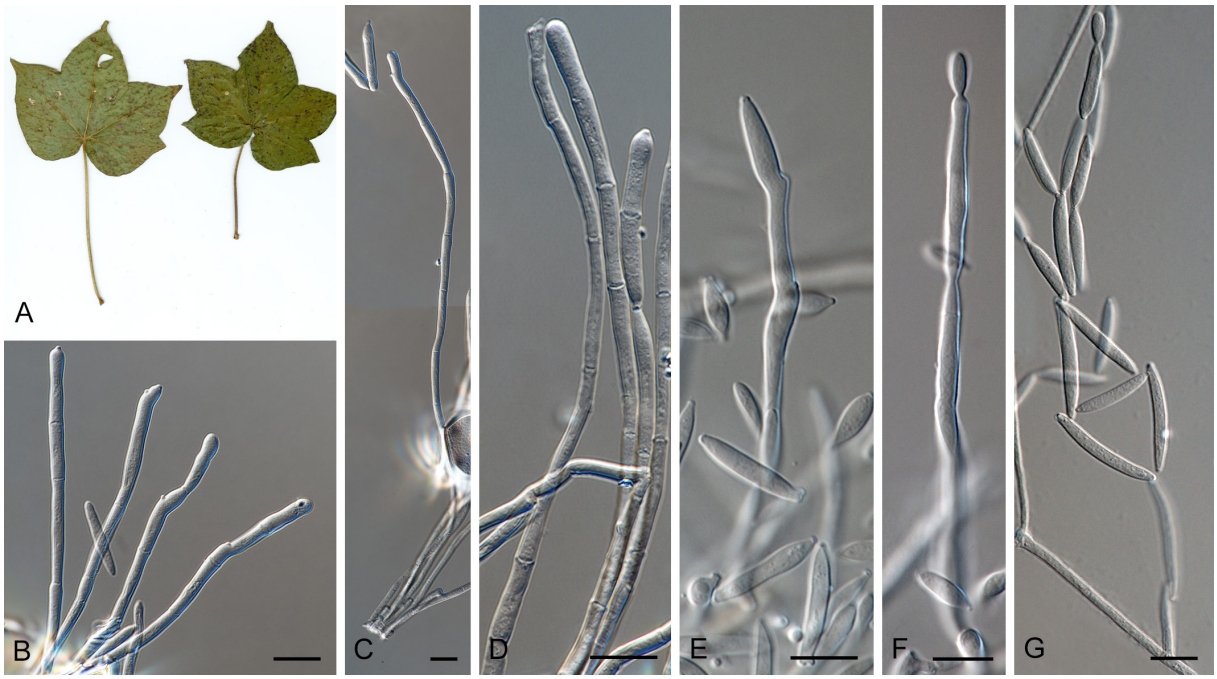


Fig. 11. *Ramulariopsis pseudoglycines* (CBS 141100). A–D. Observations from herbarium material. E–G. Structures formed in culture. A. Leaf spot symptoms on the host. B–G. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

Culture characteristics: On MEA, 10 mm diam, surface raised, lumpy, smooth, pale olivaceous grey with whitish areas, with margins undulate and fimbriate, colony reverse iron-grey; on OA, 10 mm diam, surface low convex, smooth, smoke grey in the centre and a pale olivaceous margin, with margins entire, colony reverse iron-grey; on PDA, 10 mm diam, surface low convex, lumpy, olivaceous grey with pale olivaceous grey patches, with margins undulate, colony reverse olivaceous grey.

Specimens examined: **Brazil**, on *Gossypium* sp., 2000, unknown collector (holotype CBS H-22546, culture ex-type CBS 141100 = CPC 18242); *idem*. CPC 18241. **Togo**, Kara region, on *Gossypium barbadense*, 31 Oct. 2011, M. Piatek, culture CPC 20036.

Notes: These strains were initially identified as *R. gossypii* but observations of the conidiogenous structures in culture and in the herbarium specimen revealed this species to have very long conidiophores, rather similar to *Ramulariopsis glycines* but much longer (Fig. 11). *Ramulariopsis glycines*, however, was originally described from *Glycine javanica*, Zambia, and has not been previously reported on *Gossypium* from Brazil (Braun 1998). This species clade is highly supported by the phylogenetic analysis (Fig. 1, clade XI, 1/100/100).

Clade XII: *Pseudocercospora* Speg., Anales Mus. Nac. Buenos Aires, Ser. 3, 20: 437. 1910.

Notes: *Pseudocercospora* was established by Spegazzini (1910) to accommodate species that produce pigmented conidiophores and conidia with neither thickened nor darkened conidiogenous loci and conidial hila (Braun 1995, Crous *et al.* 2013a). The genus was based on the type species *P. vitis*, a foliar pathogen of grapevines, but also includes species that are endophytes or saprobes. The generic circumscription of *Pseudocercospora* has been emended in recent years due to the publication of DNA sequence data of various gene regions (Crous *et al.* 2000, 2001b, 2013a). Based on these studies the genera *Cercostigmina*, *Phaeoisariopsis* and *Pseudophaeoramularia* have been reduced to synonymy under *Pseudocercospora* and the name *Pseudocercospora* was conserved over *Stigmina*, which represented an older generic name (Braun & Crous 2006).

Clade XIII: *Pallidocercospora* Crous, Stud. Mycol. 75: 73. 2013.

Note: See Crous *et al.* (2013a).

Clade XIV: *Ramularia* Unger, Exanth. Pflanzen (Wien): 169. 1833. emend. U. Braun (nom. cons.).
= *Didymaria* Corda, Icon. fung. (Prague) 5: 9. 1842.
≡ *Septocylindrium* Bonord. ex Sacc., Michelia 2: 15. 1880.
= *Acrotheca* Fuckel, Jahrb. Vereins Naturk. Herzogth. Nassau 15: 43. 1860.
= *Phacellium* Bonord., in Rabenh., Fungi Eur. Exs., Edn. 2, ser. 2: no. 288. 1860.
= *Ovularia* Sacc., Michelia 2: 17. 1880.
= *Ophiocladium* Cav., Z. Pflanzenkrankh. 3: 26. 1893.
= *Pseudovularia* Speg., Anales Mus. Nac. Buenos Aires, Ser. 3, 20: 418. 1910.
For additional synonyms see Braun (1998).

Mostly phytopathogenic (leaf spots, chlorosis or necrosis), sometimes saprobic or mycophilic.

Conidiophores individual or synnematous, sometimes forming small to sporodochial caespituli, emerging through stomata or through the cuticle, straight, subcylindrical to geniculate-sinuous, continuous or septate, hyaline or in some species with a faintly reddish tinge, occasionally branched, thin-walled, usually smooth but rarely rough. *Conidiogenous cells* integrated, terminal, polyblastic, sympodially elongating, straight to geniculate-sinuous, conidiogenous loci conspicuously thickened, darkened and refractive, coronate (cladosporoid). *Conidia* consistently solitary or in simple or branched chains, solitary conidia 0–1-septate, catenate conidia aseptate to multiseptate (mostly 1–4 eusepta), hyaline, in a few species with a faintly reddish tinge, usually ellipsoid-ovoid, cylindrical-fusiform, rarely filiform, occasionally constricted at the septa, thin-walled, smooth to verruculose-echinulate, hila distinct, slightly to conspicuously thickened, darkened, refractive; conidial secession schizolytic.

Type species: *Ramularia pusilla* Unger.

Notes: The genus *Ramularia* was described by Unger (1833) to include two species *R. pusilla* and *R. didyma*, of which *R. pusilla* on *Poa nemoralis*, Austria, was later designated as lectotype (Unger 1836). The confused taxonomic history of *Ramularia* has been addressed by several authors (Hughes 1949, Braun 1988, Sutton & Waller 1988), and the genus was monographed by Braun (1995, 1998). *Ramularia* species are usually described as hyphomycetes with hyaline conidiophores and conidia with distinct, thickened, darkened and refractive conidial loci and hila. Braun (1998) divided the genus *Ramularia* in two morphologically circumscribed subgenera, one with conidia consistently solitary (*Ramularia* subgen. *Ramularia*) and another with catenate conidia (*Ramularia* subgen. *Septocylindrium*, type species *R. septata*). Within *Ramularia* subgen. *Ramularia*, two sections were established, one with conidiogenous cells straight to geniculous-sinuous (Sect. *Ramularia*, type *Ramularia pusilla*) and one with conidiogenous cells strongly curved like a swan's neck (Sect. *Ophiocladium*, type species *R. collo-cygni*).

Ramularia species are phytopathogenic and mostly cause leaf spots but they can also be endophytic, saprobic and mycophilic. There are about 325 species accepted in this genus (Braun 1998, or MycoBank) of which only six have thus far been experimentally linked to a *Mycosphaerella* sexual morph (Videira *et al.* 2015b). Currently *Ramularia* is accepted as being a host-specific genus of phytopathogenic fungi (Braun 1998), although some exceptions are known (e.g. *R. vizellae*, Videira *et al.* 2015b).

Phacellium was described by Bonorden (1861) and currently includes 27 species (Braun 1998, Seifert *et al.* 2011 or MycoBank). The type species, *Ph. alborosellum* (Fig. 12) was described from *Cerastium holosteoides* in France and is characterised by forming synnematous conidiomata that can be hyaline or slightly pigmented. The *Phacellium* strains in this study cluster within *Ramularia* (Fig. 1, clade XIV; Fig. 2, clade 64, clade 82) and a new *Ramularia* species that forms synnemata is described (Fig. 2, clade 76). These results support the hypothesis that, as in *Pseudocercospora*, synnematous conidiophores is a feature that is unreliable at generic level. Therefore, the genus *Phacellium* is tentatively synonymised with *Ramularia* until the exact phylogenetic position of its type species becomes known.

Clade XV: *Xenoramularia* Videira, H.D. Shin & Crous, **gen. nov.** MycoBank MB816822.

Etymology: Named after its morphological similarity to the genus *Ramularia*, composed of xeno- (xenos, Greek for strange) and the latter genus name.

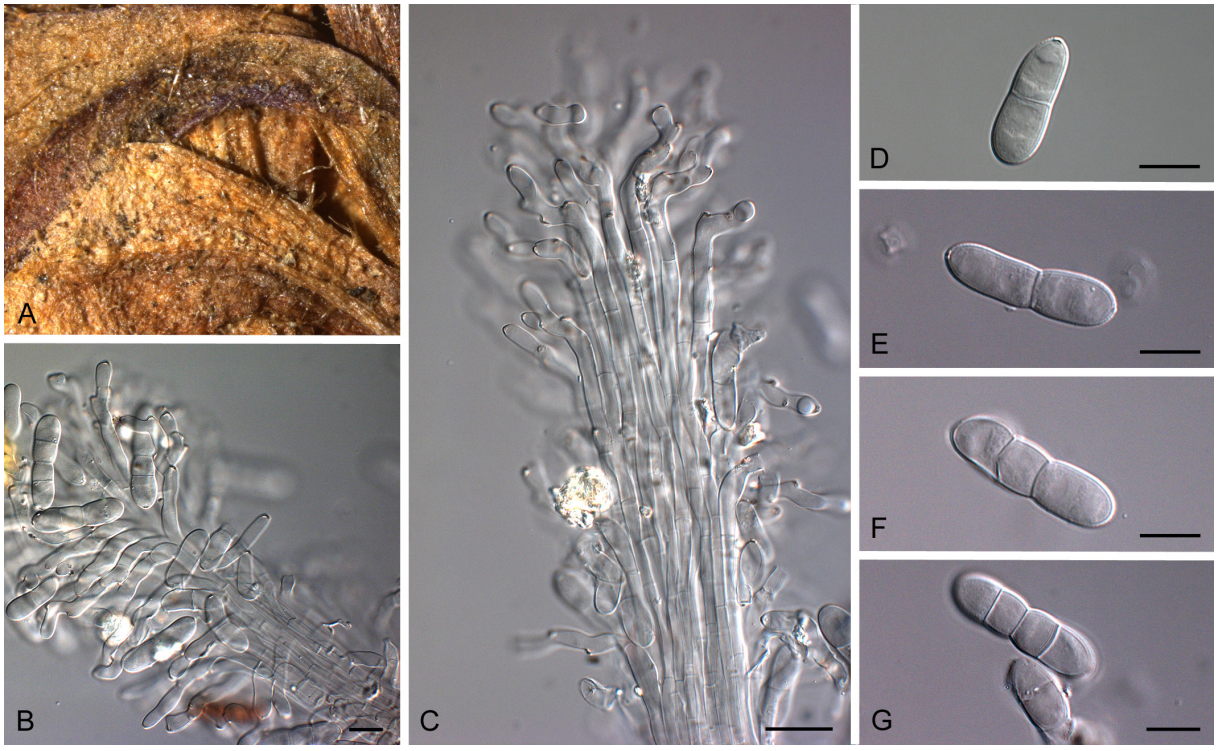


Fig. 12. *Phacellium alborosellum* (PC herbarium PC0084649, type specimen). A. Disease symptom on host leaf. B, C. Synnematous conidiophores, conidiogenous cells and conidia. D–G. Single and multiseptate conidia. Scale bars = 10 μm.

Phytopathogenic, causing leaf spots. *Mycelium* composed of hyaline, septate, branched hyphae. *Conidiophores* hyaline to pigmented, solitary, simple, straight or slightly curved, often reduced to conidiogenous cells, thin-walled, smooth. *Conidiogenous cells* hyaline, integrated in the mycelium or terminal in the conidiophores, subcylindrical to geniculate-sinuous, with one or multiple thickened but not darkened conidiogenous loci. *Conidia* hyaline, thin-walled, smooth, formed singly or catenate, aseptate or 1-septate, subcylindrical, apex obtuse to subacute, base truncate; hila thickened but not darkened.

Type species: *Xenoramularia polygonicola* Videira, H.D. Shin & Crous.

Notes: The genus *Xenoramularia* (Fig. 1, clade XV, 0.59/–/–) is very close to *Zymoseptoria* (Fig. 1, clade XVI, 0.92/–/–) and their individual support by the phylogeny is low but they are maintained apart due to morphological differences. Morphologically *Xenoramularia* is similar to *Ramularia* but can be distinguished by the following set of characters: it tends to have reduced conidiophores that are mostly solitary (always solitary in culture, rarely with weakly developed fascicles on host tissue), hyaline, but at times somewhat pigmented, and conidial hila and conidiogenous loci that are thickened, but not darkened and refractive as in *Ramularia*.

Xenoramularia arxii Videira & Crous, **sp. nov.** MycoBank MB816927. Fig. 13.

Etymology: Named after Josef Adolf von Arx, who collected this species.

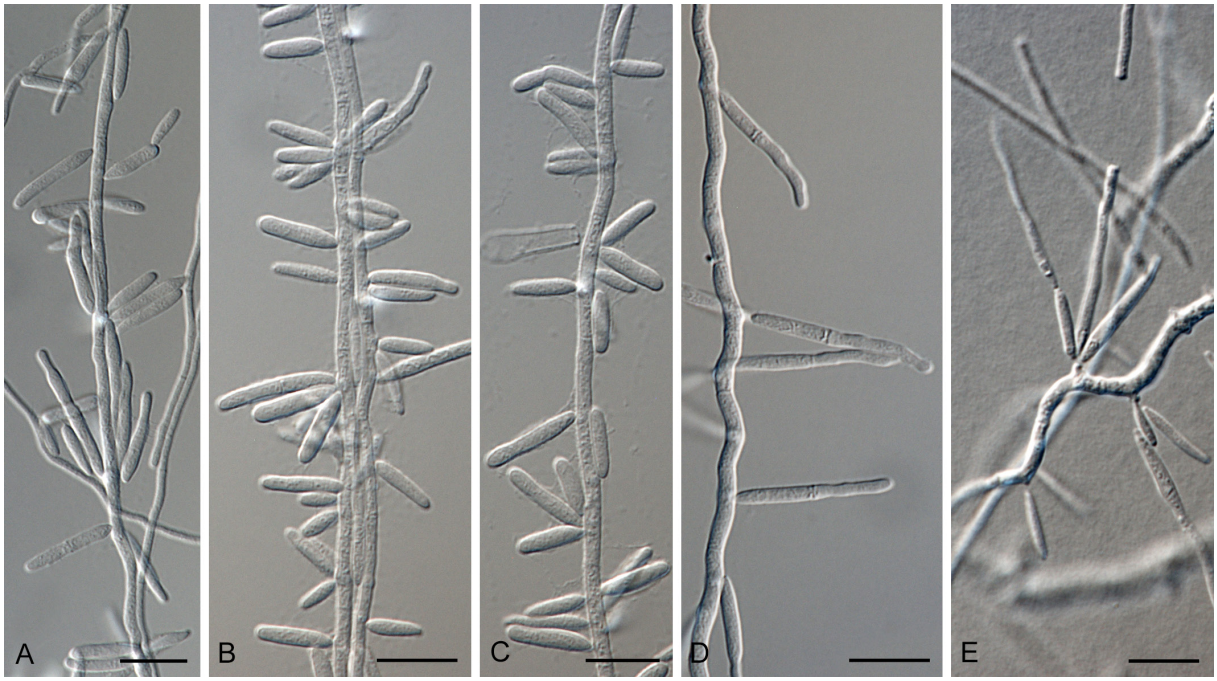


Fig. 13. *Xenoramularia arxii* (CBS 342.49). A–E. Conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

Mycelium consisting of hyaline, septate, branched hyphae, 1–3 µm diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium, hyaline, thin-walled, smooth, subcylindrical, (4–)8–10(–14) × 1.5–2 µm, with single or multiple conidiogenous loci that are thickened but not darkened. *Conidia* formed singly, aseptate or 1-septate, hyaline, thin-walled, smooth, subcylindrical, with a rounded apex and an acute base, (5–)9–12(–21) × (1.5–)2(–3) µm; hila thickened but not darkened.

Culture characteristics: On MEA, 47 mm diam, surface raised, smooth mycelium, white with buff tinge with margins entire and feathery, colony reverse iron grey in the centre and ochreous towards the margin; on OA, 45 mm diam, surface flat, feathery white mycelium in the centre becoming sparse and hazel towards the margin, margin undulate, almost naked, colony reverse hazel; on PDA, 50 mm diam, surface low convex, centre white turning pale olivaceous grey and erumpent towards the margin, with margin olivaceous grey and sparse mycelium, colony reverse olivaceous black in the centre and olivaceous towards the buff margin.

Specimen examined: **Netherlands**, Utrecht Prov., Baarn, Eemufer, on leaf spot of *Acorus calamus*, 5 Sep. 1949, J.A. von Arx (holotype CBS H-4925, culture ex-type CBS 342.49).

Notes: *Xenoramularia arxii* (Fig. 13) forms a basal single lineage to other taxa in the genus (Fig. 1, clade XV), but is retained in *Xenoramularia* as it is morphologically similar. For a morphological comparison see notes under *X. polygonicola*.

Xenoramularia neerlandica Videira & Crous, **sp. nov.** MycoBank MB816928. Fig. 14.

Etymology: Named after the country from where it was collected, the Netherlands.

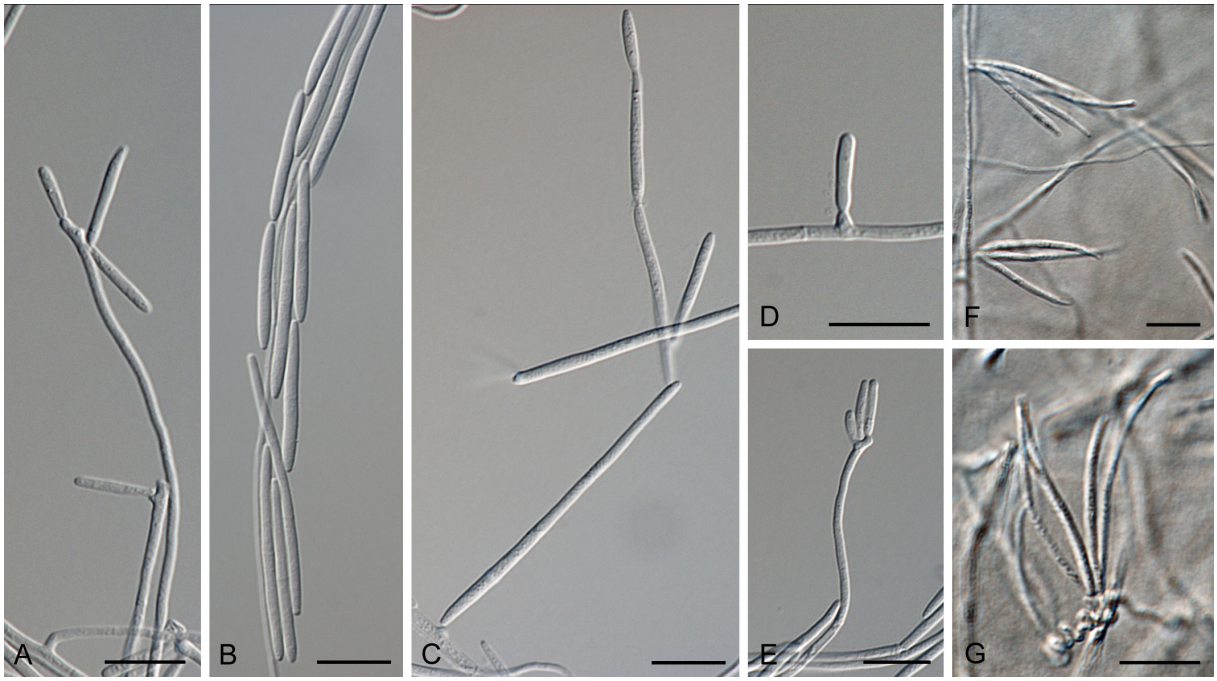


Fig. 14. *Xenoramularia neerlandica* (CBS 113615). A–G. Structures formed in culture. A, C–G. Conidiogenous cells and conidia. B. Conidia. Scale bars = 10 µm.

Mycelium consisting of hyaline, septate, branched, hyphae, 0.5–1 µm diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium, hyaline, thin-walled, smooth, subcylindrical, (8–)11–13.5(–16) × (1–)1.5(–2) µm, with single or multiple conidiogenous loci that are thickened but not darkened. *Conidia* formed singly or catenate and ramoconidia scarce. *Ramoconidia* hyaline, thin-walled, smooth, aseptate or 1-septate, subcylindrical to fusiform, (9–)13.5–18(–23) × (0.5–)1(–1.5) µm. *Intercalary conidia* hyaline, smooth, aseptate or 1-septate, subcylindrical to fusiform, (7–)10–12(–19) × (0.5–)1 µm. *Terminal conidia* hyaline, smooth, aseptate or 1-septate, subcylindrical to fusiform, (3–)11–17(–32) × (0.5–)1(–2) µm; hila thickened but not darkened.

Culture characteristics: On MEA, 20 mm diam, surface raised, smooth, white with pale grey and olivaceous grey tinge, margins undulate, colony reverse olivaceous grey; on OA, 22 mm diam, surface with fluffy mycelium pale grey and olivaceous grey, margins undulate and with sparse aerial mycelium, reverse iron-grey; on PDA, 18 mm diam, surface flat, smooth aerial mycelium, centre white turning pale olivaceous grey towards the margin, margin undulate with sparse mycelium, reverse olivaceous grey.

Specimens examined: **Netherlands**, Utrecht Prov., Breukelen, on *Sparganium ramosum*, Sep. 2003, W. Gams, culture CBS 113615; Utrecht, De Uithof, on *Iris pseudacorus*, 26 Jun. 2006, P.W. Crous (holotype CBS H-22540, culture ex-type CBS 141101 = CPC 18377); *idem*. CPC 18378.

Notes: *Xenoramularia neerlandica* (Fig. 14) is highly supported in the phylogenetic analysis (Fig. 1, clade XV, 1/100/100). For morphological comparison with the other species in this genus see notes under *X. polygonicola*.

Xenoramularia polygonicola Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB 816929. Fig. 15.

Etymology: Named after the host genus from which it was described, *Polygonum*.

Mycelium consisting of hyaline, septate, branched, hyphae, 0.5–1 µm diam. *Conidiophores* hyaline, thin-walled, smooth, solitary, simple, sometimes branched, straight to slightly curved, sometimes reduced to conidiogenous cells, (13.5–)23–29(–42) × (0.5–)1 µm. *Conidiogenous cells* integrated in the mycelium, lateral or terminal in the conidiophores, subcylindrical to geniculate-sinuous, (6.5–)9–11(–17) × (0.5–)1 µm, with conidiogenous loci thickened but not darkened. *Conidia* formed singly or catenate, but no ramoconidia were observed. *Intercalary conidia* hyaline, smooth, subcylindrical, aseptate or 1-septate, (6–)8.5–11(–16) × (0.5–)1 µm. *Terminal conidia* hyaline, smooth, formed singly or catenate, aseptate or 1-septate, subcylindrical, apex obtuse to subacute, base truncate, (4–)6.5–8(–11) × (0.5–)1 µm; hila thickened but not darkened.

Culture characteristics: On MEA, 8 mm diam, surface raised, lumpy, smooth mycelium, pale olivaceous grey, with margins undulate, buff, convex, colony reverse iron grey; on OA, 8 mm diam, surface flat, smooth mycelium, pale olivaceous grey, with margins entire, with sparse aerial mycelium, colony reverse olivaceous grey; on PDA, 10 mm diam, surface low convex, smooth, grey olivaceous, radially striated and cutting into the agar, with margins undulate, convex and buff, colony reverse olivaceous grey.

Specimens examined: **South Korea**, Pyeongchang, on *Polygonum* sp., 20 Sep. 2003, H.D. Shin (holotype KUS-F19688, isotype CBS H-22541, culture ex-type CBS 141102 = CPC 10852); *idem*. CPC 10853, CPC 10854.

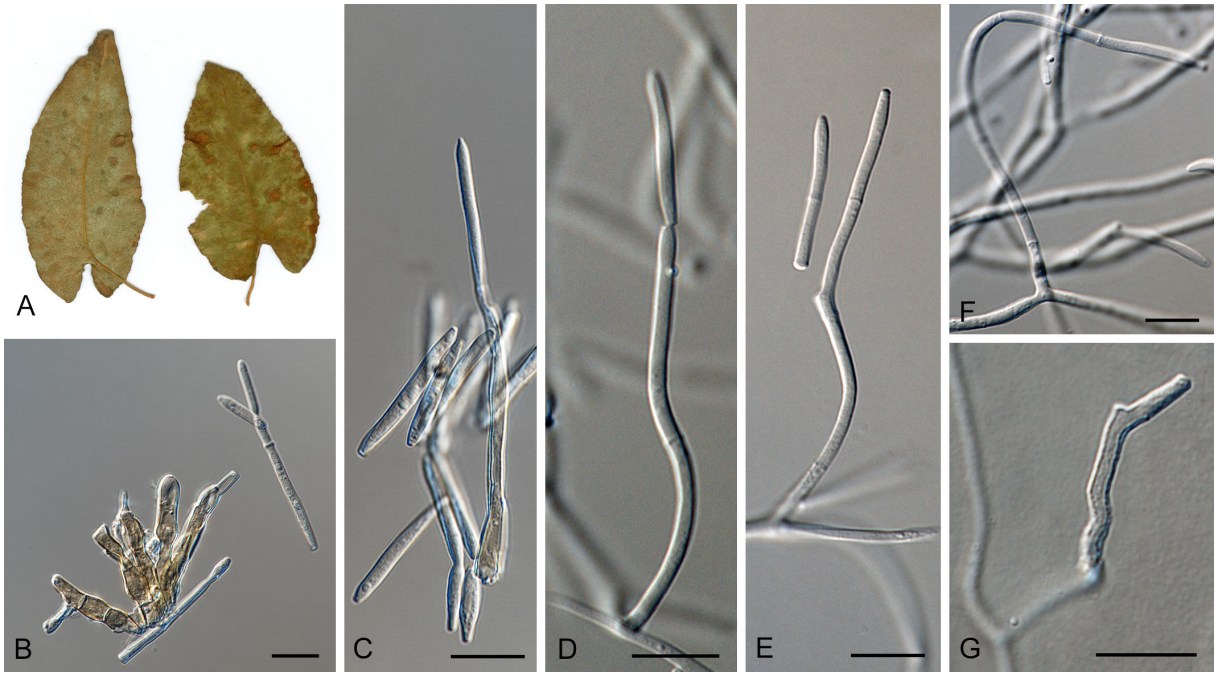


Fig. 15. *Xenoramularia polygonicola* (CBS 141102). A–C. Observations from herbarium material. D–G. Structures formed in culture. A. Leaf spot symptoms on host. B–F. Conidiophores, conidiogenous cells and conidia. G. Conidiophore. Scale bars = 10 µm.

Notes: The species *X. polygonicola* is highly supported in the phylogenetic analysis (Fig. 1, clade XV, 1/100/100). *Xenoramularia polygonicola* (Fig. 15) forms conidiophores while *X. arxii* (Fig. 13) and *X. neerlandica* (Fig. 14) have conidiophores reduced to conidiogenous cells. *Xenoramularia polygonicola* and *X. arxii* do not produce ramoconidia and in *X. neerlandica* they were rarely observed. *Xenoramularia polygonicola* and *X. neerlandica* produce both single and catenate conidia while *X. arxii* produces only single, wider conidia.

Clade XVI: *Zymoseptoria* Quaedvl. & Crous, Persoonia 26: 64. 2011.

Note: See Quaedvlieg *et al.* (2011) and Stukenbrock *et al.* (2012).

Clade XVII: *Dothistroma* Hulbary, Bull. Illinois Nat. Hist. Surv. 21: 235. 1941.

Note: See Barnes *et al.* (2004).

Clade XVIII: *Stromatoseptoria* Quaedvl., Verkley & Crous, Stud. Mycol. 75: 353. 2013.

Note: See Quaedvlieg *et al.* (2013).

Clade XIX: *Pseudocercosporella* Deighton, Mycol. Pap. 133: 38. 1973.

Colonies in vivo. *Mycelium* consisting of hyaline to pale brown, septate and smooth hyphae. *Conidiophores* solitary to fasciculate, emerging through stomata or through the cuticle, arising from inner hyphae or from stromata, sometimes arising from superficial hyphae or forming subglobose sporodochia, aseptate or septate, straight and subcylindrical to geniculate-sinuous, rarely branched, mostly hyaline but occasionally faintly pigmented, thin-walled, mostly more or less smooth. *Conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, mono- to polyblastic, sympodial; conidiogenous loci inconspicuous, unthickened and hyaline. *Conidia* formed singly, subcylindrical, filiform to obclavate, 1- multi-euseptate, hyaline, thin-walled, mostly smooth, apex obtuse to subacute, base subtruncate, hilum unthickened, not darkened nor refractive. Adapted from Frank *et al.* (2010).

Type species: *Pseudocercosporella bakeri* (Syd. & P. Syd.) Deighton (= *Pseudocercosporella ipomoeae* Deighton).

Notes: *Pseudocercosporella* was described by Deighton (1973), and is characterised by solitary conidia, rarely in chains, with unthickened, inconspicuous conidial loci (Braun 1995). Braun (1990) confined *Pseudocercosporella* to species with solitary conidia and the species with catenate conidia were transferred to *Thedgonia*. However, the conidial ontogeny in *Thedgonia* is thallic (i.e. conidia form in disarticulating chains) while the species in question had polyblastic conidiogenesis and conidia in acropetal chains (Crous *et al.* 2009a). Braun (1995) placed these species back in *Pseudocercosporella* under a different subgenus: *Pseudocercosporella* subgen. *Pseudocercocatenella* (type: *Pseudocercosporella dioscoriae*). Braun (1995) also established another subgenus based on morphology to include species with superficial secondary mycelium and solitary conidiophores: *Pseudocercosporella* subgen. *Cercovellosiella* (type: *Pseudocercosporella crataegi*). The type species *Pseudocercosporella bakeri* (= *P. ipomoea*) has recently been epitypified (on *Ipomoeae* sp., Philippines, ex-epitype

culture CBS 125685; Frank *et al.* 2010) and forms a single species clade (Fig. 1, clade XIX) that clusters close to *Dothistroma* (Fig. 1, clade XVII) and *Stromatoseptoria* (Fig. 1, clade XVIII). The pseudocercosporella-like morphology is polyphyletic (see Frank *et al.* 2010, Crous *et al.* 2011c, 2012a), and new taxonomically useful morphological features will need to be found to delineate all the genera presently accommodated in other clades.

Clade XX: *Microcyclosporella* J. Frank *et al.*, Persoonia 24: 101. 2010.

Mycelium consisting of pale brown, smooth to finely verruculose, branched, septate hyphae, sometimes covered in a mucoid layer. *Conidiophores* mostly reduced to conidiogenous cells. *Conidiogenous cells* integrated in hyphae, cylindrical to doliiform, pale brown to hyaline if occurring in yeast-like sectors of colonies, thin-walled, smooth, mono- or polyblastic, proliferating sympodially; conidiogenous loci lateral, inconspicuous, truncate, unthickened, not darkened. *Conidia* hyaline, thin-walled, smooth, subcylindrical to narrowly obclavate or narrowly fusoid with acutely rounded apex and obconically truncate base, guttulate, 0–6 transversely septate; microcyclic conidiation common. Adapted from Frank *et al.* (2010).

Type species: *Microcyclosporella mali* J. Frank, Schroers & Crous.

Specimens examined: **Slovenia**, Senozeti, Dolsko, on fruit surface *Malus domestica*, 7 Aug. 2007, J. Frank (holotype CBS H-20413, culture ex-type 300-07 = CBS 126136 = CPC 16184). **USA**, Georgia, Ellijay, on *Malus* sp., 29 Aug. 2005, M. Wheeler, culture CBS 125654; Illinois, Chester, on unknown host, Sep. 2000, J. Batzer, culture CBS 119461; Illinois Rockford, Illinois, on unknown host, Sep. 2000, J. Batzer, culture CBS 118960; Michigan, Fennville, on *Malus* sp., 1 Sep. 2005, G. Sundin, culture CBS 125653; Missouri, New Franklin, on unknown host, Sep. 2000, J. Batzer, culture CBS 118969; Ohio, Wooster on *Malus* sp., 5 Sep. 2005, M. Ellis, culture CBS 125651.

Notes: *Microcyclosporella* was described by Frank *et al.* (2010) to accommodate species with hyaline conidiophores and long scolecosporous conidia with inconspicuous conidiogenous loci and unthickened, non-pigmented hila, resembling *Pseudocercosporella*, but also displaying microcyclic conidiation. More work needs to be done in this genus since the variation observed in the phylogeny (Fig. 1, clade XX) indicates that more than one species may be present.

Clade XXI: *Mycosphaerelloides* Videira & Crous, gen. nov. MycoBank MB816819.

Etymology: Named after the morphological similarity to the genus *Mycosphaerella*.

Ascomata pseudothecial, single, black, immersed, becoming erumpent, globose, apical ostiole, wall with medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid to narrowly ellipsoid. *Ascospores*, straight to fusoid-ellipsoid, hyaline, guttulate, thin-walled, with sub-obtuse ends, medianly 1-septate, widest in the middle of the apical cell. *Ascospore germination* from both ends, with germ tubes parallel to the long axis of the spore. *Mycelium* consisting of smooth, branched, septate, pale to medium brown hyphae.

Conidiomata fasciculate, medium brown. *Conidiophores* arising from mycelium or from the upper cells of a brown stroma, pale to medium brown, smooth, unbranched or branched, sub-

cylindrical, straight to variously curved. *Conidiogenous cells* terminal or lateral, solitary, pale brown, smooth, proliferating sympodially or percurrently; conidiogenous loci inconspicuous. *Conidia* smooth, subcylindrical, multiseptate; hila neither thickened nor darkened-refractive. Adapted from Crous *et al.* (2004b).

Type species: *Mycosphaerelloides madeirae* (Crous & Denman) Videira & Crous.

Notes: The strains in this genus represent a mycosphaerella-like species lacking a ramularia-like asexual morph, and also not being congeneric with *Ramularia* based on *R. pusilla* (Fig. 1, clade XIV). This monotypic genus is highly supported by the phylogenetic analysis (Fig. 1, clade XXI, 1/100/100).

Mycosphaerelloides madeirae (Crous & Denman) Videira & Crous, **comb. nov.** MycoBank MB817150.
Basionym: *Mycosphaerella madeirae* Crous & Denman, Stud. Mycol. 50: 204. 2004.

Specimens examined: **Portugal**, Madeira, Party Farm, on leaves of *Eucalyptus globulus*, Apr. 2000, S. Denman (holotype CBS H-9898, culture ex-type CBS 112895 = CPC 3745); *idem*. CBS 112301 = CPC 3747. **Netherlands**, Utrecht, Soest, endophytic on green leaves of *Quercus robur*, 2002, G. Verkley, cultures CBS 115936, CBS 116068, CBS 116066.

Notes: *Mycosphaerelloides madeirae* was isolated from *Eucalyptus globulus* collected in Madeira (Portugal), and is very similar to *M. heimioides* (Crous 1998), but can be distinguished by its ascospore germination pattern as well as its cultural characteristics.

Clade XXII: *Epicoleosporium* Videira & Crous, **gen. nov.** MycoBank MB816817.

Etymology: Named after the host its type species was isolated from, *Coleosporium*.

Colonies growing on uredinia of *Coleosporium*, mycophilic. *Mycelium* superficial, consisting of hyaline, septate, thin-walled, smooth hyphae. *Conidiophores* hyaline, loose, straight, subcylindrical, unbranched, septate, thin-walled, smooth. *Conidiogenous cells* hyaline, terminal in the conidiophore, cylindrical-oblong, proliferation sympodial, with conspicuous conidiogenous loci, thickened, darkened and refractive. *Conidia* hyaline, smooth, solitary or in short chains, cylindrical-oblong, clavate, obovate, aseptate, thin-walled, smooth, with hila thickened, darkened and refractive.

Type species: Epicoleosporium ramularioides Videira, H.D. Shin & Crous.

Notes: This monotypic genus is highly supported by the phylogenetic analysis (Fig. 1, clade XXII, 1/100/100) and represents a mycophilic species that is ramularia-like in its morphology but is not congeneric with *Ramularia* based on *R. pusilla* (Fig. 1, clade XIV).

Epicoleosporium ramularioides Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816847. Fig. 16.

Etymology: Named after its morphological similarity with the genus *Ramularia.*

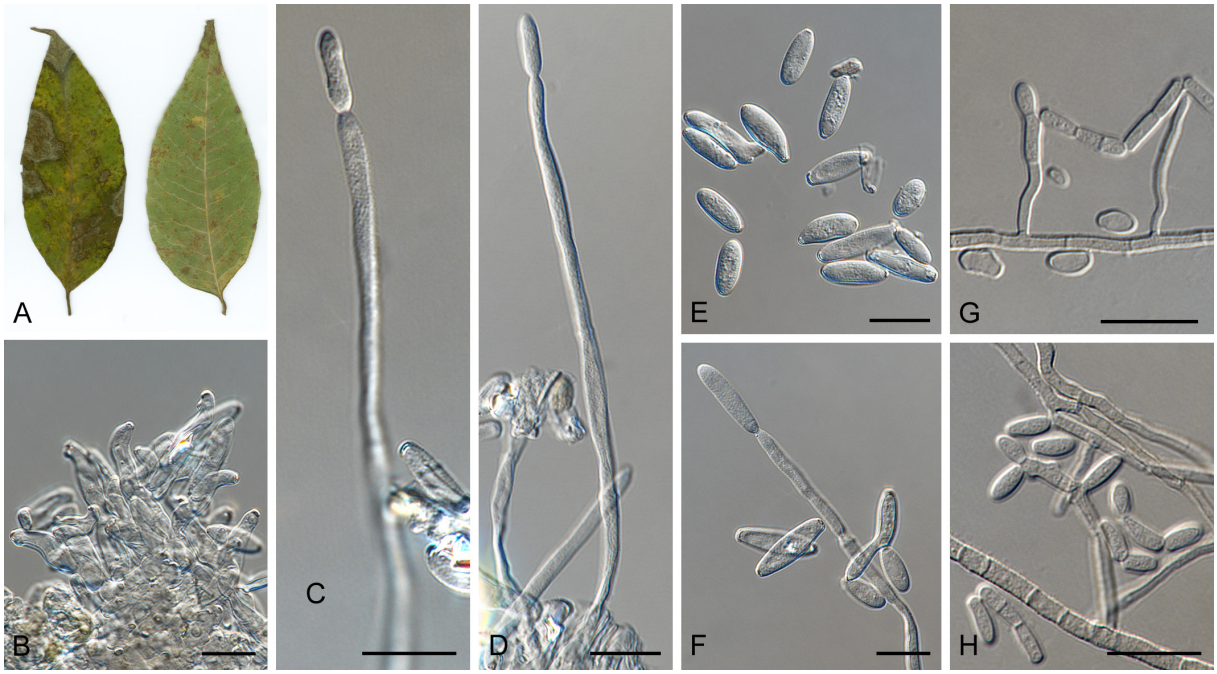


Fig. 16. *Epicoleosporium ramularioides* (CBS 141103). A–F. Observations from herbarium material. G, H. Structures formed in culture. A. Leaf spot symptoms on host. B. Conidiophores. C, D, F–H. Conidiophore and conidia. E. Conidia. Scale bars = 10 µm.

Colonies on uredinia of *Coleosporium*, mycophilic, whitish. *Mycelium* superficial, consisting of hyaline, septate, thin-walled, smooth hyphae, 1.5–2 µm diam. *Conidiophores* hyaline, loose, erect, straight, subcylindrical, unbranched, (37–)65–83(–129) × 2–3 µm, septate, thin-walled, smooth. *Conidiogenous cells* hyaline, integrated, terminal on the conidiophore, cylindrical-oblong, (9–)11–13(–15) × 1.5–2(–2.5) µm, conidiogenous loci thickened, darkened and refractive, 1 µm diam. *Conidia* hyaline, thin-walled, smooth, solitary or in short chains, cylindrical-oblong, clavate, obovate, aseptate, (6–)10–13(–21) × (2.5–)3–4(–5) µm, apex obtuse, base obtuse to slightly elongated, with hila thickened, darkened and refractive, 1 µm diam.

Specimens examined: **South Korea**, Pyeongchang, on *Coleosporium phellodendri* on leaves of *Phellodendron amurense*, 4 Sep. 2003, H.D. Shin (holotype KUS-F19603, isotype CBS H-22542, culture ex-type CBS 141103 = CPC 10672); *idem*. CPC 10673.

Notes: *Epicoleosporium ramularioides* is morphologically ramularia-like (Fig. 16) and represents another addition to the list of known mycophilic cercosporoid species. It differs from *R. coleosporii* that produces conidiophores occasionally branched, longer and wider [(20–)30–200(–270) × 3–6 µm]. In addition, the conidia of *R. coleospori* are catenate, ellipsoid-ovoid, smooth to rough, longer and wider [8–35(–45) × 3–8 µm] and 0–1(–3)-septate (Braun 1998). The development of the conidial structures of *E. ramularioides* in culture is unusual (Fig. 16).

Clade XXIII: *Uwebraunia* Crous & M.J. Wingf., Mycologia 88: 446. 1996.

Note: See Crous and Wingfield (1996) and Li *et al.* (2012).

Clade XXIV: *Dissoconium* de Hoog *et al.*, Proc. Kon. Ned. Akad. Wetensch. C 86(2): 198. 1983.

Note: See Crous *et al.* (1999), Jackson *et al.* (2004) and Li *et al.* (2012).

Clade XXV: *Ramichloridium* Stahel ex de Hoog, Stud. Mycol. 15: 59. 1977.

Note: See Arzanlou *et al.* (2007).

Clade XXVI: *Acrodontium* de Hoog, Stud. Mycol. 1: 23. 1972.

Saprobic or mycophilic. *Mycelium* consisting of subhyaline, brownish or olivaceous, smooth, thin-walled, septate hyphae. *Conidiophores* when present arising from hyphae, erect or procumbent, sometimes thick-walled and dark brown at the base, paler brown towards the apex, branched verticillately or dichotomously. *Conidiogenous cells* integrated, terminal in conidiophores and often forming whorls or conidiophores reduced to conidiogenous cells, arising from hyphae, basal part flask-shaped or elongate, tapering towards the tip forming a sympodial denticulate rachis, straight to flexuous. *Conidia* formed singly, hyaline or pigmented, smooth, subglobose to fusiform, with an apiculate base. Adapted from Hoog (1972).

Type species: *Acrodontium crateriforme* (J.F.H. Beyma) de Hoog.

Notes: The genus *Acrodontium* was introduced by Hoog (1972), and currently accommodates 10 species varying in lifestyle from saprobic to mycophilic (Seifert *et al.* 2011). *Acrodontium* species have conidiogenous cells that bear conidia on a sympodially proliferating rachis, straight or slightly flexuous, bearing alternating denticles at regular intervals (Hoog 1972). According to the present study, the type species of the genus, *A. crateriforme* (CBS 144.33), belongs to the *Teratosphaeriaceae* (Fig. 1, clade XXVI, 1/100/100). The LSU sequences of isolates belonging to *A. antarcticum*, *A. abietis*, *A. griseum*, *A. hydnicola*, *A. salmoneum*, *A. simplex* and *A. virelum* currently housed in the CBS collection (data not shown) place them in different orders (e.g. *Sordariomycetes* and *Leotiomycetes*) and will not be treated here.

Acrodontium crateriforme (J.F.H. Beyma) de Hoog, Stud. Mycol. 1: 26. 1972. Fig. 17.
Basionym: *Chloridium crateriforme* J.F.H. Beyma, Zentralbl. Bakteriol., 2 Abt., 89: 241. 1933.
≡ *Tritirachium crateriforme* (J.F.H. Beyma) Matsush., Icon. microfung. Matsush. lect.: 160. 1975.
= *Acrodontium neolitseae* Crous & Summerell, Persoonia 32: 209. 2014.

Description in vitro: See de Hoog (1972: 26)

Specimens examined: **Australia**, Nightcap National Park, on *Neolitsea australiensis*, 9 Mar. 2013, B. Summerell, culture CBS 137975 = CPC 22172. **Germany**, Hesse, Schlangenbad, on leaves of *Betula* sp., 2012, W. Quaedvlieg, culture CPC 25895; on leaves of *Ranunculus* sp., 2012, W. Quaedvlieg, culture CPC 25894. Java, Tjibodas Hortus Botanicus, on leaf of *Citrus* sp., 1969, J.H. van Emden, culture CBS 842.71. **South Korea**, Hoengseong, on *Agrimonia pilosa*, 21 Ago. 2004, H.D. Shin, culture CPC 11519; Hongcheon, on *Fraxinus chinensis* subsp. *rhynchophylla* (≡ *F. rhynchophylla*), 11 Aug. 2004, H.D. Shin, culture CPC 11509. **Netherlands**,

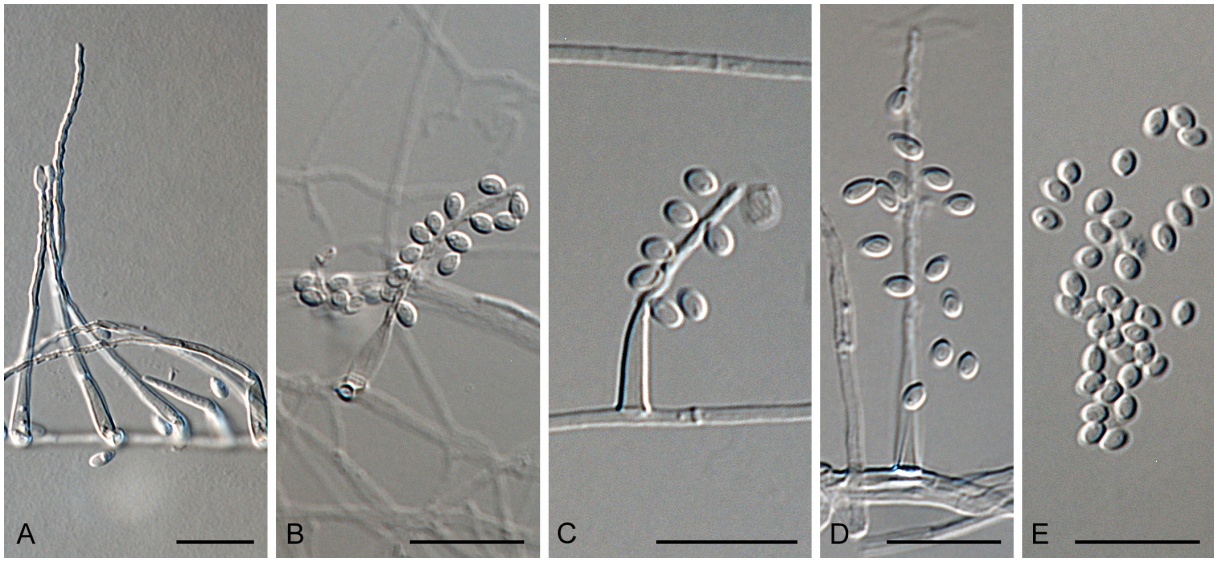


Fig. 17. *Acrodontium crateriforme* (CBS 144.33). A–E. Structures formed in culture. A–D. Conidiophores, conidiogenous cells and conidia. E. Conidia. Scale bars = 10 µm.

on foodstuff, unknown collector and date, isol. M. van Schothorst, dep. RIV, Bilthoven, Oct. 1971, culture CBS 840.71; Baarn, isolated from sputum, unknown collector and date, isol. G.A. de Vries, dep. Jul. 1958, culture CBS 151.58; Baarn, associated with *Tuberculina maxima*, unknown collector and date, isol. H.A. Diddens, dep. F.H. van Beyma, Jun. 1933 (culture ex-type CBS 144.33 = ATCC 15679 = MUCL 15748 = MUCL 8978). **UK**, Westmorland, Meathop Wood, on living leaflet of *Fraxinus excelsior*, unknown date, J.C. Frankland, culture CBS 985.70.

Notes: The recently described species *A. neolitseae* (CPC 22172) is 100 % identical to *A. crateriforme* on LSU but differs on 3 nucleotides on ITS and 7 nucleotides on *rpb2*. The morphological description of *A. neolitseae* also fits with *A. crateriforme* (Fig. 17) since this taxon can sometimes have slightly pigmented conidiophores and conidia. At the time *A. neolitsiae* was described, the ITS BLAST resulted in a 99 % similarity to a strain identified as *Pseudocercosporella fraxini* (GenBank GU214682; CPC 11509) and *Acrodontium crateriforme* (GenBank FN666566), which we show here to represent the same species (Fig. 1, clade XXVI). Since the strain CPC 11509 was not used in a morphological study before two scenarios are possible, namely that the fungus isolated from the specimen was the wrong one or that the culture was contaminated previous to storage and is no longer *P. fraxini* but *A. crateriforme*. The phylogenetic analysis strongly supports this species clade (Fig. 1, clade XXVI, 1/100/ 100).

Acrodontium fagicola Videira & Crous, **sp. nov.** MycoBank MB817151. Fig. 18.

Etymology: Named after the host genus *Fagus*, from which it was collected.

Mycelium hyaline, consisting of septate, branched, smooth, 1–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, subulate to slightly ampulliform, sometimes with a transverse septum, straight to flexuous, proliferating sympodially and forming a rachis in the upper part, (16.5–)31–38(–61) × (1–)1.5–2 µm, with

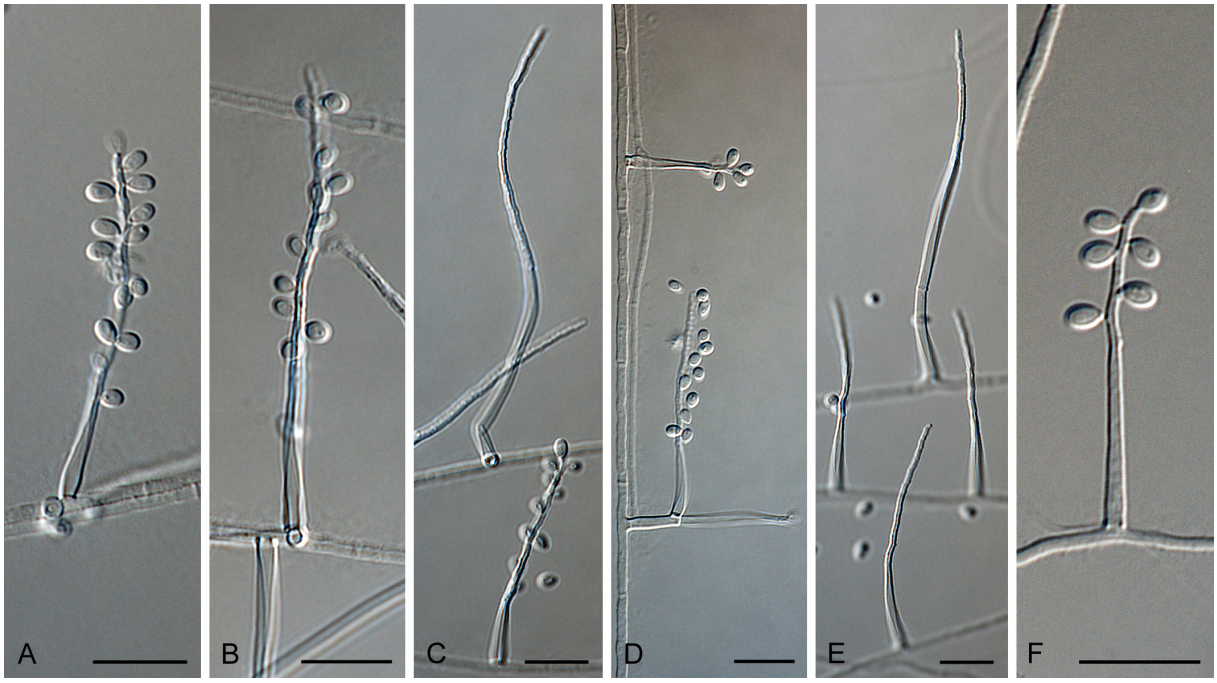


Fig. 18. *Acrodontium fagicola* (CBS 714.79). A–F. Conidiophores, conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

multiple conidiogenous loci slightly thickened but not darkened. *Conidia* hyaline, thin-walled, smooth, solitary, ellipsoid with obtuse apex, (2–)2.5–3 × 1.5–2 µm; hilum slightly thickened but not darkened.

Culture characteristics: On MEA, 10 mm diam, surface raised, smooth, with erumpent aerial mycelium, olivaceous, margins undulate, reverse sepia; on OA, 11 mm diam, surface raised, smooth, with erumpent aerial mycelium, olivaceous and sepia, margins undulate, reverse umber; on PDA, 10 mm diam, surface flat, smooth, with erumpent aerial mycelium, olivaceous and sepia, margins entire, reverse sepia.

Specimen examined: **Germany**, on *Fagus sylvatica*, isol. G. Arnold, Oct. 1978, dep. G. Arnold, Dec. 1979 (holotype CBS H-8534, culture ex-type CBS 714.79).

Note: This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade XXVI) and differs from *A. crateriforme* by having longer conidiogenous cells and smaller conidia (Fig. 18).

Acrodontium luzulae Videira & Crous, **sp. nov.** MycoBank MB816844. Fig. 19.

Etymology: Named after the host genus *Luzula*, from which the ex-type strain was collected.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, elongate ampulliform, straight to flexuous, proliferating sympodially and forming a rachis in the upper part, (23–)44–56(–98) × (1.5–)2(–3) µm, with multiple conidiogenous loci slightly thickened

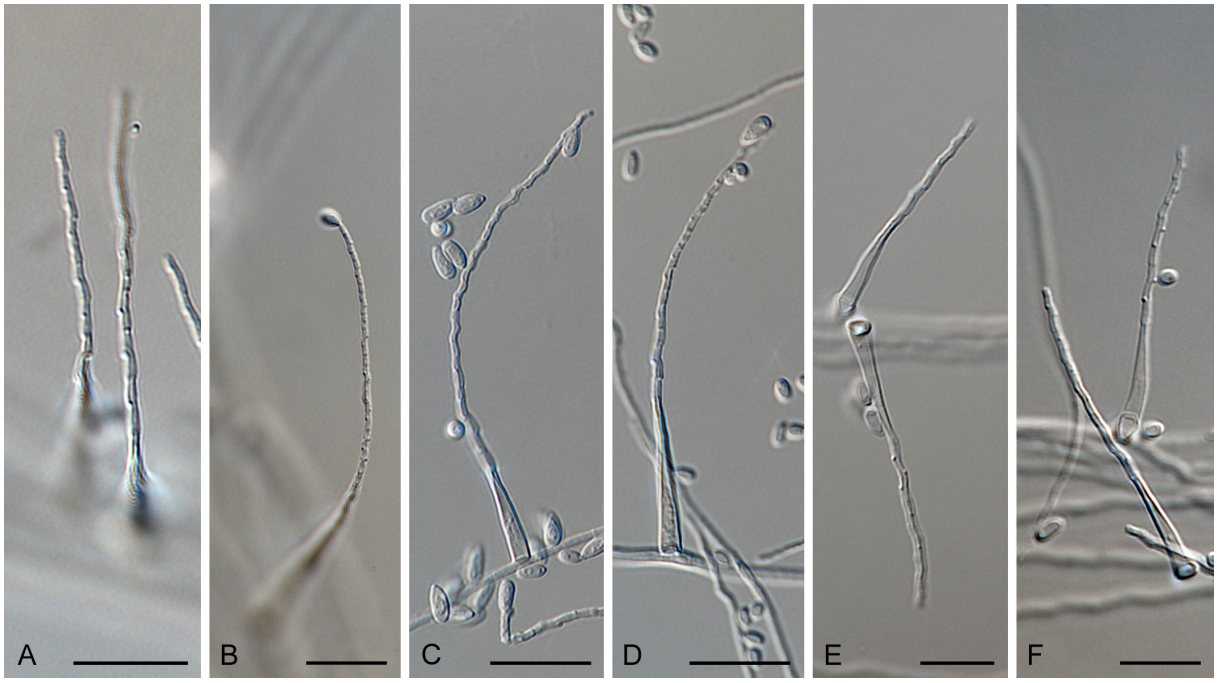


Fig. 19. *Acrodontium luzulae* (CBS 839.71). A–F. Structures formed in culture. A. Conidiogenous loci in the rachis. B–F. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

but not darkened. *Conidia* hyaline, thin-walled, smooth, solitary, ellipsoid with obtuse apex, (2.5–)3–4(–5) × (1–)2(–2.5) µm, hilum slightly thickened but not darkened.

Culture characteristics: On MEA, 10 mm diam, surface flat, smooth, with sparse erumpent aerial mycelium, buff, margins entire, reverse umber; on OA, 10 mm diam, surface flat, smooth, greyish sepia, margins undulate, reverse fawn; on PDA, 10 mm diam, surface flat, smooth, with sparse erumpent aerial mycelium, buff, margins entire, reverse sepia.

Specimens examined: **England**, Devon, East Lyn River, on dead leaf of *Luzula sylvatica*, unknown collector and date, isol. W. Gams, Sep. 1971, dep. Nov. 1971, (holotype CBS H-8529, culture ex-type CBS 839.71). **Netherlands**, Beerze, near Campina, on leaf of *Carex* sp., unknown collector and date, isol. W. Gams, Apr. 1968, dep. Nov. 1971, culture CBS 841.71.

Notes: Although initially identified as *A. crateriforme*, these strains are not conspecific with the type species, and the phylogenetic analysis strongly supports this clade (Fig. 1, clade XXVI, 1/97/100). Morphologically it differs from *A. pigmentosum* by having longer conidiogenous cells and conidia (Fig. 19).

Acrodontium pigmentosum Videira & Crous, **sp. nov.** MycoBank MB817152. Fig. 20.

Etymology: Named after its pigmented mycelium.

Mycelium consisting of hyaline to slightly olivaceous, septate, branched, thin-walled, smooth hyphae, 0.8–1.5 µm diam. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, subulate, sometimes with a transverse septum, arising from the mycelium or from a

Fig. 20. *Acrodontium pigmentosum* (CBS 111111). A–G. Conidiophores, conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

subtending cell in groups of two, straight to flexuous, proliferating sympodially and forming a rachis in the upper part, (9.5–)15.5–19(–31) × (1–)1.5–2 µm, with multiple conidiogenous loci slightly thickened but not darkened. *Conidia* hyaline, thin-walled, smooth, solitary, subglobose to broadly ellipsoidal, 2–3 × 1–2 µm, hilum slightly thickened but not darkened.

Culture characteristics: On MEA, 8 mm diam, surface raised, smooth, with erumpent aerial mycelium, smoke-grey, margins entire, reverse iron grey; on OA, 11 mm diam, surface raised, smooth, with erumpent aerial mycelium, greyish sepia, margins undulate, reverse fuscous black; on PDA, 10 mm diam, surface flat, smooth, with erumpent aerial mycelium, olivaceous and greyish sepia, margins entire, reverse olivaceous black.

Specimen examined: **Finland**, from outdoor air, unknown date, S. Haatainen (holotype CBS H-22637, culture ex-type CBS 111111).

Notes: Initially identified as *A. griseum*, the micro- and macro- morphology of *A. pigmentosum* differs significantly from *A. griseum* by not forming markedly differentiated conidiophores with a thick stalk, smooth and thick-walled, bearing multiple brown conidiogenous cells in side branches and also by not forming olivaceous conidia (Hoog 1972). This species is represented by a single lineage in the phylogenetic analysis (Fig. 1, clade XXVI) and differs from the closest species, *A. fagicola* by having wider conidiogenous cells, larger conidiophores and pigmented mycelium (Fig. 20), as well as 47 nucleotides in *rpb2*, and 5 in LSU.

Clade XXVII: *Parapenidiella* Crous & Summerell, Persoonia 29: 185. 2012.

Note: See Crous *et al.* (2012a).

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

Note: See Crous *et al.* (2009d) and Quaedvlieg *et al.* (2014).

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

Note: See Crous *et al.* (2009d).

Clade XXX: *Teratoramularia* Videira, H.D. Shin & Crous, gen. nov. MycoBank MB816821.

Etymology: Composed of *Terato*- from *Teratosphaeriaceae* and *Ramularia*.

Mycelium consisting of smooth, branched, septate, hyaline hyphae, or swollen pale to brown hyphae. *Conidiophores* at times synnematal, but mostly reduced to conidiogenous cells or consisting of one supporting cell and conidiogenous cell. *Conidiogenous cells* hyaline, thin-walled, smooth, terminal or lateral, subcylindrical, straight, proliferating sympodially; conidiogenous loci conspicuous, thickened and darkened. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia (type I)* hyaline, thin-walled, smooth, subcylindrical, long, aseptate to 1-septate, with conspicuous hila, thickened and darkened. *Conidia (type II)*, sometimes formed, brown, multiseptate, constricted at the septa, with thickened and darkened hila, germinating to form pigmented mycelium.

Type species: *Teratoramularia persicariae* Videira, H.D. Shin & Crous.

Notes: This is the first time that the ramularia-like morphology is observed outside the *Mycosphaerellaceae*. Like in *Ramularia*, species of *Teratoramularia* produce catenate, hyaline conidia with conspicuous hila, but differ by having conidiophores mostly reduced to conidiogenous cells, and by producing very long intercalary conidia and ramoconidia that usually appear immediately next to the conidiogenous cell. In addition, on OA, sometimes pigmented mycelium as well as conidia are observed, that are brown, multiseptate and constricted at their septa. The pigmented conidia were not observed in association with the hosts in the herbarium material. The phylogenetic analysis strongly supports this genus clade (Fig. 1, clade XXX, 1/100/98).

Teratoramularia infinita Videira & Crous, **sp. nov.** MycoBank MB817153. Fig. 21.

Etymology: The epithet "*infinita*" indicates its ability to infect a wide host range.

Mycelium consisting of hyaline, septate, branched, thin-walled, smooth, 1–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, integrated in hyphae, cylindrical-oblong, (6.5–)11.5–14(–19) × 1–1.5(–2) µm, with 1 thickened and darkened apical locus, 1 µm diam. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia (type I)* hyaline, thin-walled, smooth, aseptate, *hila* thickened and darkened, 1 µm diam; *ramoconidia* subcylindrical to fusiform, (4.5–)8.5–11(–17) × (1–)1.5–2 µm, with two apical hila; *intercalary conidia*, subcylindrical to fusiform, sometimes curved, (5–)10–14.5(–25.5) × (1–)1.5–2 µm, in chains of up to 11 conidia; *terminal conidia* obovoid, (3–)4(–6) × (1–)1.5–2 µm. *Conidia (type II)* not observed.

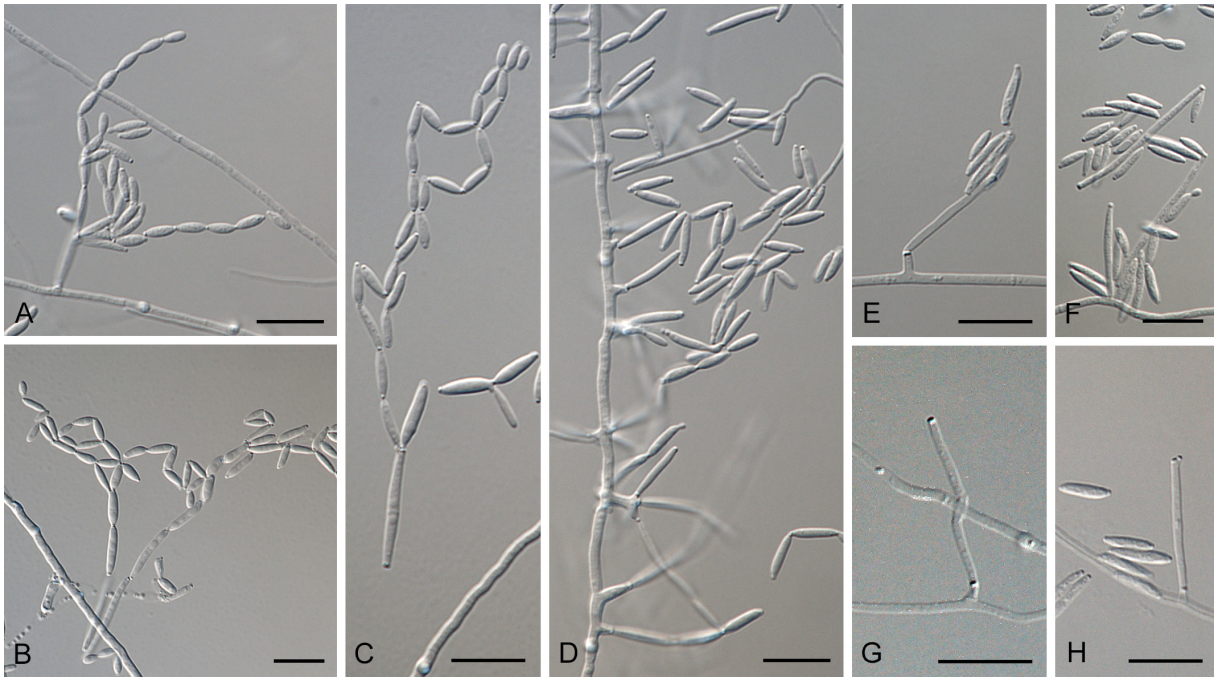


Fig. 21. *Teratoramularia infinita* (CBS 120815). A–H. Conidiophores, conidiogenous cells and conidia observed in culture. Scale bars = 10 µm.

Culture characteristics: On MEA, 18 mm diam, surface raised, folded, smooth, pale grey, with margins crenate, convex, underneath olivaceous grey; on OA, 14 mm diam, surface flat, smooth, pale olivaceous grey, with margins undulate, with sparse olivaceous grey mycelium, reverse iron-grey; on PDA, 15 mm diam, surface, smooth, pale olivaceous grey, with margins crenate, reverse olivaceous grey.

Specimens examined: **Brazil**, on *Conyza canadensis*, 2000, unknown collector (holotype CBS H-22536, culture ex-type CBS 141104 = CPC 19488). **Taiwan**, Chiayi, Meishan, Taixingcun, on living leaves of *Thladiantha punctata*, unknown date, R. Kirschner & C.-J. Chen, culture CBS 120815.

Notes: The two strains in this clade have been isolated from two very distinct hosts, *Conyza canadensis* (*Asteraceae*) and *Thladiantha punctata* (*Cucurbitaceae*), and from two very distinct locations, Brazil and Taiwan, respectively. Nevertheless, they are identical on five genes suggesting this species has a wide host range and distribution. The phylogeny supports their separation from the closest neighbour, *T. rumicicola* (Fig. 1, clade XXX, 1/ 100/100) from which it also differs morphologically by producing longer conidiogenous cells, shorter and slightly narrower ramoconidia and terminal conidia (Fig. 21).

Teratoramularia persicariae Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB817154. Fig. 22.

Etymology: Named after the host genus *Persicaria*, from which the ex-type strain of this taxon was collected.

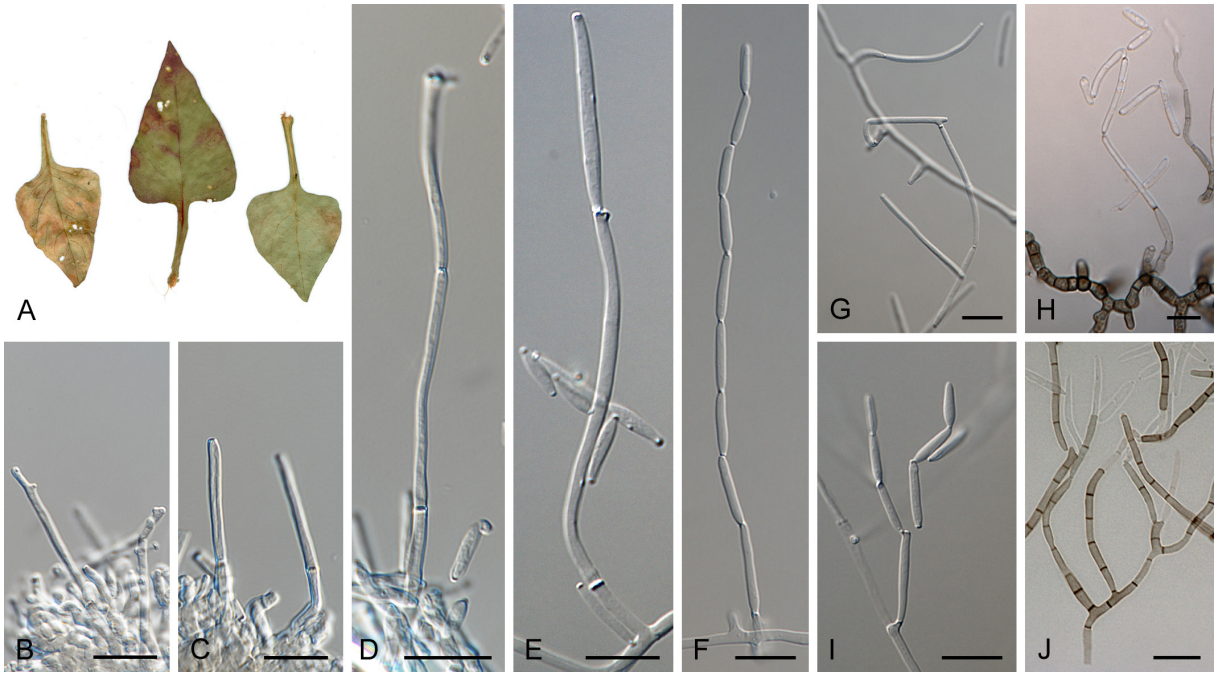


Fig. 22. *Teratoramularia persicariae* (CBS 141105). A–D. Observations from herbarium material. E–J. Structures formed in culture. A. Leaf spot symptoms on the host. B, C. Conidiophores and conidiogenous cells. D–H. Conidiophores, conidiogenous cells and conidia. H, J. Pigmented conidiogenous structures developed on OA culture medium. Scale bars = 10 µm.

Mycelium consisting of hyaline, septate, branched, thin-walled, smooth, 1–2 µm diam hyphae, but on OA also brown, pigmented hyphae are formed. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, integrated in hyphae, cylindrical-oblong, (4.5–)9–11(–15) × (1–)1.5(–2) µm, with one thickened and darkened conidiogenous locus, 1 µm diam. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia (type 1)* hyaline, thin-walled, smooth, aseptate, with *hila* thickened and darkened, 1 µm diam; *ramoconidia* subcylindrical to fusiform, (9.5–)17–20(–30) × (1.5–)2(–2.5) µm, with 2 apical hila; *intercalary conidia* subcylindrical to fusiform, sometimes curved, (8.5–)14–18(–30) × (1–)1.5–2(–2.5) µm, in chains of up to eight conidia; *terminal conidia* hyaline, smooth, aseptate, subcylindrical, (3–)7–8(–10) × (1.5–)2(–3) µm. *Conidia (type II)* not observed.

Culture characteristics: On MEA, 15 mm diam, surface smooth, raised, lumpy, olivaceous grey with buff and white patches, with margins crenate and convex, reverse iron-grey with ochreous patches; on OA, 10 mm diam, surface concave, smooth, pale olivaceous grey, with margins raised, undulate, with sparse aerial mycelium, reverse olivaceous grey; on PDA, 13 mm diam, surface smooth, lumpy, irregular, iron-grey with pale vinaceous patches, margins undulate, reverse rosy buff and olivaceous grey.

Specimens examined: **South Korea**, Hongcheon, on *Persicaria nepalensis*, 29 Jul. 2004, H.D. Shin (holotype KUS-F20536, isotype CBS H-22537, culture ex-type CBS 141105 = CPC 11410); *idem*. CPC 11408, CPC 11409. **Unknown country**, on leaf spot of *Fagopyrum esculentum*, isol. and dep. M.W. Gardner, Jul. 1927, culture CBS 195.27.

Notes: The host species, *Persicaria nepalensis*, is distributed worldwide but a broader sampling is required to show whether the fungal species follows this distribution. The phylogenetic analysis supports the separation of *Teratoramularia persicariae* from *T. rumicicola* (Fig. 1, clade XXX, 0.99/95) and, morphologically, *T. persicariae* (Fig. 22) produces longer conidia than *T. rumicicola*.

Teratoramularia rumicicola Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB817155. Fig. 23.

Etymology: Named after the host genus *Rumex*, from which it was collected.

Mycelium consisting of hyaline, septate, branched, thin-walled, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, integrated in hyphae, cylindrical-oblong, (5–)10–12.5(–16.5) × (1–)1.5(–2) µm, with 1 thickened and darkened apical locus, 1 µm diam. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia (type I)* hyaline, thin-walled, smooth, catenate, aseptate or occasionally 1-septate, with *hila* conspicuous, thickened and darkened, 1 µm diam; *ramoconidia* subcylindrical to fusiform, (8.5–)12–15(–23) × (1.5–)2(–2.5) µm, with 2 apical hila; *intercalary conidia* subcylindrical, sometimes slightly curved, (6.5–)10–13(–20) × (1.5–)2(–2.5) µm, in chains of up to five conidia; *terminal conidia* subcylindrical to obovoid, (3–)5.5–6(–8) × (1.5–)2(–3) µm. *Conidia (type II)* brown, smooth, catenate, 1–4-septate, constricted at the septa, (5–)11.5–14.5(–18.5) × (2–)2.5–3 µm, with *hila* thickened and darkened.

Culture characteristics: On MEA, 20 mm diam, surface raised, strongly folded, smooth, white with greyish tinge in the centre, with margins crenate, convex, olivaceous grey, reverse iron-

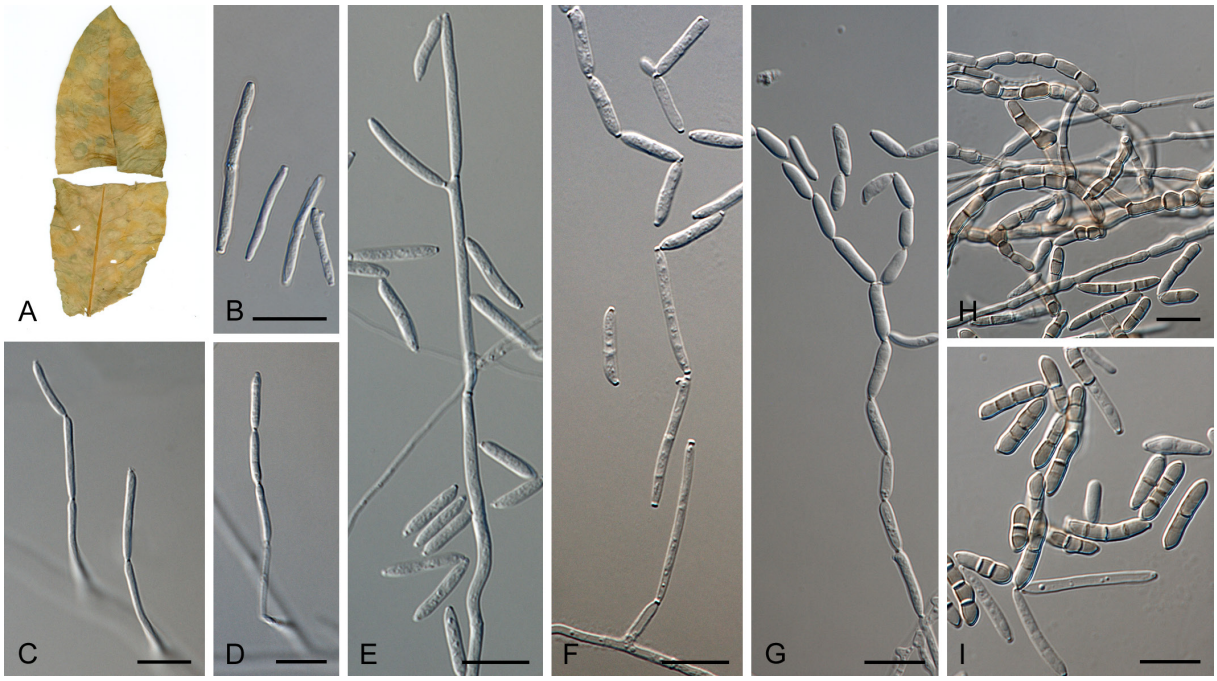


Fig. 23. *Teratoramularia rumicicola* (CBS 141106). A–B. Observations from herbarium material. C–I. Structures formed in culture. B. Conidia. C–G. Conidiophores, con- idiogenous cells and conidia. H, I. Pigmented conidiogenous structures and conidia formed on OA culture medium. Scale bars = 10 µm.

grey; on OA, 15 mm diam, surface flat, smooth, pale olivaceous grey, with margins undulate, with sparse olivaceous grey mycelium, reverse iron-grey; on PDA, 16 mm diam, surface with smooth and folded portions, pale olivaceous grey, with margins crenate and smoke grey, reverse olivaceous grey.

Specimens examined: **South Korea**, Jecheon, on *Rumex crispus*, 19 Oct. 2007, H.D. Shin (holotype KUS-F23080, isotype CBS H-22538, culture ex-type CBS 141106 = CPC 14653); *idem*. CPC 14652, CPC 14654.

Notes: A total of seven *Ramularia* species have been described from *Rumex* worldwide (Braun 1998) and two of these species form filiform, long conidia, i.e. *R. pseudodecipiens* and *R. pratensis*. *Ramularia pseudodecipiens* is only known from the type collection in the USA (Wyoming), has larger conidia [(10–)25–45(–55) × 2–5 µm] that are consistently septate and, although sometimes constricted at the septa, they are always hyaline. *Ramularia pratensis* has a worldwide distribution and produces conidia of approximately the same size, (6–)8–25(–35) × (1.5–)2–4(–5) µm, but they are never constricted at the septa or pigmented. In addition, the conidiophores in *T. rumicicola* (Fig. 23) were consistently reduced to conidiogenous cells while both *R. pseudodecipiens* and *R. pratensis* produce long conidiophores. The phylogenetic analysis supports this species clade (Fig. 1, clade XXX, 1/100/100).

Teratoramularia kirschneriana Videira & Crous, **sp. nov.** MycoBank MB817156. Fig. 24.

Etymology: Named after the mycologist Roland Kirschner, who has contributed greatly to our knowledge of cercosporoid fungi.

Mycelium consisting of hyaline, septate, branched, thin-walled, smooth, 0.5–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, integrated in hyphae, cylindrical-oblong, (13.5–)14–15(–16) × 1(–1.5) µm, with 1 thickened and darkened apical locus, 1 µm diam. *Conidia* are catenate, forming ramoconidia, intercalary conidia and terminal conidia. *Conidia (type I)* hyaline, thin-walled, smooth, aseptate, *hila* thickened and darkened, 1 µm diam.; *ramoconidia* subcylindrical to fusiform, (7–)8.5–10(–15) × (1–)1.5–2 µm, with two apical hila; *intercalary conidia*, fusiform, (6–)8–10(–17) × (1–)1.5–2 µm, in chains of up to five conidia; *terminal conidia*, fusiform to obovoid, (3.5–)5–6(–7) × (1–)1.5–2 µm. *Conidia(type II)* not observed.

Culture characteristics: On MEA, 16 mm diam, surface folded, smooth, pale grey, with margins crenate, convex, colony reverse iron-grey; on OA, 15 mm diam, surface flat, smooth, pale grey, with margins undulate, colony reverse iron-grey; on PDA, 13 mm diam, surface smooth, pale grey, with margins crenate, colony reverse iron-grey.

Specimen examined: **Taiwan**, Tahsuehshan, on leaves of *Setaria palmifolia*, 13 Apr. 2002, R. Kirschner & C.-J. Chen (holotype TNM No. F0016568, isotype CBS H-22539, culture ex-type CBS 113093).

Notes: The strain representing this species was originally identified as *Phacellium paspali*. The characteristic *Phacellium* synnemata are sometimes also formed in culture. This species is represented by a single basal lineage in the *Teratoramularia* clade in the phylogenetic analysis

(Fig. 1, clade XXX). Morphologically (Fig. 24), it is nearly impossible to distinguish it from the closest sister species *T. infinita*.

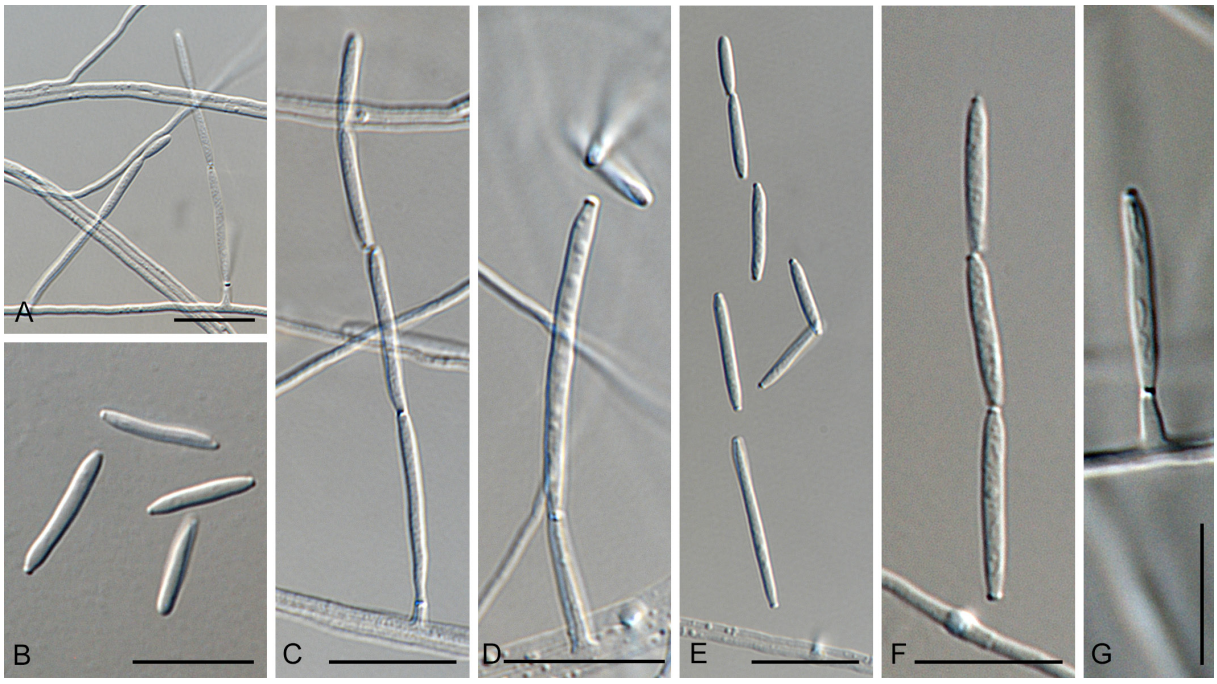


Fig. 24. *Teratoramularia kirschneriana* (CBS 113093). A–G. Structures formed in culture. A, C–G. Conidiogenous cells and conidia. B. Conidia. Scale bars = 10 µm.

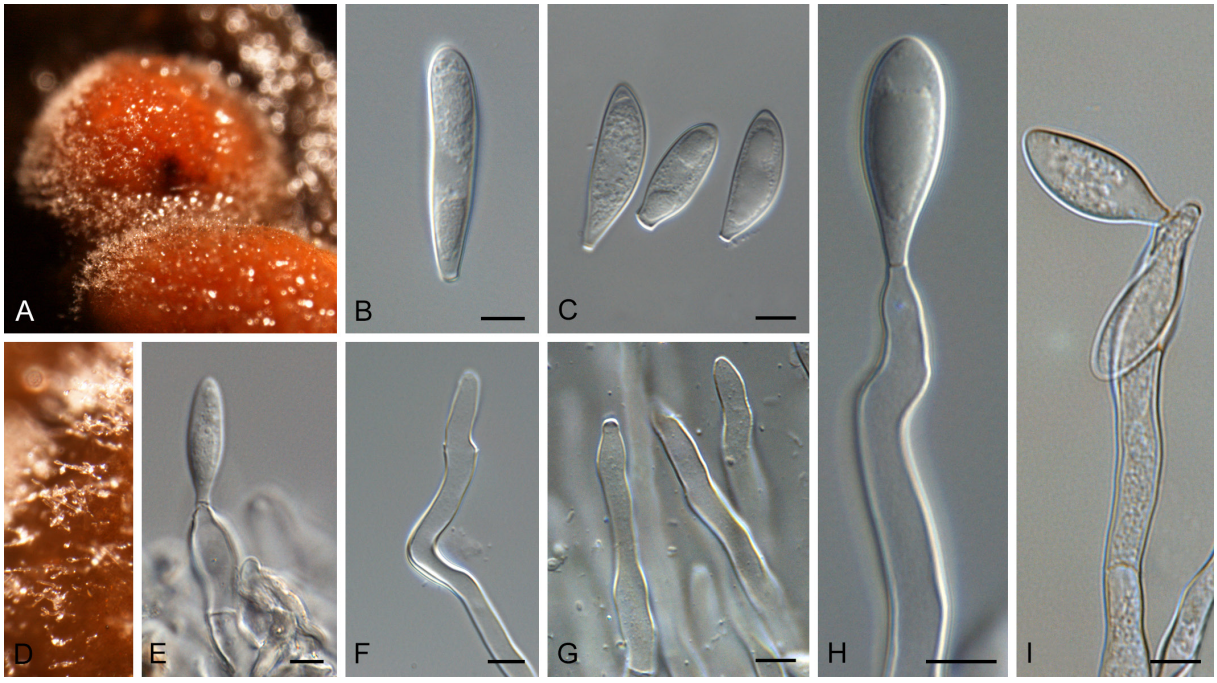


Fig. 25. *Hawksworthiana peltigericola* (herbarium Paul Diederich). A–I. Observations from herbarium material. A, D. Conidiogenous structures developing on the host. B, C. Conidia. E, H, I. Conidiophores and conidia. F, G. Conidiophores. Scale bars = 10 µm.

Genera allied to Ramularia lacking cultures

Hawksworthiana U. Braun, Int. J. Mycol. Lichenol. 3: 276. 1988. Fig. 25.

Lichenicolous, forming gall-like deformations. *Mycelium* consisting of hyaline, septate, sparsely branched, thin-walled hyphae. *Conidiophores* reduced to the conidiogenous cells, erumpent, usually ampulliform but sometimes subcylindrical, aseptate, hyaline, thin-walled, mono- or polyblastic, sympodial, conidiogenous loci conspicuous, thickened and darkened. *Conidia* formed singly, acrogenous, oblong-clavate to subcylindrical, hyaline, thin-walled, smooth, aseptate or 1-septate, hilum conspicuous, thickened and darkened.

Type species: *Hawksworthiana peltigericola* (D. Hawksw.) U. Braun.

Specimens examined: **Luxembourg**, on lichen *Peltigera rufescens*, 7 May 2008, P. Diederich. **Scotland**, Isle of Mull, Killiemore, on *Peltigera polydactyla*, 16 Jun. 1979, Clark (holotype K(M) IMI 239715a).

Notes: *Hawksworthiana* is monotypic and was described based on *H. peltigericola* on a specimen of *Peltigera polydactyla* from the Isle of Mull in Scotland. It forms gall-like deformations on lichens of the genus *Peltigera*, and has been reported from Europe and North America. *Hawksworthiana* differs from *Ramularia* by its lichenicolous habit and morphological characters such as the wide ampulliform conidiogenous cells, the conidiogenous loci and hila are not refractive, the absence of stroma-like structures and the symptoms caused on the host (Fig. 25). All attempts to culture this fungus from fresh collections have thus far proven unsuccessful.

Monodidymaria U. Braun, Nova Hedwigia 58: 195. 1994. Fig. 26.

Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline, septate, branched, thin-walled hyphae; stromata absent or small. *Conidiophores* macronematous, solitary or in fascicles, arising from internal hyphae or hyphal aggregations, emerging through stomata or erumpent through the cuticle, filiform and straight or flexuous to sinuous, but not geniculate, usually aseptate, thin-walled, hyaline and smooth, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, monophialidic. *Conidia* formed singly, ellipsoid-ovoid, obovoid, subcylindrical, fusoid or subclavate, aseptate or 1(–3)-septate, hyaline, thin-walled, smooth to rough, base rounded to truncate.

Type species: *Monodidymaria canadensis* (Ellis & Everh.) U. Braun.

Specimens examined: **Canada**, Ontario, London, on *Carex conoidea*, Aug. 1890, Dearness (lectotype NY 01293230, syntypes NY 01293231, 01293232 and 01293233).

Notes: While *Ramularia* has polyblastic, sympodial and cicatrised conidiogenous cells, *Monodidymaria* has monophialidic conidiogenous cells (Fig. 26). This character excludes *Monodidymaria* from the *Cercosporella*/*Ramularia* complex, but due to their common taxonomical history, they are still studied together. *Monodidymaria* is in fact morphologically more similar to *Cephalosporiopsis*, but the latter genus comprises saprobic soil hyphomycetes and its taxonomic status is not yet certain (Braun 1998). As a consequence, the genus is

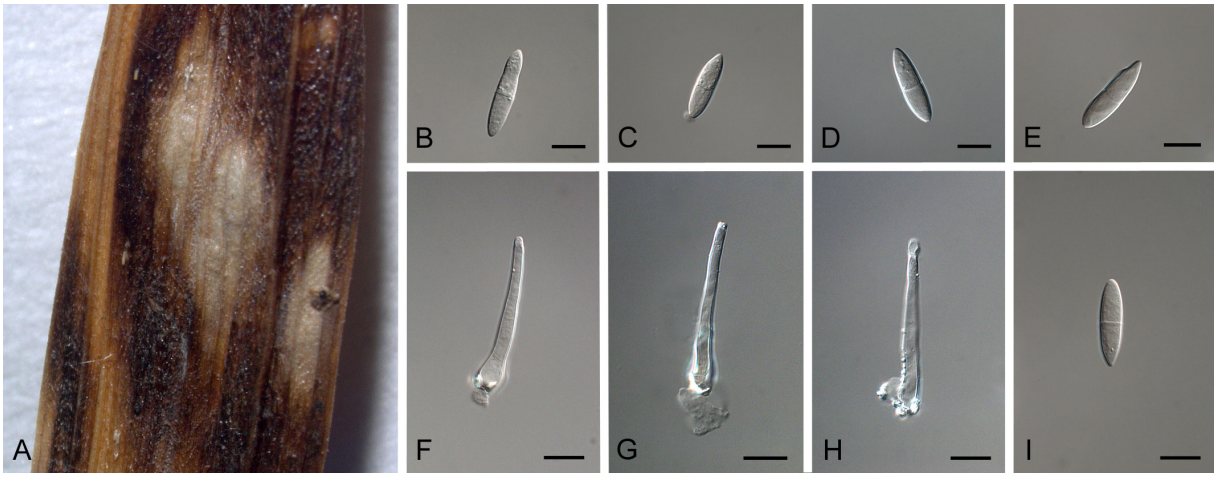


Fig. 26. *Monodidymaria canadensis* (NY herbarium, 01293230, lectotype specimen). A. Leaf spot lesion on the host. B–E, I. Conidia. F–H. Conidiophores. Scale bars = 10 µm.

maintained until more data is available to clarify its taxonomic position (Braun 1998). Five species are known to belong in this genus and were isolated from several hosts (*Chenopodium*, *Equisetum*, *Scirpus* and *Vitex*) from Asia, Europe, North and South America (Braun 1998, Seifert *et al.* 2011).

Neoovularia U. Braun, Nova Hedwigia 54: 473. 1992. Fig. 27.

Phytopathogenic, causing leaf spots. *Caespituli* amphigenous, whitish to pink or ochraceous. *Mycelium* consisting of hyaline to faintly pigmented, septate, branched, thin-walled hyphae forming well-developed stromata. *Conidiophores* arising from stromata, emerging through stomata or erumpent through the cuticle, often forming sporodochia, subcylindrical, subclavate, simple, thin-walled, smooth, hyaline or lightly pigmented, continuous or septate. *Conidiogenous cells* integrated, terminal, straight to moderately geniculate-sinuous, polyblastic and sympodial, conidiogenous loci numerous, conspicuous, bulging, papilla-like, but not thickened and darkened, at most slightly refractive. *Conidia* formed singly, subglobose, obovoid, ellipsoid, aseptate, hyaline to faintly pigmented, thin-walled, smooth to verruculose; basal hilum not thickened or darkened; conidial secession schizolytic. Adapted from Braun (1998).

Type species: *Neoovularia nomuriana* (Sacc.) U. Braun.

Specimens examined: **Hungary**, Sükösd, on leaves of *Astragalus cicer*, Sep. 1913, leg. F. Greinich, det. G. Moesz., Flora Hungarica exsiccata 106, cent. II, Fungi 16, M-0177904. **Japan**, Mino Prov., Kawanyemura, on *Astragalus sinicus*, May 1912, leg. K. Hara, com. P. Sydow, Kabát et Bubák: Fungi Imperfecti exsiccati 835, M-0177907; Kikotaru, on *Astragalus sinicus*, 1903, Nomura (holotype PAD). **Russia**, Ufa, Jabalakly, on leaves of *Astragali cicer*, 29 Jun. 1910, leg. Serebrianikow, Tranzschel et Serebrianikow Mycotheca Rossica 195, M-0177906, M-0177905.

Notes: *Neoovularia* species are characterised by having unthickened but bulging and refractive conidiogenous loci, and by producing single, subglobose conidia with unthickened but refractive hila (Fig. 27). There are six species described in this genus that are phytopathogenic

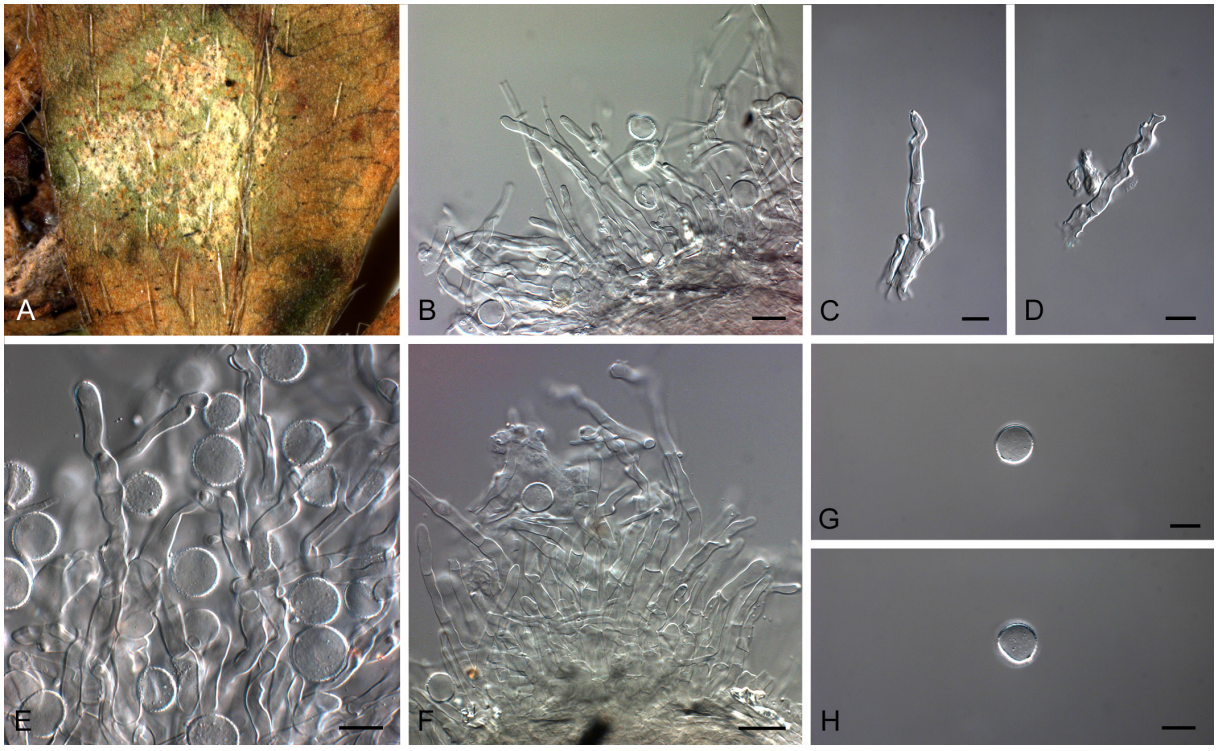


Fig. 27. *Neovularia nomuriana* (M-0177907). A. Leaf spot lesion on the host. B, E, F. Conidiophores and conidia. C, D. Conidiogenous cells. G, H. Conidia. Scale bars = 10 µm.

and cause distinct lesions on leaves and stems (Braun 1998). They have been observed from hosts belonging to four different families (*Asteraceae*, *Fabaceae*, *Lamiaceae* and *Malvaceae*) and located in Europe, Asia, Caucasus and N. America.

Neoramularia U. Braun, Nova Hedwigia 53: 291. 1991. Fig. 28.

Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline or subhyaline, septate, branched, thin-walled hyphae forming stromata or not. *Conidiophores* macronematous, usually in large fascicles, sometimes forming sporodochial and basistromatic conidiomata, emerging through stomata or erumpent through the cuticle, straight, subcylindrical to geniculate-sinuous, simple, hyaline or faintly pigmented, continuous or septate, thin-walled, smooth or occasionally rough. *Conidiogenous cells* integrated, terminal, polyblastic, percurrent and sympodial, conidiogenous loci inconspicuous, not thickened or darkened. *Conidia* solitary or catenate, ellipsoid-ovoid, sub-cylindrical or fusoid, hyaline or slightly pigmented, aseptate to 3-septate, thin-walled, smooth or almost so, hila unthickened and hyaline, conidial secession schizolytic.

Type species: *Neoramularia eurotiae* (Gamalizk.) U. Braun [= *N. kochiae* (Woron.) U. Braun].

Specimen examined: **Russia**, Central Tien-Shan, 5 Jun. 1958, Gamalitzkaja (holotype of *Ramularia eurotiae* LE 41968).

Notes: The genus *Neoramularia* was introduced by Braun (1991) to include species with inconspicuous, unthickened, hyaline conidiogenous loci and hila. The circumscription

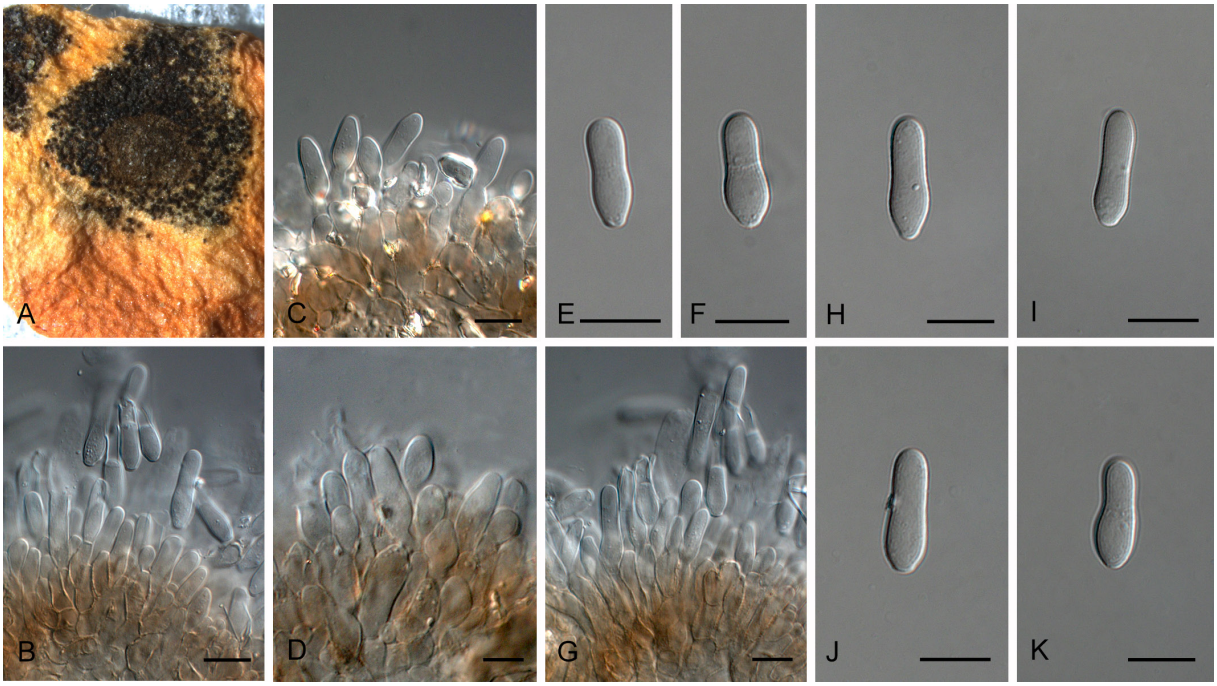


Fig. 28. *Neoramularia eurotiae* (No. 41968, LE herbarium, holotype of *Ramularia eurotiae*). A–K. Observations from herbarium material. A. Leaf spot symptoms on the host. B–D, G. Conidiogenous cells and conidia. E, F, H–K. Conidia. Scale bars = 10 µm.

of *Neoramularia* was later modified to include species forming catenate conidia such as *Neoramularia esfandiarii* (Braun 1992). Ten species are currently known in this genus and have been isolated from different hosts in Asia, Europe and North America (Braun 1998, Seifert *et al.* 2011). The type species is known from *Kochia* sp., Azerbaijan, and a photoplate based on the holotype of *R. eurotia*, a synonym of *Neoramularia kochiae* is presented (Fig. 28).

Pseudodidymaria U. Braun, Cryptog. Bot. 4: 110. 1993. Fig. 29.

Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline or faintly pigmented, septate, thin-walled and branched hyphae, forming well developed stromata. *Conidiomata* basistromatic and sporodochial. *Conidiophores* arranged in palisade-like fascicles, subcylindrical, subclavate, straight to flexuous, sinuous, rarely septate, hyaline to faintly pigmented, thin-walled, smooth, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, polyblastic, sympodial, conidiogenous loci bulging, unthickened or with a thickened rim, not darkened but refractive. *Conidia* formed singly, ellipsoid-obovoid, subclavate, aseptate to 2-septate, base rounded to broadly truncate, hyaline to faintly pigmented, thin-walled, smooth to verruculose, hilum unthickened, not darkened but refractive, conidial secession schizolytic.

Type species: *Pseudodidymaria wyethiae* (Ellis & Everh.) U. Braun.

Specimens examined: **USA**, California, Santa Rosa, on leaves of *Wyethia glabra*, 25 May 1894, WC Blasdale (lectotype NY 01087025, isolectotypes NY 01087026, 01087027, 01087028).

Notes: *Pseudodydimaria* was established to accommodate *Didymaria wyethiae*, since it did

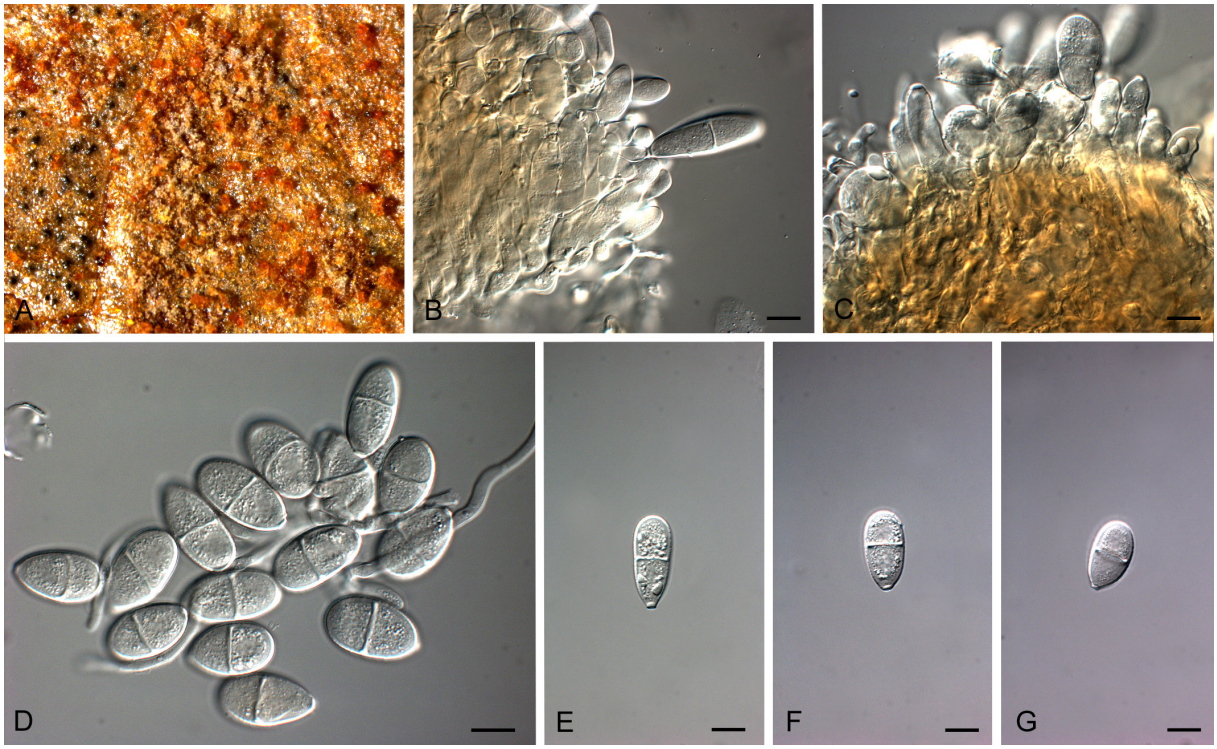


Fig. 29. *Pseudodidymaria wyethiae* (NY herbarium 01087025, lectotype specimen). A. Leaf spot lesion on the host. B, C. Conidiogenous cells and conidia. D–G. Conidia. Scale bars = 10 µm.

not fit comfortably with the description of *Ramularia*, *Pseudocercosporidium* or *Neoovularia*. *Pseudocercosporidium* differs by having very long, branched conidiophores, formed singly or loosely grouped. *Neoovularia* differs by having aseptate, subglobose to ovoid conidia with narrow, darkened, refractive hila. Two species are currently known to belong to this genus, *P. wyethiae* (Fig. 29) and *P. clematidis*, reported from North America (Braun 1998).

Tretovularia Deighton, Trans. Brit. Mycol. Soc. 82: 743. 1984. Fig. 30.

Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline, septate, branched, thin-walled hyphae; stromata absent or small. *Conidiophores* macronematous, growing singly or in fascicles, arising from internal hyphae or stromata, emerging through stomata, subcylindrical to sinuous, fertile part usually strongly geniculate-sinuous, hyaline, continuous or sometimes septate, thin-walled, smooth. *Conidiogenous cells* integrated, terminal, sometimes becoming intercalary, polytretic, indeterminate, proliferation sympodial, conidiogenous loci are minute pores located in small shoulders that are later covered by a colourless cap. *Conidia* solitary, subglobose, broad ellipsoid-ovoid, pyriform, aseptate, hyaline, base rounded or with a small protrusion.

Type species: *Tretovularia villiana* (Magnus) Deighton.

Specimen examined: **Germany**, Unterfranken, Hassfurt near Nürnberg, on *Vicia cassubica*, Sep. 1898, A. Vill [Allesch. & Schn., Fungi bavar. 691], ex-herb. P. Magnus acc.1918 (holotype HBG).

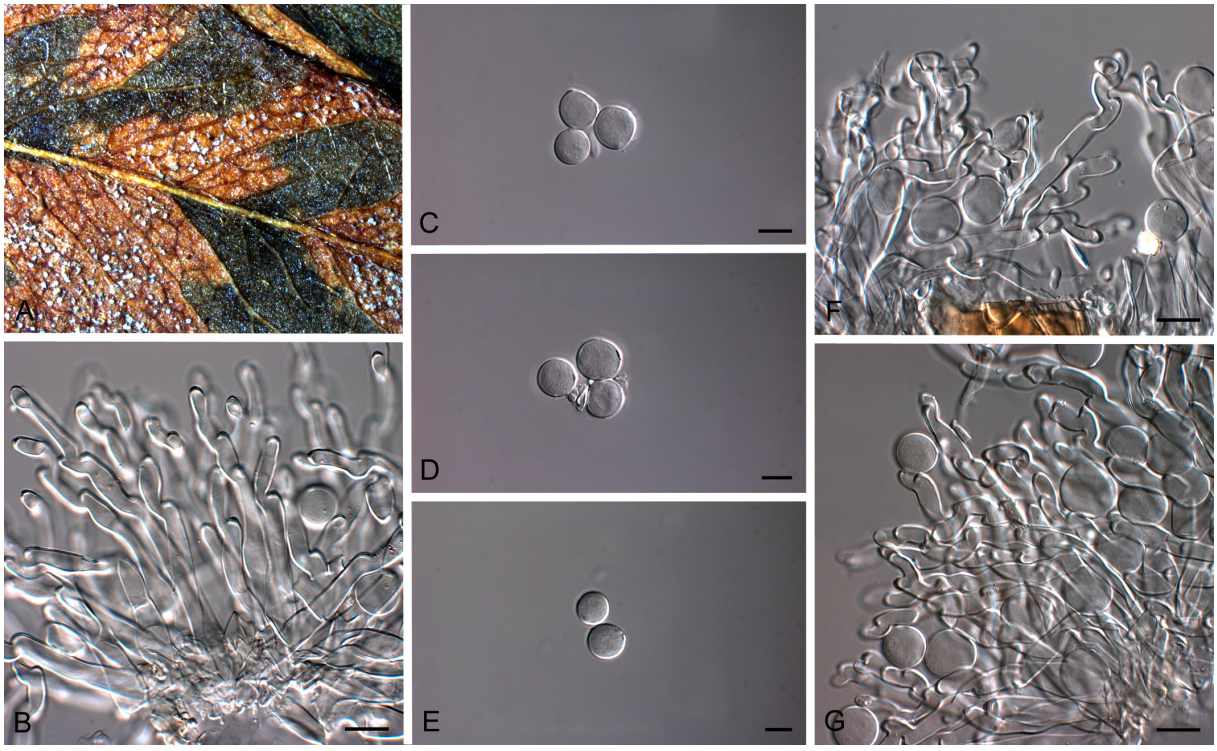


Fig. 30. *Tretovularia viliana* (holotype, HBG). A. Leaf spot lesion on the host. B, F, G. Conidiogenous cells and conidia. C–E. Conidia. Scale bars = 10 µm.

Notes: This monotypic genus was established to accommodate *Ovularia villiana* (Fig. 30), a phytopathogenic species that forms polytretic conidiogenous cells with sympodial proliferation, a characteristic very different from *Ramularia* and other similar genera.

Ramularia sensu stricto

Ramularia abscondita (Fautrey & F. Lamb.) U. Braun, Int. J. Mycol. Lichenol. 3: 280. 1988. Fig. 31.
Basionym: *Ovularia abscondita* Fautrey & F. Lamb., Rev. Mycol. (Toulouse) 18: 144. 1896.
= *Ramularia filaris* f. *lappae* Sacc., Syll. Fung. 4: 210. 1886.
= *Ramularia filaris* var. *lappae* Bres., Hedwigia 36: 200. 1896.
≡ *Ramularia lappae* (Bres.) Ferraris, Fl. Ital. Crypt., Fungi 1(6): 837. 1913.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, cylindrical-oblong, straight to geniculate-sinuous, unbranched, (10–)15.5–20.5(–44.5) × (1.5–)2 µm, or reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium or terminal on the conidiophore, cylindrical-oblong to geniculate-sinuous, (7–)11–14(–22.5) × (1–)1.5–2(–3) µm, with multiple conidiogenous loci almost flat to protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth to slightly verruculose, catenate, with *hila* thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong, clavate, sometimes curved, oval, (5.5–)8–9.5(–15) × 2–2.5(–3) µm, aseptate, with 2–3 apical hila. *Intercalary conidia* cylindrical-oblong, oval, ellipsoid, aseptate, (4.5–)6.5–7(–10) × 2(–2.5) µm, in branched chains of up to five conidia.

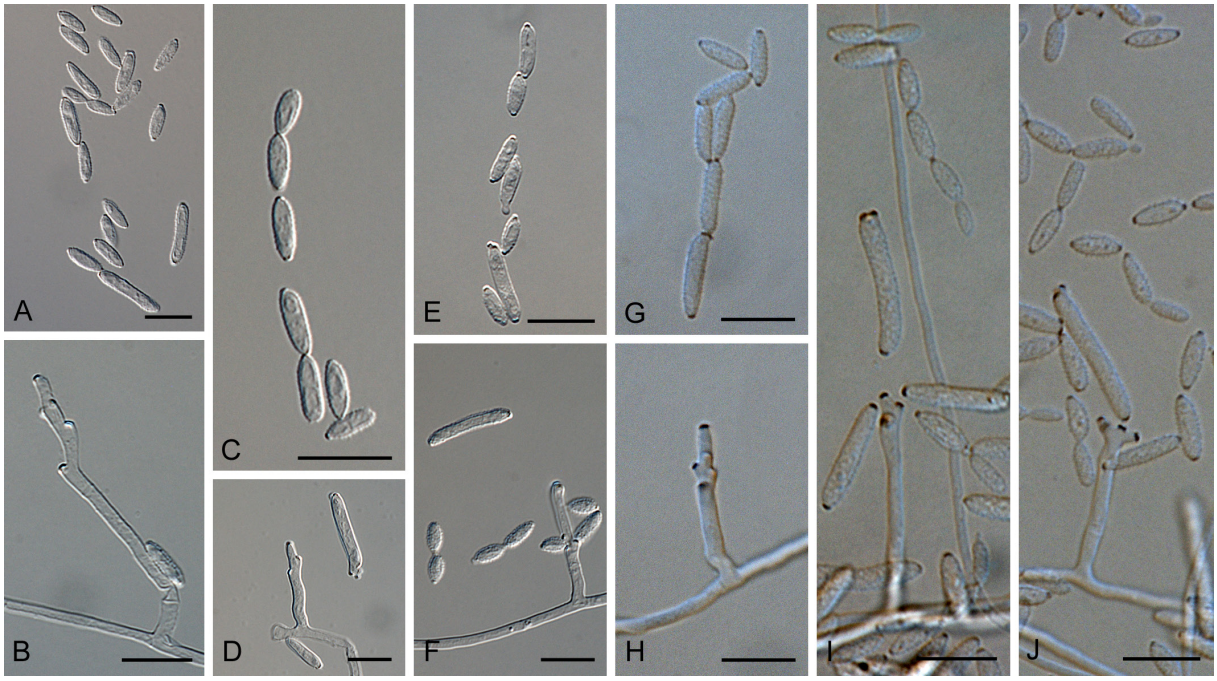


Fig. 31. *Ramularia abscondita* (CBS 114727). A–J. Structures formed in culture. A, C, E, G. Conidia. B, D, F, I, J. Conidiophores, conidiogenous cells and conidia. H. Conidiophore. Scale bars = 10 µm.

Terminal conidia obovoid, aseptate, (4–)5(–6) × (1.5–)2–2.5 µm (on SNA, CBS 114727).

Culture characteristics: On MEA, 8 mm diam, surface raised, fluffy aerial mycelium, dirty white, with margins undulate, colony reverse ochreous; on OA, 8 mm diam, surface raised, folded, fluffy aerial mycelium, white, margins undulate, colony reverse buff; on PDA, 8 mm diam, surface raised, folded, fluffy aerial mycelium pale grey, with margins undulate, colony reverse buff.

Description in vivo: See Braun (1998: 84).

Specimens examined: **France**, Viserny, Côte-d'Or, on *Arctium lappa*, 1896, Fautrey [Roum., Fungi Sel. Gall. Exs. 7245] (lectotype, designated in Braun 1998, PC). **Sweden**, Uppland, Dalby, on leaves of *Arctium tomentosum*, 20 Sep. 1990, E. Gunnerbeck, culture CBS 114727.

Substrate and distribution: On *Arctium* spp. (*Asteraceae*); Caucasus, Central Asia, Europe.

Notes: *Ramularia abscondita* was originally described on *Arctium lappa* from France (lectotype in PC). It has a wide geographical distribution but has only been isolated from hosts belonging to the genus *Arctium* (*Asteraceae*), a plants genus commonly known as thistle burdock. Burdock root was used as bittering agent of beer before the introduction of hop and is very much used in Asian cuisine. *Ramularia abscondita* has been reported on *Arctium tomentosum* from Sweden (Braun 1998). The morphological description of this strain (Fig. 31) differs from the one in literature (Braun 1998) based on collections *in vivo* by having longer conidiophores and narrower conidiophores and conidia. These differences may be related to the fungus growing in culture and not being associated with its host. This strain forms a single lineage in the phylogenetic analysis (Fig. 2, clade 43) but will be tentatively considered as a good representative of this

species until material from the type host and location is collected and cultured.
Ramularia acris Lindr., Acta Soc. Fauna Fl. Fenn. 22(1): 14. 1902.
= *Septocylindrium ranunculi* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 34: 46. 1881.
= *Ramularia aequivoca* f. *ranunculi-acris* C. Massal., Atti Mem. Accad. Agric. Sci. Art. Verona: 156. 1902.
= *Ramularia aequivoca* var. *andrei* M. Morelet, Bull. Soc. Sci. Nat. Archéol. Toulon Var: 9. 1967.

Description in vivo: See Braun (1998: 234).

Specimens examined: **Netherlands**, Gelderland Prov., Wageningen, on living leaves of *Ranunculus acris*, Aug. 2012, S.I.R. Videira, cultures CBS 141107 = CPC 25899 and CPC 25898; Utrecht Prov., Utrecht, Rhijnauwen, on living leaves of ?*Ranunculus* sp., May 2013, U. Damm, culture CPC 25900; Zeeland Prov., Borsele, Vladijk near Nisse, on *Ranunculus* sp., 27 Aug. 2001, G. Verkley, culture CBS 109794.

Substrate and distribution: On *Ranunculus* (*Ranunculaceae*); Asia, Europe and N. America.

Notes: The strains in this clade were previously identified as *R. didyma.* Authentic strains of *R. didyma* cluster in clade 72 (Fig. 2) and, besides *R. didyma*, *R. acris* is also common on *Ranunculus acris*. Since the strains were sterile in culture and no herbarium specimens were preserved, the morphological characters could not be compared with the description available in literature. The strains in this clade cluster in a highly supported clade (Fig. 2, clade 7, 1/100/100) and are tentatively treated as *R. acris*.

Ramularia acroptili Bremer, Sydowia 2: 315. 1984.
≡ *Cercosporella acroptilli* (Bremer) U. Braun, Nova Hedwigia 56: 439. 1993.
= *Cercosporella centaureicola* D. Berner *et al.*, Mycologia 97: 1122. 2006.

Description in vivo: See Braun (1995: 72).

Specimens examined: **Greece**, Macedonia region, Kozani, on leaves of *Centaurea solstitialis*, 28 Apr. 2004, D. Berner, culture CBS 120253 = BPI 844247. **Turkey**, Ankara, on *Acroptilon repens*, 14 Jul 1947, Bremer [Reliquiae Petrakianae 363] (lectotype W, No. 11177); near Isparta, on *Acroptilon repens*,1 Sep. 1997, R. Sobhian (epitype designated here BPI 745883, MBT130827, culture ex-epitype CBS 120252). **USA**, California, on *Cynara cardunculus*, Oct. 2010, L. Davenport, cultures CPC 18723, CPC 18724.

Substrate and distribution: On *Acroptilon repens, Centaurea solstitiales* and *Cynara cardunculus* (*Asteraceae*); Central Asia, Europe and N. America.

Notes: Russian knapweed (*Acroptilon repens*) and yellow starthistle (*Centaurea solstitialis*) are invasive weeds in the western USA. Berner *et al.* (2005) studied two potential biological control agents for these weeds namely *Cercosporella acroptili* for *A. repens*, and a morphologically similar *Cercosporella* sp. on *Centaurea solstitialis*. The culture of *Cercosporella acroptili* (CBS 120252) from the same host and country as the type (*Acroptilon repens*, Turkey) was compared with the herbarium type material and found to be identical.

Both *Cercosporella acroptili* (CBS 120252) and *Cercosporella* sp. (CBS 120253) were morphologically cryptic, the infection symptoms were phenotypically similar and the ITS sequences were 99 % similar with only 3 base pairs difference. Pathogenicity tests showed they were only pathogenic to their respective hosts, growth studies showed some culture morphology differences, and that they were vegetatively incompatible (Berner *et al.* 2006). At the time, the combination of these minor differences in morphology, pathogenicity, growth and genetics (ITS sequences) between *C. acroptili* and *Cercosporella* sp. were found sufficient to describe the new species as *Cercosporella centaureicola* (CBS 120253). However, previous studies have shown that a strain isolated from one host that was not able to colonise the other host did not necessarily mean they were different species; they can be the same species with different physiological specialisations to the host in which case a *forma specialis* is usually proposed (Macedo *et al.* 2013). In this study, the strains CBS 120252 and CBS 120253 show minimal nucleotide differences for the six genes amplified: 0 (LSU), 5 (ITS), 3 (*rpb2*), 2 (*actA*), 2 (*gapdh*) and 5 (*tef1*-α). We propose that this is the same species and synonymise *Cercosporella centaureicola* and *C. acroptili* under *R. acroptili*, since this is the older name. These strains fall in the *Ramularia* clade (Fig. 1, clade XIV, 1/100) and cluster in a highly supported clade based on BA, ML and PA phylogenetic analysis (Fig. 2, clade 2, 1/100).

Ramularia actinidiae Ablak., Bot. Mater. Otd. Sporov. Rast. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 13: 244. 1960. Fig. 32.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, intermediate in the mycelium, cylindrical-oblong, (6–)11.5–15(–20) × (1.5–)2(–3) µm, with one *conidiogenous locus*, almost flat to protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with *hila* thickened, darkened and refractive. *Ramoconidia* subcylindrical, fusoid, (15–) 18–20(–28) × (1.5–)2–3 µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, fusoid, 0–1-septate, slightly narrower at the septa, (11–)17–20(–27) × 2–3 µm, in branched chains of up to four conidia. *Terminal conidia* subcylindrical, obovoid, aseptate, (7–)10–12.5(–20) × (1.5–)2(–3) µm (on SNA).

Culture characteristics: On MEA, 17 mm diam, surface convex, pale olivaceous grey, smooth flat mycelium, radially striated close to the margin, margins white and lobate, colony reverse olivaceous grey with a buff margin and radially striated; on OA, 15 mm diam, surface flat, short and uniform aerial mycelium, livid vinaceous in the centre and smoke-grey towards margin, with margins olivaceous grey, undulate and with scarce aerial mycelium, colony reverse iron-grey; on PDA, 18 mm diam, surface low convex, short and uniform aerial mycelium, pale olivaceous grey, with margins undulate, feathery, white, colony reverse iron-grey.

Description in vivo: See Braun (1998: 46).

Specimen examined: **South Korea**, Yangpyeong, on *Actinidia polygama*, 24 Oct. 2004, H.D. Shin, KUS-F20880, CBS H-22543, cultures CBS 141108 = CPC 11675, and CPC 11674.

Substrate and distribution: On *Actinidia polygama*; Russia and South Korea.

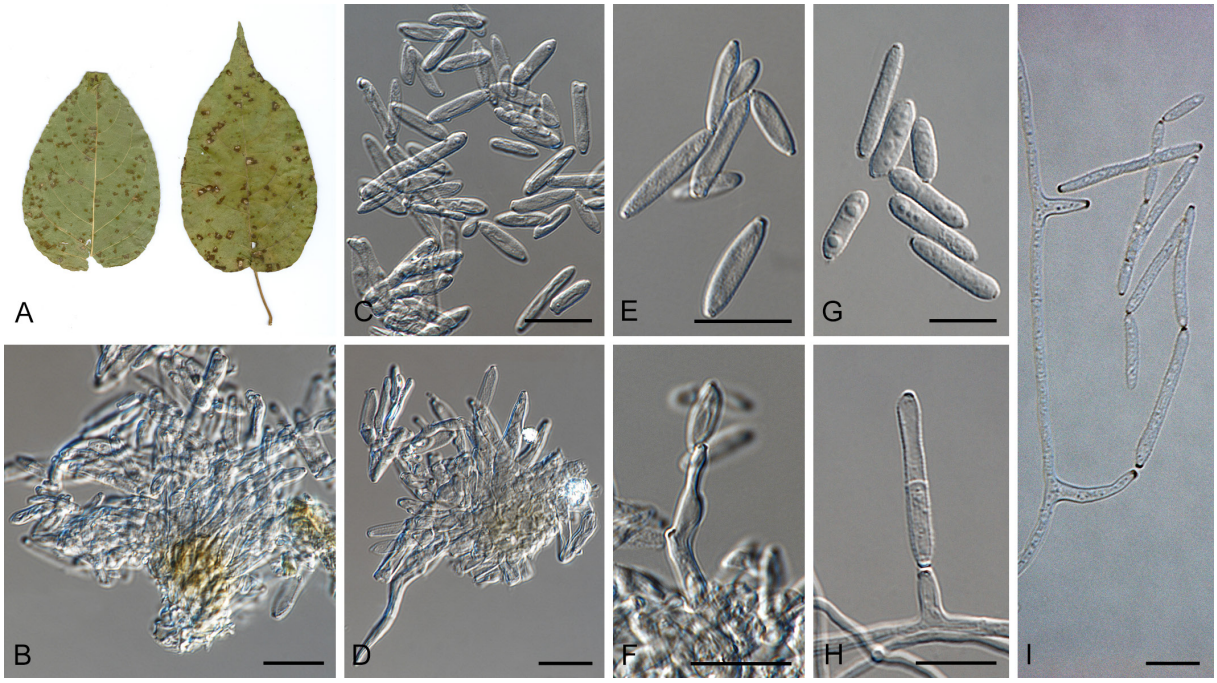


Fig. 32. *Ramularia actinidiae* (CBS 141108). A–F. Observations from herbarium material. G–I. Structures formed in culture. A. Leaf spot lesion on the host. B, D, F, H, I. Conidiophores and conidia. C, E, G. Conidia. Scale bars = 10 µm.

Notes: The description of *R. actinidiae* available in literature includes greyish caespituli, conidiophores, hyaline, simple, 20–40 µm long, conidia cylindrical, aseptate, 10.5–17 × 3 µm. The specimen observed has short conidiophores (12–)19–23(–35) × (1.5)–2–2.5(–3) µm and conidial dimensions matching the ones in culture (5–)10–12(–21) × (1.5–)2(–3) µm. *Ramularia actinidiae* was originally described on *Actinidia polygama* from Russia. Braun (1998) commented on this species being insufficiently known, and that the type material was not available for study. The strain used in this study is from a different location to that of *R. actinidiae* but the description of the morphology is quite similar (Fig. 32). It forms a single lineage supported by the Bayesian multigene analysis (Fig. 2, clade 77) and is tentatively maintained as *Ramularia actinidiae* until fresh material from the same location and host as the type has been recollected (*Actinidia polygama*, Russia).

Ramularia agastaches Sawada, Bull. Gov. Forest Exp. Sta., Meguro 105: 85. 1958. Fig. 33.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, terminal or intermediate in the mycelium, cylindrical-oblong, (8.5–)11–13(–16) × 1.5–2(–2.5) µm, with one or two conidiogenous loci, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical, clavate, ovoid, (11–)15–18(–27) × (2.5–)3–3.5(–4) µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, 0–1-septate, (11–)13.5–15.5(–21) × 3(–4) µm, in branched chains of up to six conidia. *Terminal conidia* subcylindrical, obovoid, aseptate, (4–)8–10(–13)

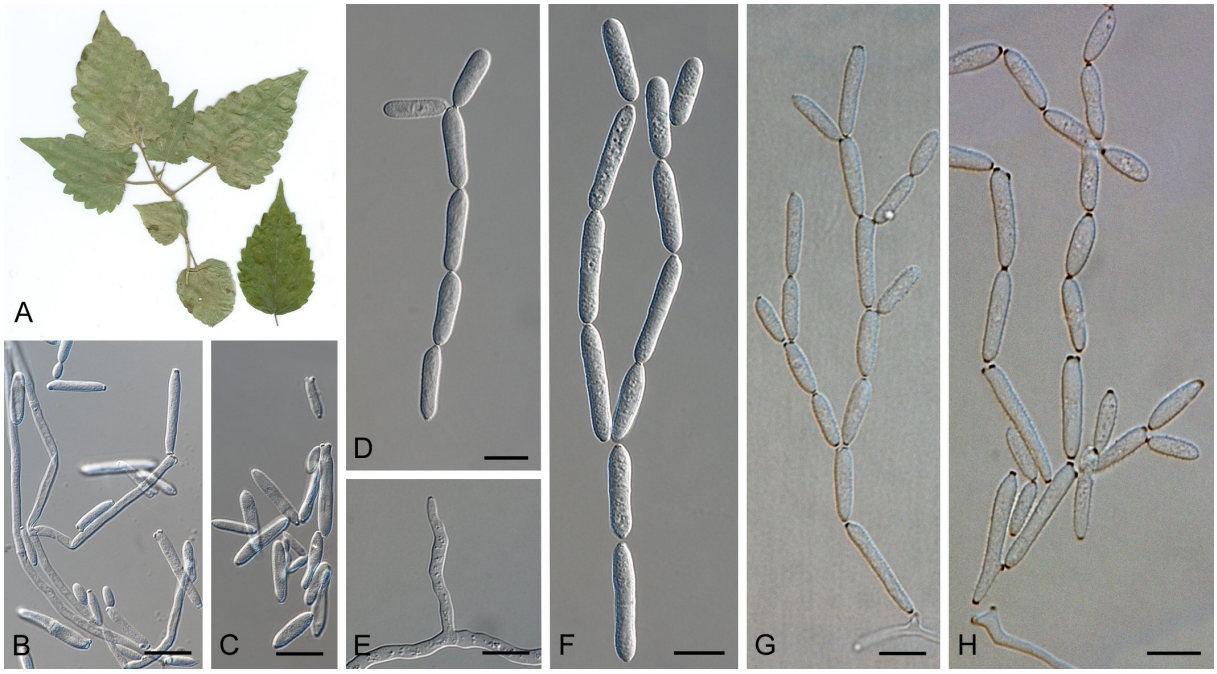


Fig. 33. *Ramularia agastaches* (CPC 10820). A–C. Observations from herbarium material. D–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, G, H. Conidiophores, conidiogenous cells and conidia. C, D, F. Conidia. E. Conidiophore. Scale bars = 10 µm.

× (2–)3(–4) µm (on SNA).

Culture characteristics: On MEA, 12 mm diam, surface raised, strongly folded, pale olivaceous grey, smooth, with margins crenate, reverse olivaceous grey; on OA, 10 mm diam, surface convex, pale olivaceous grey, fluffy aerial mycelium, with margins undulate, reverse olivaceous grey; on PDA, 10 mm diam, surface raised, pale olivaceous grey with white patches, fluffy aerial mycelium, with margins undulate, reverse rosy buff with olivaceous grey patches.

Specimen examined: **South Korea**, Hoengseong, on *Agastache rugosa*, 10 Oct. 2003, H.D. Shin, KUS-F19865, cultures CPC 10819–10821.

Substrate and distribution: On *Agastache rugosa*, East Asia (Japan, South Korea).

Notes: *Ramularia agastaches* was originally described on *Agastache rugosa* from Japan and was synonymised with *R. lamii* var. *lamii* by Braun (1998) who was not able to examine the type specimen. The strains in this clade were previously identified as *R. lamii*, which is now restricted to species in clade 67 (Fig. 2). The strains in this clade form a highly supported clade by all three methods of phylogenetic analysis (Fig. 2, clade 46, 1/100/100). Morphologically (Fig. 33) the description does not match that of *R. lamii* available in literature (Braun 1998).

Ramularia agrimoniae Sacc., Malpighia 10: 277. 1896.

Leaf spots almost absent to subcircular, pale to brownish occasionally with reddish border. *Mycelium* consisting of hyaline, branched, smooth, septate hyphae, sometimes forming small stromata internally. *Conidiophores* in loose fascicles arising from stromata, through stomata, or

solitary arising from secondary hyphae, straight, subcylindrical to geniculate-sinuous, simple, 4–30 × 1.5–4 µm, 0–1(–2)-septate, hyaline, thin-walled, smooth; *conidiogenous loci* slightly thickened and darkened. *Conidia* formed in chains, occasionally branched, ellipsoid-ovoid, fusiform, subcylindrical, 6–19.5 × 1.5–3.5(–5) µm, 0–1-septate, hyaline, thin-walled, smooth to faintly rough, ends obtuse to subacute; *hila* minute, slightly thickened and darkened. Adapted from Braun (1998).

Specimens examined: **South Korea**, Hoengseong, on *Agrimonia pilosa*, 4 Aug. 2004, H.D. Shin, KUS-F20540, cultures CPC 11450–11452, CPC 11651–11653. **Russia**, Siberia, Paseka, on *Agrimonia* sp., 19 Jun., herb. Saccardo (holotype PAD).

Substrate and distribution: On *Agrimonia* spp. (*Rosaceae*), Asia, Caucasus, Europe.

Note: *Ramularia agrimoniae* was originally described on *Agrimonia* sp. from Siberia, Russia. Despite the reported distribution of this species across Europe and Asia, the available strains in this study all originate from South Korea (Fig. 2, clade 8, 1/100/100).

Ramularia alangiicola Videira, H.D. Shin & Crous, **nom. nov.** MycoBank MB817157. Fig. 34.
Basionym: *Phacellium alangii* H.D. Shin & J.D. Kim, Mycotaxon 81: 341. 2002, non *Ramularia alangii* Hasija, 1962.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, cylindrical-oblong, straight, unbranched, (11–)24.5–35.5(–67) × (1.5–)2(–3) µm, or reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium or terminal on the conidiophore, cylindrical-oblong, (6–)11–15.5(–27) × (1.5–)2(–3) µm, with 1–2 conidiogenous loci almost flat to protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth to slightly verruculose, catenate, aseptate, with hila thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong to clavate, (10–)12.5–14(–19) × (1.5–)2(–2.5) µm, with 2–3 apical hila. *Intercalary conidia* cylindrical-oblong, (8.5–)11–12(–16) × (1.5–)2(–2.5) µm, in branched chains of up to five conidia. *Terminal conidia* obovoid, (6–)8.5–9.5(–11.5) × (1.5–)2 µm.

Specimens examined: **South Korea**, Chuncheon, on leaves of *Alangium platanifolium* var. *macrophyllum*, 11 Oct. 2002, H.D. Shin, KUS-F19227, culture CPC 10299; Chuncheon, on living leaves of *Alangium platanifolium* var. *macrophyllum*, 29 Sep. 2000, H.D. Shin (holotype KUS-F17673, isotype HAL 1656 F).

Substrate and distribution: Only known from the type collection.

Notes: *Phacellium alangii* was originally described on *Alangium platanifolium* var. *macrophyllum* from South Korea (holotype in KUS). *In vivo*, this species produced long and septate conidiophores grouped in synnemata (90–340 × 20–50 µm) and conidia solitary or in short chains (5–42 × 2–5 µm) (Shin & Kim 2002). At the time it was described (Shin & Kim 2002), it was compared with *Ramularia alangii* but found different since the later has short and aseptate conidiophores (10–35 × 3–6.5 µm) and longer and wider catenate conidia (20–45 × 3–4.5 µm). *Ramularia alangii* was only known from the type location (on *Alangium salviifolium*

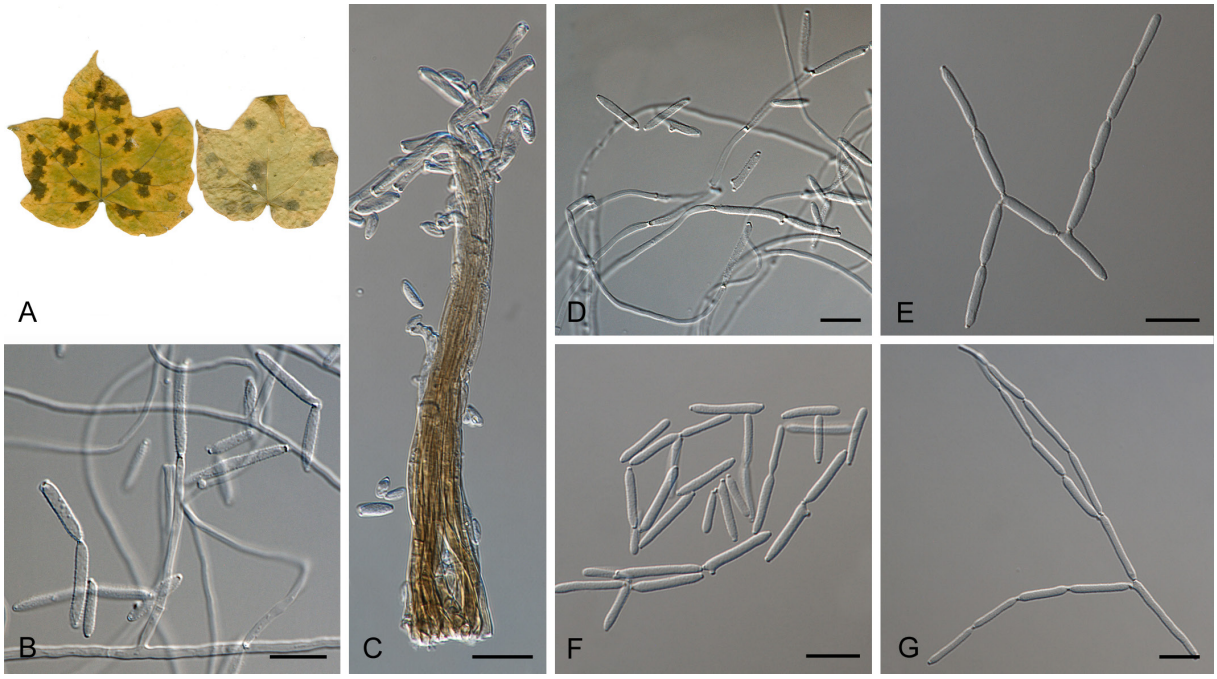


Fig. 34. *Ramularia alangiicola* (CPC 10299). A, C. Observations from herbarium material. B, D–G. Structures formed in culture. A. Leaf spot symptoms on the host. B, C, D. Conidiophores and conidia. E–G. Conidia. Scale bars = 10 µm.

[= *A. lamarckii*] from India) and this fact, together with the morphological differences, supported *Phacellium alangii* as a new species. In the herbarium specimen from which isolate CPC 10299 was derived, we observed that the conidiophores grow in synnemata that are hyaline to pale brown (Fig. 34, C). In culture, the synnemata were not observed, the conidiophores and conidia were shorter and narrower than the ones described in the original publication (Shin & Kim 2002). Since the species formed a distinct single lineage in the *Ramularia* clade (Fig. 1, clade XIV) and the production of synnemata is no longer considered a reliable character to separate *Ramularia* from *Phacelium*, a new combination is proposed. Because the epithet "*alangii*" is already occupied in *Ramularia* for a different species, the new epithet "*alangiicola*" is introduced.

Ramularia aplospora Speg., Dec. Mycol. Ital. no. 105. 1879. Fig. 35.
≡ *Ovularia aplospora* (Speg.) Magnus, Hedwigia 44: 17. 1904.
= *Ramularia schroeteri* J.G. Kühn, Hedwigia 20: 147. 1881.
≡ *Ovularia schroeteri* (J.G. Kühn) Sacc., Syll. Fung. 4: 140. 1886.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–3(–5)-septate, cylindrical-oblong, straight and apically geniculate-sinuous, unbranched (22–)40–60(–135) × (1–)2(–3) µm. *Conidiogenous cells* terminal in conidiophores, cylindrical-oblong to sinuous, narrower at the top, (10.5–)19–24(–40) × (1–)1.5–2(–2.5) µm, with multiple conidiogenous loci almost flat to protuberant in a terminal and lateral position, thickened, darkened, refractive. *Conidia* hyaline, thin-walled, smooth to slightly verruculose, catenate, with hila thickened, darkened and refractive. *Ramoconidia* ellipsoidal to oval, (8.5–)10–11(–13) × (3.5–)5–6(–7) µm, aseptate, with 2 apical

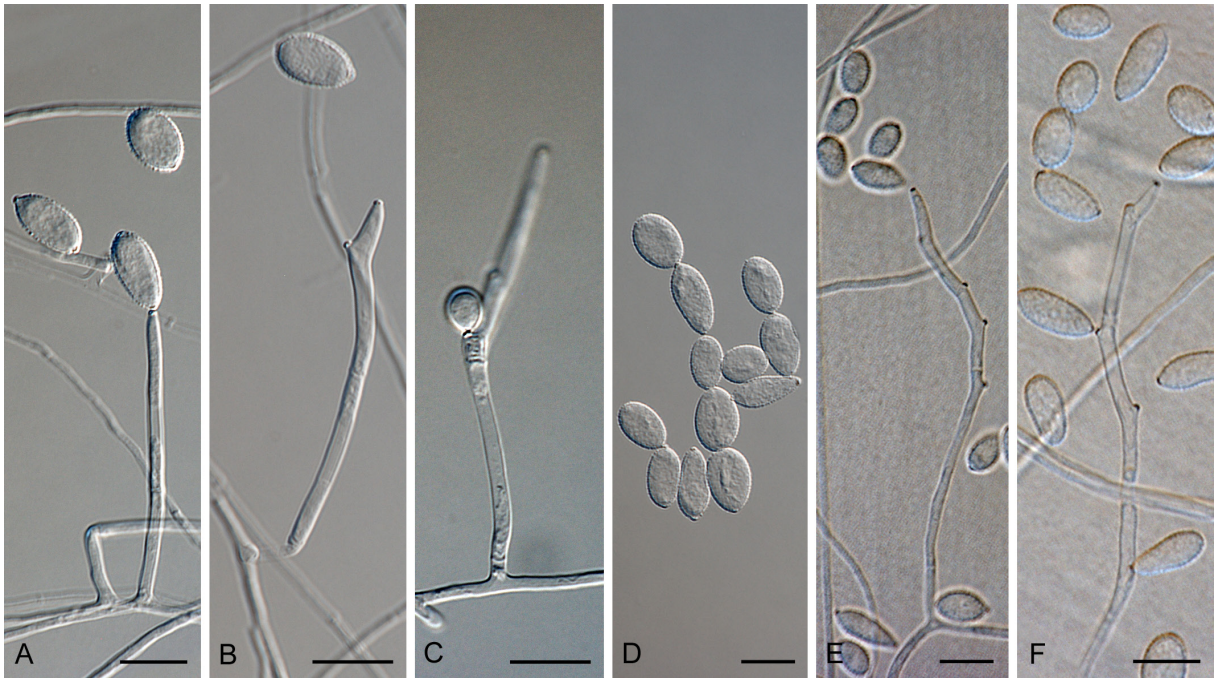


Fig. 35. *Ramularia aplospora* (CBS 545.82). A–F. Structures formed in culture. A–C, E, F. Conidiophores, conidiogenous cells and conidia. D. Conidia. Scale bars = 10 µm.

hila. *Intercalary conidia* ellipsoidal to oval, 0–1-septate, (8–)10–11(–14) × (4–)5–5.5(–7) µm, in branched chains of up to five conidia. *Terminal conidia* ellipsoidal to obovoid, aseptate, (5.5–)7.5–8.5(–11) × (3.5–)4.5–5.5(–6.5) µm.

Culture characteristics: On MEA, 20 mm diam, surface low convex, smooth, greenish grey, producing small droplets of hyaline exudate on top of the mycelium, radially striated with margins undulate and concave, colony reverse olivaceous grey, broken radially; on OA, 16 mm diam, surface low convex, smooth, pale olivaceous grey producing small droplets of hyaline exudate on top of the mycelium, with margins with an entire edge and with sparse buff mycelium, with a discolouration halo in the media around the colony margins, colony reverse buff and olivaceous grey; on PDA, 18 mm diam, surface low convex, smooth, grey olivaceous, margins feathery with an entire edge, colony reverse olivaceous grey.

Description in vivo: See Braun (1998: 242).

Specimens examined: **Austria**, Tirol, Ober Inntal, Samnaum Gruppe, Lazidalm near Serfaus, on leaf spot from *Alchemilla vulgaris*, 8 Aug. 2000, G. Verkley, cultures CBS 109120, CBS 109121; Ötztal, Hoch-Sölden, on leaf spot from *Alchemilla vulgaris*, 25 Jul. 2000, G. Verkley, cultures CBS 109013, CBS 109014. **Former Czechoslovakia**, on *Alchemilla xanthochlora*, unknown collector and date, isol. L. Marvanová, Nov. 1972, dep. L. Marvanová, Jan. 1973, culture CBS 237.73. **Germany**, Gössweinstein, Ober-Franken, on *Alchemilla vulgaris*, unknown collector and date, isol. T. Hijwegen, 3 Aug. 1982, dep. T. Hijwegen, Oct. 1982 (epitype, designated here, CBS H-1743, MBT204828, culture ex-epitype CBS 545.82). **Italy**, on *Alchemilla vulgaris* L., Speg., Decad. Mycol. Ital. 105 (lectotype designated in Braun 1998, PAD). **Sweden**, Uppland, Haga, Årtopet, on *Alchemilla vulgaris*, 14 Aug. 1988, E. Gunnerbeck, culture CBS 114118.

Substrate and distribution: On *Alchemilla* and *Aphanes* (*Rosaceae*); Asia, Caucasus, Europe.
Notes: In literature, *R. aplospora* is linked to the sexual morph named *Mycosphaerella alchemillicola* (Vassiljevsky 1925, Braun 1998), but experimental proof is still lacking (Videira *et al.* 2015b). The strain CBS 545.82 has previously been indicated as the type strain of the latter (Crous *et al.* 2007c) but this was not formally proposed. Therefore, and since the morphological characteristics are in agreement with the original description (Fig. 35), we formally designate CBS 545.82 as the ex-epitype strain of *R. aplospora*. This species formed a highly supported clade (Fig. 2, clade 27, 1/100/100). *Ramularia aplospora* is the only species in this genus known from the host *Alchemilla* (*Rosaceae*). *Alchemilla* plants are herbaceous perennials commonly known as "lady's mantle" and highly appreciated in gardens for their flowers and foliage (Hawke 2004).

Ramularia archangelicae Lindr., Acta Soc. Fauna Fl. Fenn. 23: 22. 1902. Fig. 36.
= *Ramularia angelicae* Höhn., Hedwigia 42: 178. 1903.
= *Cylindrosporium vaccarianum* Sacc., Nuovo Giorn. Bot. Ital., N.S., 24: 41. 1917.
= *Ramularia grantii* Dearn., Mycologia 21: 326. 1929.
= *Septocylindrium angelicae* Katsuki, Kyushu Agric. Res. 6: 42. 1953.

Mycelium consisting of hyaline, septate, branched, smooth, 0.5–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, straight, cylindrical-oblong, unbranched, (11.5–)26.5–36(–46.5) × 1.5–2(–2.5) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong, (5.5–)9.5–12(–16) × (1–)1.5–2 µm, with 1–2 apical conidiogenous loci, almost flat to short cylindrical thickened, darkened, refractive. *Conidia* hyaline, thin-walled, smooth, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, (15–)22–25(–

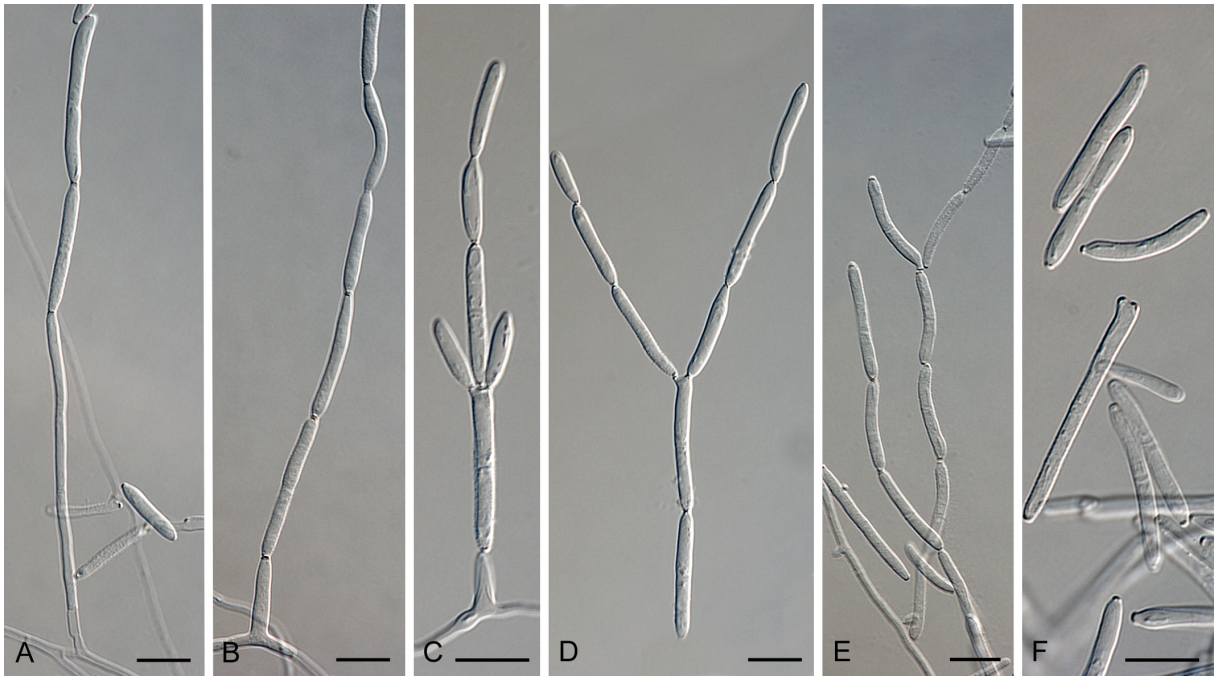


Fig. 36. *Ramularia archangelicae* (CBS 108991). A–F. Structures formed in culture. A–C. Conidiophores, conidiogenous cells and conidia. D, F. Conidia. E. Conidiogenous cell and conidia. Scale bars = 10 µm.

35) × (1.5–)2–2.5(–3) µm, 0–3-septate, with 2–3 apical hila. *Intercalary conidia* aseptate or 0–1(–2)-septate, subcylindrical, sometimes curved, (14–)18–22(–37) × (1.5–)2(–2.5) µm, in branched chains of up to seven conidia. *Terminal conidia* aseptate, subcylindrical to obovoid, (6–)10–12(–16) × 1.5–2(–2.5) µm, *hila* thickened, darkened, refractive.

Culture characteristics: On MEA, 13 mm diam, surface raised, folded, smooth, light smoke grey with pale vinaceous tinge with margins undulate, convex, feathery, colony reverse brick and with dark vinaceous patches; on OA, 16 mm diam, surface low convex, fluffy aerial mycelium, dirty white to smoke-grey, with margins crenate, producing a brick coloured pigment imbued in the agar forming a 13 mm band surrounding the colony, colony reverse dark vinaceous centre; on PDA, 16 mm diam, surface flat, smooth, pale smoke-grey with pale vinaceous tinge, forming tiny droplets of pale vinaceous exudate, with margins undulate, colony reverse pale vinaceous centre turning lighter shade towards the margin. Strains CBS 108992 and CBS 288.49 did not produce any pigment.

Description in vivo: See Braun (1998: 55).

Specimens examined: **Austria**, Ötztal, Ötz near Habichen, on leaf spot of *Angelica sylvestris*, 24 Jul. 2000, G. Verkley, cultures CBS 108991, CBS 108992, CBS 109011, CBS 109012; on stem of *Angelica sylvestris*, unknown collector and date, isol. and dep. J.A. von Arx, Jun. 1949, culture CBS 288.49. **Sweden**, Lapponia Lulensis, Sarvestjakko, on *Angelica archangelica*, 12 Aug. 1900 [Verstergr., Micromyc. Rar. Sel. Praec. Scand. 549] (neotype, designated in Braun 1998, B).

Substrate and distribution: On *Angelica* (*Apiaceae*); Asia, Europe, North America.

Notes: This species was described from *Argelica archangelica* collected in Sweden (neotype at B). The representative strains of this species cluster in a clade highly supported by BA and ML phylogenetic analyses (Fig. 2, clade 19, 1/100/100). Morphologically, the structures observed in culture (Fig. 36) are slightly narrower than those described in literature based on material *in vivo* (Braun 1998) but similar in all other characters. The strain CBS 288.49 was initially identified as *Mycosphaerella rubella*, and the type of this species was isolated from *Angelica sylvestris* from Germany. However, there is no evidence in literature of a link between these sexual and asexual names, and further studies are necessary to evaluate whether these species are conspecific.

Ramularia armoraciae Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 361 "1869" (1870) emend. U. Braun (1998). Fig. 37.
≡ *Ovularia armoraciae* (Fuckel) Massee, Brit. Fung.-Fl. 3: 321: 1893.
≡ *Cylindrospora armoraciae* (Fuckel) J. Schröt., in Cohn, Krypt.-Fl. Schlesien, 3.2(4): 485: 1897.
≡ *Entylomella armoraciae* (Fuckel) Cif., Ann. Mycol. 26: 17. 1928.
= *Ramularia matronalis* Sacc., Michelia 2(6): 123. 1880.
= *Ramularia cochleariae* Cooke, Grevillea 11(60): 155. 1883.
= *Ramularia hesperidis* Svavul. & Sandu, Mem. Sect. Şti. Acad. Română, Ser. 3, 15: 477. 1940.
For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth, 1.5–3 µm diam hyphae.

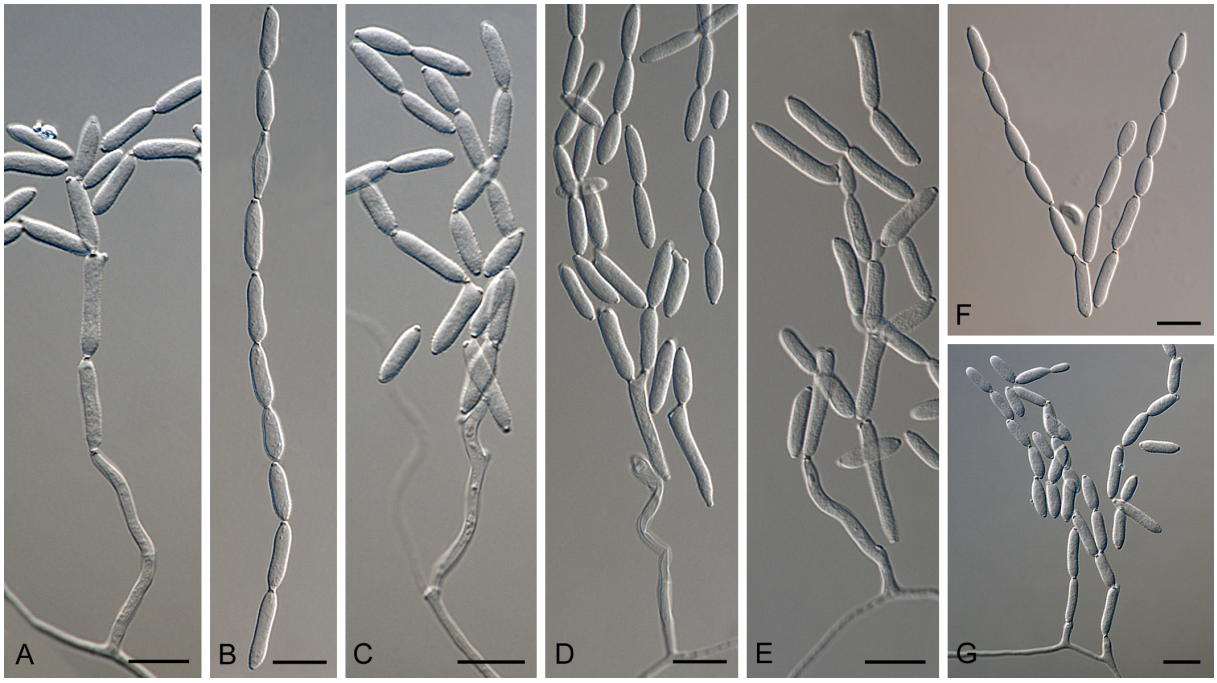


Fig. 37. *Ramularia armoraciae* (CBS 241.90). A–G. Structures formed in culture. A, C–E, G. Conidiophores, conidiogenous cells and conidia. B, F. Conidia. Scale bars = 10 µm.

Conidiophores hyaline, thin-walled, smooth, erect, septate, straight, cylindrical-oblong, geniculate-sinuous, unbranched, (12–)20–29(–41) × (1.5–)2(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong, geniculate-sinuous, (2–)12–17(–30) × (1–)1.5–2.0(–3) µm, with one to multiple apical conidiogenous loci, almost flat or slightly protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, aseptate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, (10.5–)13–14.5(–18.5) × (2.5–)3(–4) µm, with two apical hila. *Intercalary conidia* fusoid, ovoid, ellipsoid, (8–)10.5–12(–16) × (2.5–)3–3.5(–4) µm, in branched chains of up to ten conidia. *Terminal conidia* obovoid, (5–)7–8(–10) × (2–)3–3.5(–4) µm (on SNA).

Culture characteristics: On MEA, 13 mm diam, surface irregular, raised, smooth, white, with margins crenate feathery and olivaceous green, colony reverse olivaceous green; on OA, 14 mm diam, surface flat, smooth, with sparse aerial mycelium, white with olivaceous green patches, with margin irregular, with sparse aerial mycelium, colony reverse iron-grey; on PDA, 13 mm diam, surface flat, smooth, white with pale olivaceous grey patches, margins undulate, colony reverse olivaceous grey.

Description in vivo: See Braun (1998: 120).

Specimens examined: **Germany**, on *Armoracia rusticana* [Fuckel, Fungi Rhen. Exs. 133; lectotype, designated in Braun (1998), HAL]; on *Armoracia rusticana*, S. Petzoldt, unknown date (epitype designated here, CBS H-22518, MBT204829, culture ex-epitype CBS 241.90). **Netherlands**, on *Armoracia rusticana*, unknown collector and date, isol. and dep. A.L. Houwink, Nov. 1928, culture CBS 253.28.

Substrate and distribution: On various crucifers (*Brassicaceae*); Asia, Caucasus, Europe, Africa (Kenya), N. America.

Notes: *Ramularia armoraciae* was first described on *Armoracia rusticana* from Germany (lectotype in HAL). Strain CBS 241.90 originates from the same country and was isolated from the same host as the holotype, and is therefore chosen as ex-epitype (Fig. 37). Phylogenetically, this species is highly supported by the BA and ML analysis (Fig. 2, clade 55).

Ramularia asteris (W. Phillips & Plowr.) Bubák, in Kabát & Bubák, Fungi Imperf. Exs., Fasc. 8, no. 388. 1906.
Basionym: *Fusidium asteris* W. Phillips & Plowr., Grevillea 6: 23. 1877.
= *Ramularia rudbeckiae* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 34: 47. 1881.
= *R. macrospora* var. *asteris* Trel., Preliminary list of the parasitic fungi of Winsconsin: 13. 1884.
= *Ramularia asteris-tripolii* Jaap, Verh. Bot. Vereins Prov. Brandenburg 50: 48. 1908.
= *R. serotina* var. *stomaticola* U. Braun, Nova Hedwigia 58: 199. 1994.
For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 259).

Specimens examined: **Netherlands**, on *Aster tripolium*, unknown collector and date, isol. v.d. Molen, dep. Oct. 1921, culture CBS 131.21. UK, Kings Lynn, on *Aster tripolium*, 10/5, Plowright (holotype K).

Substrate and distribution: On *Aster*, *Galatella*, *Grindelia*, *Heteropappus*, *Rudbeckia*, *Solidago* (*Asteraceae*); Asia, Europe, N. America.

Notes: *Ramularia asteris* was first observed on *Aster tripolium* from England (holotype in K). There are specimens of *Ramularia asteris* with narrow conidia (3–5 µm) that are referred to as *R. asteris* var. *asteris*, and broader conidia (5–7 µm) that are usually referred to as *R. asteris* var. *latispora* (Braun 1998). Only one isolate was available in this study (CBS 131.21) and it forms a single lineage (Fig. 2, clade 11). The culture was unfortunately sterile and no morphological observations could be made.

Ramularia bellunensis Speg., Michelia 1(5): 475. 1879.

Description in vivo: See Braun (1998: 95).

Specimens examined: **Italy**, Belluno, on *Tanacetum parthenium*, Oct. 1878, Spegazzini [lectotype, designated in Braun (1998), PAD]. **Netherlands**, on *Argyranthemum frutescens* (≡ *Chrysanthemum frutescens*), unknown collector and date, isol. H.C. Koning, dep. Dutch Plant Protection Services, Jan. 1943, culture CBS 116.43. **New Zealand**, Auckland, Grey Lynn, on *A. frutescens*, unknown collector and date, isol. C.F. Hill, Jun. 2005, dep. C.F. Hill, culture CBS 118417.

Substrate and distribution: On *Argyranthemum*, *Chrysanthemum*, *Leucanthemum*, *Tanacetum*

(*Asteraceae*); Africa, Asia, Caucasus, Europe.
Notes: *Ramularia bellunensis* was described in 1879 from *Tanacetum parthenium*, from Italy [lectotype, designated in Braun (1998), in PAD]. This species is represented in a single lineage (Fig. 2, clade 75). This is a new report for the Netherlands and New Zealand, as well as a first report on the host *Argyranthemum frutescens* (Braun 1998). Although strain CBS 118417 is not in the phylogenetic trees, it is identical to CBS 116.43, except on one nucleotide in *gapdh* and one nucleotide in *tef1*-α. It was not included because at the time the trees were prepared we did not possess all the gene sequences. No ex-type strain of this species is available, and collections on *Tanacetum* from Italy are required to resolve its identity.

Ramularia beticola Fautrey & Lambotte, Rev. Mycol. (Toulouse) 19: 54. 1897. Fig. 38.
= *Ramularia betae* Rostr., Bot. Tidskr. 22: 272. 1898 (1899).

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–2(–4)-septate, straight to sinuous, cylindrical-oblong, unbranched (19.5–)43–58(–83) × 2–2.5(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong and narrower at the top, (7–)16.5–20(–30) × 2–2.5(–3) µm, with 1–4 apical conidiogenous loci, almost flat or protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth to slightly verruculose, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, (8–)12–14.5(–22) × 3–4 µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, sometimes curved, ovoid, 0–1-septate, (8.5–)10.5–12.5(–20) × (2.5–)3(–4) µm, in branched chains of up to eight conidia. *Terminal conidia* subcylindrical to obovoid, aseptate, (3.5–)6.5–8(–11) × (2–)3(–5) µm (on SNA).

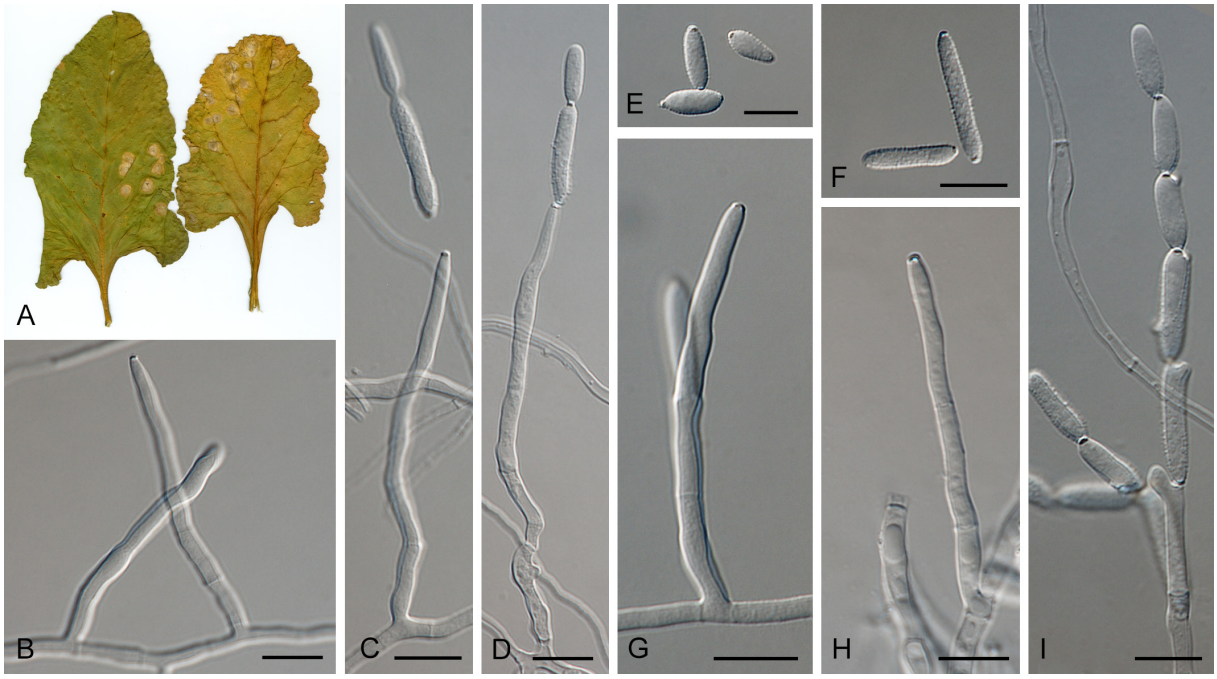


Fig. 38. *Ramularia beticola* (CBS 141109). A. Observations from herbarium material. B–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, G, H. Conidiophores and conidiogenous cells. C, D, I. Conidiophores, conidiogenous cells and conidia. E, F. Conidia. Scale bars = 10 µm.

Culture characteristics: On MEA, 13 mm diam, surface irregular, raised, smooth, white, with margins crenate feathery and olivaceous green, colony reverse olivaceous green; on OA, 14 mm diam, surface flat, smooth, with sparse aerial mycelium white with olivaceous green patches, with margin irregular, with sparse aerial mycelium, colony reverse iron-grey; on PDA, 13 mm diam, surface flat, smooth, with white to pale olivaceous grey patches, margins undulate, colony reverse olivaceous grey.

Description in vivo: See Braun (1998: 136).

Specimens examined: **Denmark**, Holeby, on leaf spot on *Beta vulgaris*, 2011, A.L. Hansen, culture CPC 30065; Jungshoved, on leaf spot on *Beta vulgaris*, 2011, A.L. Hansen, culture CPC 30653. **France**, Dumont, on *Beta vulgaris* L., 1896, Fautrey [Roum., Fungi Sel. Exs. 7261; lectotype, designated in Braun (1998), PC]; Fresney-l'Évêque, on leaf spot on *Beta vulgaris*, 2011, A. Champeil, epitype designated here CBS H-22519, MBT204830, culture CBS 141109 = CPC 30066). **Germany**, Bonn, on unknown host, unknown collector and date, isol. and dep. H.A. Diddens, Jan. 1929, culture CBS 341.29. **Netherlands**, Groningen, leaf spot on *Beta vulgaris*, 2011, S.I.R. Videira, culture CPC 30067; Steenbergen, leaf spot on *Beta vulgaris*, 2011, S.I.R. Videira, cultures CPC 30063, CPC 30064. **Switzerland**, Nyon, on *Beta vulgaris*, unknown collector and date, isol. B. Lieberherr, dep. R. Corbaz, Feb. 1967, culture CBS 151.67.

Substrate and distribution: On *Beta* (*Chenopodiaceae*); Asia, Europe, North America.

Notes: *Ramularia beticola* (Fig. 38) is the causal organism of Ramularia leaf spot disease in sugar beet, table beet and fodder beet. The fungus forms pale brown leaf spots and affected leaves turn yellow, become necrotic and die. The impact of Ramularia leaf spot disease can vary significantly from season to season. Conditions of high humidity, moderate temperature (17–20 °C), high plant density and sulphur deficiency usually increase disease intensity and damage. It has been reported from North America (Oregon, Washington, California and Colorado), Europe (Ireland, UK, the Scandinavian countries, Belgium, France, Germany) and Russia (Harveson *et al.* 2009). Worldwide, yield losses in sugar beet due to plant pathogens and pests are estimated in general to be 26 % with, and more than 80 % without crop protection (Oerke & Dehne 2004). In the Netherlands, in spite of crop protection measures, the yield losses due to pests and diseases for top growers were 37.1 and 16.7 % on sandy and clay soils respectively (Hanse *et al.* 2011). When treatments are applied timely, programmes of disease control in Denmark increased sugar yield by 10 %. Thus far, *R. beticola* has not shown signs of developing resistance to either strobilurin or triazol fungicides, but it remains important to apply fungicides efficiently by following monitoring programmes and respecting the recommended thresholds (www.FRAC.info) (Thach *et al.* 2013). *Ramularia beticola* was described on *Beta vulgaris* from France in 1896. The strains used in this study clustered together in a single and highly supported clade (Fig. 2, clade 52, 1/100/100).

Ramularia bosniaca Bubák, Österr. Bot. Z. 53: 49. 1903. Fig. 39.
= *Ramularia scabiosae* Rostr. ex Lind, Danish Fungi: 511. 1913.
= *Ramularia scabiosae* Jaap, Ann. Mycol. 15: 122. 1917.

Mycelium consisting of hyaline, septate, branched, smooth, 1–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–2(–4)-septate, straight to geniculate-sinuous, cylindrical-

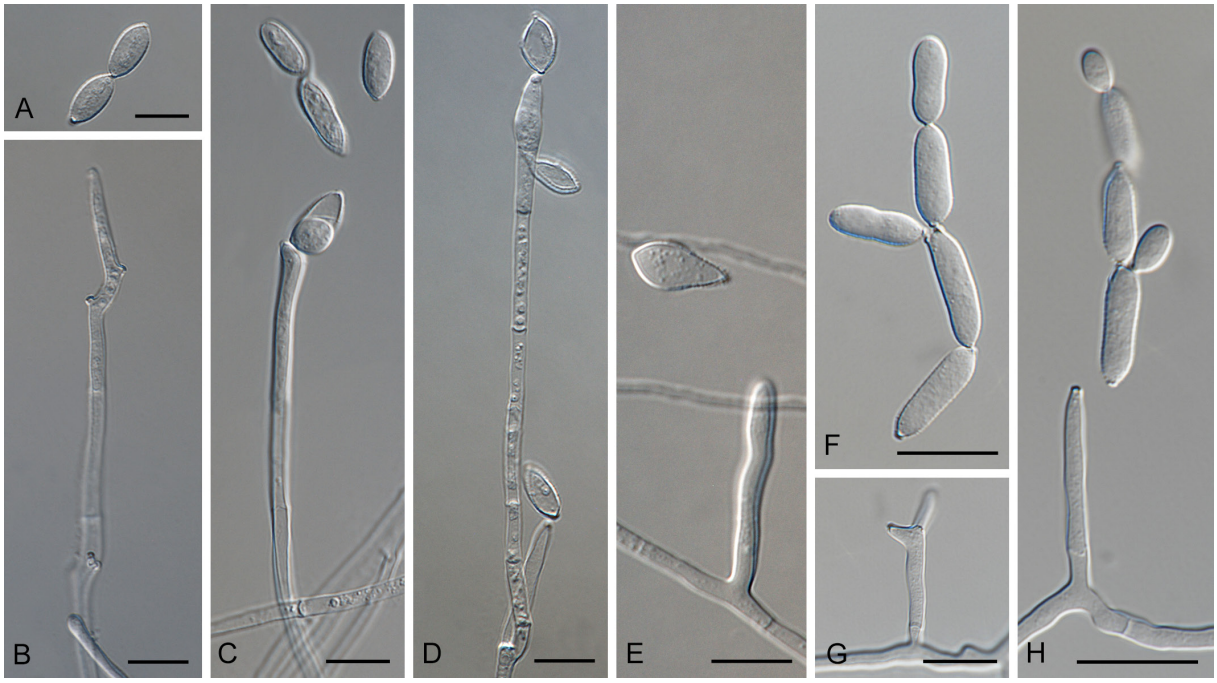


Fig. 39. *Ramularia bosniaca* (CBS 123880). A–H. Structures formed in culture. A, F. Conidia. B, G. Conidiophores. C, D, E, H. Conidiophores and conidia. Scale bars = 10 µm.

oblong, unbranched, (20–)41–60(–119) × 2–2.5(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong and narrower at the top, geniculate-sinuous, (14–)19–23(–35) × 2–2.5(–3) µm, with nidiogenous loci, almost flat or protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, solitary or catenate, aseptate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to ovoid, (7.5–)10–11(–14) × (3–)4–4.5(–5) µm, with two apical hila. *Intercalary conidia* ovoid, 0–1-septate, (8–)9.5–0.5(–13) × (3–)4–5(–7) µm, in branched chains of up to four conidia. *Terminal conidia* obovoid, (5–)7–8(–10) × (2.5–)4(–5) µm (on SNA).

Culture characteristics: On MEA, 13 mm diam, surface irregular, raised, smooth, white, with margins crenate, feathery and olivaceous green, colony reverse olivaceous green; on OA, 14 mm diam, surface flat, smooth, with sparse aerial mycelium white with olivaceous green patches, with margin irregular, with sparse aerial mycelium, colony reverse iron-grey; on PDA, 13 mm diam, surface flat, smooth, with white with pale olivaceous grey patches, margins undulate, colony reverse olivaceous grey.

Description in vivo: See Braun (1998: 143).

Specimen examined: **Czech Republic**, Moravia, Pavlov, forest around the ruin, leaf spot on *Scabiosa ochroleuca*, 18 Nov. 2008, G. Verkley, cultures CBS 123880, CBS 123881.

Substrate and distribution: On *Scabiosa* (*Dipsacaceae*); Central Asia, Caucasus, Europe.

Notes: *Ramularia bosniaca* was originally described on the host *Scabiosa columbaria* in Bosnia

(holotype BPI 416442 [the neotype designated in Braun (1998), BPI 416443, is obsolete since holotype material has been traced in BPI]) and is the only species of *Ramularia* known to infect *Scabiosa* (Braun 1998). *Ramularia bosniaca* has been reported from several European countries but this is the first time it is reported from the Czech Republic. The description of these collections fit that of *R. bosniaca* (Braun 1998), except that conidia were shorter than 28 µm (Fig. 39). Additional collections from Montenegro may well reveal the strains from the Czech Republic to represent a new species. The phylogenetic analysis provides good support to this species clade (Fig. 2, clade 60, 1/100/100).

Ramularia buniadis Vestergr., Jahreskat. Wiener Kryptog. Tauschanst.: 4. 1897.

Specimens examined: **Sweden**, Uppsala, Skottsbacke, X. 1897 [Vestergr., Micromyc. Rar. Sel. Praec. Scad. 73; lectotype, designated in Braun (1998), S-F57272]. **Sweden**, Uppland, Haga, Årtopet, on *Bunias orientalis*, 16 Sep. 1988, E. Gunnerbeck, culture CBS 114301 = UPSC 2718.

Substrate and distribution: On *Bunias orientalis* (*Brassicaceae*); Caucasus, Europe.

Notes: This species was described on *Bunias orientalis* collected in Sweden (lectotype in S). *Ramularia buniadis* (among other names) was synonymised with *R. armoraciae*, but since *R. armoraciae* clusters in clade 55 (Fig. 2), the name *R. buniadis* is again resurrected for this isolate (Fig. 2, clade 48). Although this isolate could be considered a good representative for epitypification, it is sterile in culture and no herbarium material of the CBS isolate was preserved.

Ramularia calcea Ces., in Rabenhorst, Klotzschii Herb. Viv. Mycol., Ed. 1, Cent. 17: no. 1681, Dresden 1852, emend. U. Braun (1998). Fig. 40.
= *Hormodendrum farinosum* Bonord., Bot. Zeitung 19: 196. 1861.
= *Ovularia symphyti-cordati* SVavul. & Sandu, Hedwigia 73: 107. 1933.
= *Ramularia trachystemonis* Siemaszko, Mat. Mikol. Fitopatol. Ross., I, 3: 39. 1915.
= *Ramularia noneae* Lobik, Bolez. Rast. 17: 190. 1928.
For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth, 0.5–1.5 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, intermediate in the mycelium, cylindrical-oblong, (5.5–)10.5–13(–17) × 1–1.5(–2) µm, with one or two conidiogenous loci, almost flat to protuberant, thickened, darkened and refractive, 1 µm diam. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong to oval, (7–)9.5–12(–23) × (1.5–)2(–2.5) µm, 0–1-septate, with 2–4 apical hila. *Intercalary conidia* cylindrical-oblong, ellipsoid or fusoid, aseptate, (4.5–)7–8(–11) × (1.5–)2(–2.5) µm, in branched chains of up to seven conidia. *Terminal conidia* obovoid, aseptate, (3–)4–4.5(–6) × (1–)1.5–2 µm (on SNA, CBS 101613).

Culture characteristics: On MEA, 17 mm diam, surface raised, folded, erumpent aerial mycelium, vinaceous-buff, with margins lobate, convex, feathery, colony reverse brown-vinaceous and fawn margin; on OA, 15 mm diam, surface raised, folded, erumpent aerial mycelium, vinaceous-buff, with margins undulate, rosy-vinaceous and no aerial mycelium,

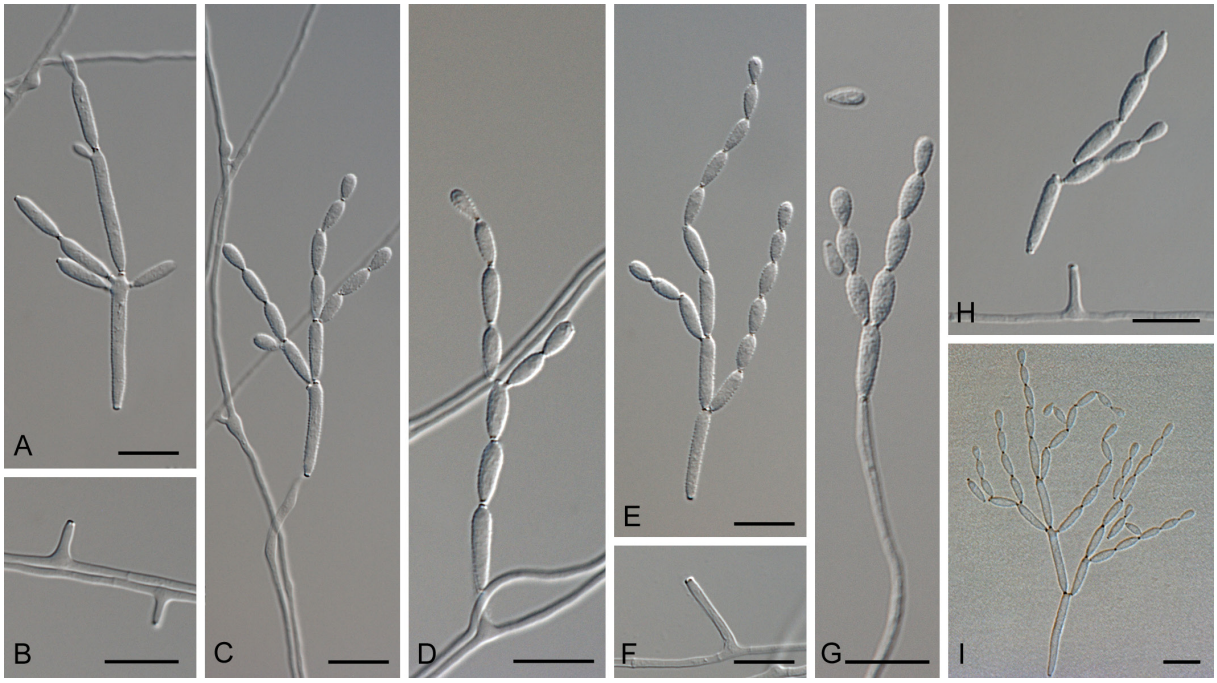


Fig. 40. *Ramularia calcea* (CBS 101613). A–I. Structures formed in culture. A, E, I. Conidia. B, F. Conidiophore reduced to conidiogenous cell. C, D, G, H. Conidiophore and conidia. Leaf spot symptoms on the host. Scale bars = 10 µm.

colony surrounded by a 0.5 cm discoloured halo, colony reverse vinaceous; on PDA, 14 mm diam, surface greyish lilac, erumpent, convex, with margins pale vinaceous, undulate, colony surrounded by pale vinaceous pigment diffusing into the media, colony reverse vinaceous.

Description in vivo: See Braun (1998: 112).

Specimens examined: **Germany**, Thüringen, Weimar, brown leaf spot on *Symphytum* sp., 1999, G. Arnold, cultures CBS 101612, CBS 101613. **Italy**, Vercellis, 1851, Cesatis [Rabenh., Klotzschii Herb. Viv. Mycol. 1681; lectotype, designated in Braun (1998), HAL]. **Sweden**, Uppland, Vassunda, on *Viola hirta*, 11 Sep. 1988, E. Gunnerbeck, culture CBS 114442.

Substrate and distribution: On *Nonea*, *Symphytum*, and *Trachystemon* spp. (*Boraginaceae*); Asia, Caucasus, Europe.

Notes: *Ramularia calcea* is a species with a wide distribution within Europe that was originally described on *Symphytum officinale* from Italy. Morphologically, the strains in this clade have conidiophores reduced to conidiogenous cells and narrower conidia (Fig. 40) than the *in vivo* description of *R. calcea* found in literature (Braun 1998), in which the conidiophores are small and sometimes deeply forked [10–80 × (2–)3–6(–7) µm], and conidia are wider [(5–)8–24(–26.5) × (2.5–)3–7(–8) µm]. Unfortunately, the herbarium specimen from which the culture was retrieved was not preserved which made it impossible to assess the morphological characters of this species on host tissue. The clade formed by these two strains is highly supported by the phylogenetic analysis (Fig. 2, clade 42). Strain CBS 299.49 (Fig. 2, clade 36) is also under the name *R. calcea* in the CBS database, but since this is sterile it will be treated as *Ramularia* sp. C.

Therefore, the correct phylogenetic placement of this species remains unresolved until material from the type host and location is recollected. *Ramularia calcea* has been reported on *Symphytum officinale* in both Germany and the Netherlands, among other countries. The morphological characteristics of CBS 114442 are identical to CBS 102612 and 102613, therefore, until more collections become available, these strains will be treated as *R. calcea* here.

Ramularia carneola (Sacc.) Nannf., in Lundell & Nannf., Fungi Exs. Suec., Fasc. XXXIX–LX, Sched.: 25. 1950.
Basionym: *Ovularia carneola* Sacc., Fungi ital. Del., Tab. 975. 1881.
= *Ovularia duplex* Sacc., Fungi ital. Del., Tab. 876. 1881.
= *Ramularia scrophulariae* Fautery & Roum., Revue Mycol. (Toulouse): 81. 1891.
= *R. nicolai* Bubák, Sitzungsber. Königl. Böhm. Ges. Wiss. Prag: 19. 1903.
= *R. borghettiana* C. Massal., Malpighia 25: 14. 1912.
= *R. nodosa* Tho, Novosti Sist. Nizsh. Rast. 9: 204. 1972.

Description in vivo: See Braun (1998: 264).

Specimens examined: **France**, Rouen, on *Scrophularia nodosa*, Letendre, herb. Saccardo (holotype PAD). **Netherlands**, Utrecht Prov., Baarn, de Hooge Vuursche, leaf spot on *Scrophularia nodosa*, 22 Jun. 2000, G. Verkley, cultures CBS 108975–108978; Goedereede, Kwade Hoek nature reserve parking, leaf spot on *Scrophularia nodosa*, 13 Sep. 2001, G. Verkley, culture CBS 109847.

Substrate and distribution: On *Scrophularia* (*Scrophulariaceae*); Asia, Caucasus, Armenia, Europe, N. America.

Notes: *Ramularia carneola* is a pathogen of *Scrophularia* spp. that are commonly known as figworts. It was first described on *Scrophularia nodosa* from France (holotype in PAD). Although *R. carneola* has a broad geographical distribution, this is the first record for the Netherlands. The strains of this species cluster together in a clade highly supported by the BA and ML phylogenetic analyses (Fig. 2, clade 49, 1/100).

Ramularia cerastiicola (Crous) Videira & Crous, **comb. nov.** MycoBank MB816933.
Basionym: *Mycosphaerella cerastiicola* Crous, IMA Fungus 2: 55. 2011.

Specimen examined: **Netherlands**, Flevoland, on *Cerastium semidecandrum*, 2 May 2004, A. Aptroot (holotype CBS H-20549, culture ex-type CBS 115913 = CPC 11290).

Notes: When this species was initially described, both the ITS and LSU sequences placed it within the genus *Ramularia* but the cryptic nature of the asexual morph, with its septoria- to pseudocercosporella-like morphology, baffled the researchers (Crous *et al.* 2011c). Based on all three phylogenetic analyses performed on the five-gene alignment, this species forms a single lineage (Fig. 2, clade 14) closely related to *Ramularia stellariicola*.

Ramularia chamaedryos (Lindr.) Gunnerb., Svensk Bot. Tidskr. 61: 135. 1967. Fig. 41.
Basionym: *Ovularia chamaedryos* Lindr., Acta Soc. Fauna Fl. Fenn. 23: 7. 1902.
= ?*Ramularia veronicae* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 361. 1869. (1870)

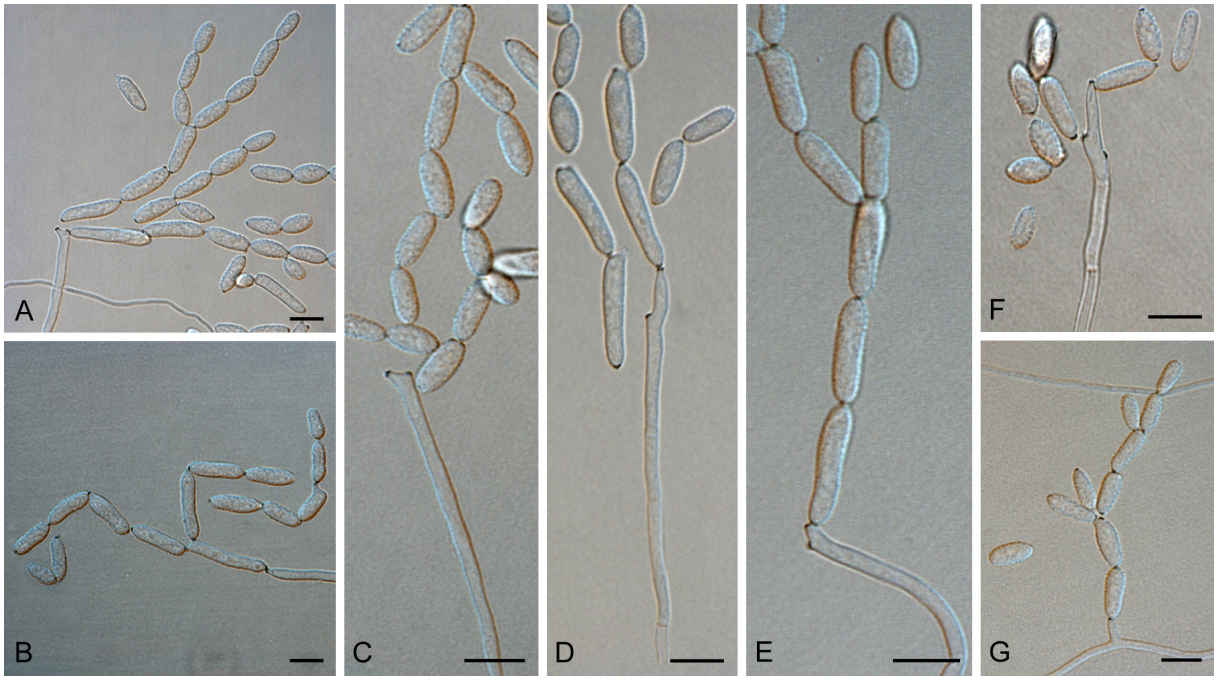


Fig. 41. *Ramularia chamaedryos* (CBS 116577). A–G. Conidiophores, conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

≡ *Ovularia veronicae* (Fuckel) Sacc., Fungi ital. Del., t. 974. 1881.
= ?*Ramularia beccabungae* Fautrey, Revue Mycol. (Toulouse) 14: 10. 1892.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, straight, cylindrical-oblong, unbranched, (24.5–)60–92(–230) × 1.5–2(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong, geniculate-sinuous, (14–)20–26(–44) × 2–3 µm, with 1–4 apical conidiogenous loci, almost flat or protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, aseptate, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical, clavate, ovoid, (9.5–)15–19(–31.5) × (3–)3.5–4(–5) µm, with two apical hila. *Intercalary conidia* subcylindrical, fusoid, ovoid, (9–)11–13(–22) × (3–)3.5–4(–4.5) µm, in branched chains of up to five conidia. *Terminal conidia* obovoid, (6.5–)8–9(–11) × (3.5–)4(–5) µm (on SNA, CBS 116577).

Culture characteristics: On MEA, 8 mm diam, surface smooth, smoke-grey, with margins undulate, feathery and olivaceous grey, colony reverse olivaceous grey; on OA, 10 mm diam. Surface smooth, with fuffy aerial mycelium, light grey with olivaceous green patches, with margin irregular, with sparse aerial mycelium, colony reverse iron-grey; on PDA, 9 mm diam, surface smooth, buff to smoke-grey, margins crenate, colony reverse olivaceous.

Description in vivo: See Braun (1998: 258).

Specimens examined: **Latvia**, Vidzeme, on *Veronica chamaedrys*, 1936, Smarods [neotype, designated in Braun (1998), JE]. **Sweden**, Uppland, Uppsala Näs parish, Vängelstra, on *Veronica chamaedrys*, 29 Sep. 1986, E. Gunnerbeck, culture CBS 116577. **New Zealand**, Auckland, St.

Johns, on *Veronica persica*, unknown collector and date, isol. C.F. Hill, Oct. 2005, dep. C.F. Hill, culture CBS 118794. **South Korea**, Samcheok, on *Veronica didyma*, 8 May 2003, H.D. Shin, KUS-F19441, culture CBS 113307; Taean, on *Veronica persica*, 17 Apr. 2007, H.D. Shin & M.J. Park, KUS-F22542, culture CBS 131773 = KACC 42885. **Sweden**, Uppland, Knivsta, on *Veronica anagallis-aquatica*, 22 Sep. 1989, E. Gunnerbeck, culture CBS 114731.

Substrate and distribution: On *Veronica* (*Scrophulariaceae*); Europe, Korea, New Zealand.

Notes: The description of CBS 116577 fits the morphology of *R. chamaedryos*. *Ramularia veronicae* and *R. beccabungae* are similar, but differ *in vivo* in having septate conidia. *Ramularia chamaedryos* is only known from *Veronica chamaedryos* (*Scrophulariaceae*) and was originally described from Finland [type not preserved, neotype designated in Braun (1998), in JE]. *Ramularia veronicae* is known from several *Veronica* spp. worldwide with the exception of Australia and Antartica. *Ramularia beccabungae* has been described from several *Veronica* spp. in Europe and Asia. Some *Ramularia* species have been shown to be plurivorous while others can be seen as host specific. Phylogeny based on five partial gene sequences places sequences retrieved from *Ramularia* on *Veronica chamaedrys* (as ?*R. chamaedryos*), *V. persica* (as ?*R. veronicae*, but not the type host) and *V. anagallis-aquatica* (as ?*R. beccabungae*) in the same clade (Fig. 2, clade 61, 1/100/100), suggesting that a single species is involved. However, this assumption is still vague and unproven since the description of the sporulation *in vitro* is only based on a culture of *R. chamaedryos* on *Veronica chamaedrys* (Fig. 41). Sporulating cultures of *R. veronicae* and *R. beccabungae* based on isolations from the type hosts are necessary for comparison and to evaluate and explain possible differences in the conidial septation between *in vivo* and *in vitro* material. Therefore, a final taxonomic conclusion is not yet possible.

Ramularia chelidonii (Jacz.) Karak., Fungi Imperfecti Parasitici. I. Hyphomycetes: 123. 1937.
Basionym: *Didymaria chelidonii* Jacz., Fungi Ross. Exs. 349. 1899.
= *Ramularia hylomeconis* Naumov, Bull. Trimestriel Soc. Mycol. France 30: 80. 1914.

Description in vivo: See Braun (1998: 197).

Specimens examined: **Russia**, Far East, Amur, near Radde Station, on *Hylomecon japonica* (≡ *Chelidonium japonicum*), 28 May/9 Jun. 1895, Komarov [Jacz. *et al*., Fungi Ross. Exs. 349; lectotype, designated in Braun (1998), LE 40741]. **South Korea**, Hongcheon, on *Hylomecon vernalis*, 6 Jun. 2005, H.D. Shin, KUS-F21198, cultures CPC 12208, CPC 12209; Yangpyeong, on *Hylomecon vernalis*, 4 Jun. 2003, H.D. Shin, KUS-F19550, culture CBS 113317.

Substrate and distribution: On *Chelidonium* and *Hylomecon* (*Papaveraceae*); Asia, Caucasus, Europe (Ukraine).

Notes: *Ramularia chelidonii* was originally described on *Chelidonium japonicum* from Russia (lectotype in LE). The strains of *R. chelidonii* used in this study cluster in a highly supported clade (Fig. 2, clade 71, 1/100/100). This is the first report of this species from South Korea and on *Hylomecon*.

Ramularia coleosporii Sacc., Michelia 2(6): 170. 1880.
≡ *Cylindrosporium coleosporii* (Sacc.) J. Schröt., Krypt.-Fl. Schlesien, Pilze, 3.2(4): 493. 1897.

= *Ramularia clerodendri* Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 87: 71. 1944, nom. inval.
= *R. fagarae* Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 87: 72. 1944, nom. inval.

Description in vivo: See Braun (1998: 39).

Specimens examined: **France**, Lyon, on *Coleosporium melampyri* on *Melampyrum nemorosum*, Sep. 1879, Therry [Thüm., Mycoth. Univ. 1566; lectotype, designated in Braun (1998), HAL]. **South Korea**, Hongcheon, on *Coleosporium horianum* on *Codonopsis lanceolata*, 9 Oct. 2007, H.D. Shin & M.J. Park, culture CBS 131757 = KACC 43185; same location, date and collectors, on *Coleosporium eupatorii* on *Eupatorium lindleyanum*, culture CBS 131764 = KACC 43182; Incheon, on *Coleosporium* sp. on *Solidago gigantea*, 24 Sep. 2009, H.D. Shin & M.J. Park, culture CBS 131762 = KACC 44860; Inje, on *Coleosporium asterum* on *Aster pilosus*, 3 Oct. 2008, H.D. Shin & M.J. Park, culture CBS 131755 = KACC 43977; Jinju, on *Coleosporium horianum* on *Codonopsis lanceolata*, 13 Oct. 2008, H.D. Shin & M.J. Park, culture CBS 131759 = KACC 44073; Jecheon, on *Coleosporium clematidis-apiifoliae* on *Clematis apiifolia*, 19 Oct. 2007, H.D. Shin & M.J. Park, culture CBS 131756 = KACC 43200; Namyangju, on *Coleosporium perillae* on *Perilla frutescens* var. *japonica*, 21 Aug. 2006, H.D. Shin & M.J. Park, culture CBS 131753 = KACC 42483; Pocheon, on *Coleosporium asterum* on *Aster pilosus*, 22 Sep. 2006, H.D. Shin & M.J. Park, culture CBS 131765 = KACC 42635; Pocheon, on *Coleosporium eupatorii* on *Eupatorium japonicum*, 2 Sep. 2003, H.D. Shin, culture CPC 10669; Pocheon, on *Coleosporium eupatorii* on *Eupatorium japonicum*, 20 Aug. 2006, H.D. Shin & M.J. Park, culture CBS 131763 = KACC 42484; Pocheon, on *Aster ageratoides*, 23 Oct. 2002, H.D. Shin, culture CPC 10085; Pyeongchang, on *Coleosporium clematidis-apiifoliae* on *Clematis apiifolia*, 20 Sep. 2003, H.D. Shin, cultures CPC 10731–10733; Pyeongchang, on *Pileolaria shiraiana* on *Rhus trichocarpa*, 22 Sep. 2008, H.D. Shin & M.J. Park, culture CBS 131767 = KACC 44053; Pyeongchang, on *Coleosporium eupatorii* on *Eupatorium lindleyanum*, 20 Sep. 2003, H.D. Shin, cultures CPC 10746–10748; Pyeongchang, on *Coleosporium cacaliae* on *Syneilesis palmata*, 14 Sep. 2009, H.D. Shin & M.J. Park, culture CBS 131758 = KACC 44854; same location, date and collectors, on *Coleosporium saussureae* on *Saussurea pulchella*, culture CBS 131761 = KACC 44855; Seoul, on *Coleosporium clerodendri* on *Clerodendron trichotomum*, 2 Sep. 2007, H.D. Shin & M.J. Park, culture CBS 131766 = KACC 43058; Suwon, on *Coleosporium asterum* on *Aster pilosus*, 1 Oct. 2007, H.D. Shin & M.J. Park, culture CBS 131754 = KACC 43177; Ulleung, on *Coleosporium horianum* on *Codonopsis lanceolata*, 21 Oct. 2008, H.D. Shin & M.J. Park, culture CBS 131760 = KACC 44081; Pocheon, on *Coleosporium eupatorii* on *Eupatorium japonicum*, 2 Sep. 2003, H.D. Shin, culture CPC 10653; Pyeongchang, on *Coleosporium phellodendri* on *Phellodendron amurense*, 4 Sep. 2003, H.D. Shin, cultures CPC 10672, CPC 10673; Hoengseong, on *Coleosporium plectranthi* on *Plectranthus japonicus*, 21 Aug. 2004, H.D. Shin, culture CPC 11516.

Substrate and distribution: Mycophilic on *Chrysomyxa*, *Coleosporium* (*Coleosporiaceae*, *Pucciniales*), *Pileolaria* (*Pileolariaceae, Pucciniales*); Asia, Europe, N. America (USA), West Indies (Puerto Rico).

Notes: Only six species of *Ramularia* have been classified as mycophilic (*R. butomi*, *R. coleosporii*, *R. cylindriopsis*, *R. dichosciadii*, *R. uredinearum*, and *R. uredines*). Ķirulis (1942) stated that *R. coleosporii* does not parasitise *Coleosporium* directly but that it is confined to the

weakened tissue around the sori and that it is unrelated to other foliicolous species on the same hosts. Braun (1998) hypothesised that *R. coleosporii* could be a separate species or a collective species composed of various races since on some hosts there are morphologically similar phytopathogenic species and in other hosts this species was morphologically distinguishable from other phytopathogenic species. *Ramularia coleosporii* was originally described parasitising *Coleosporium melampyri* on *Melampyrum nemorosum* from France (lectotype in HAL). All the strains of *R. coleosporii* used in this study cluster together in the same clade (Fig. 2, clade 66, 1/ 100/100) and are clearly separated from the other *Ramularia* spp., supporting the hypothesis that this is indeed a unique species. They were, however, all collected from South Korea, and a few isolates from other countries should be analysed to determine if it is a global species. It was the first time that this species was observed in association with the host *Pileoaria shiraiana*. To determine if *R. coleosporii* is truly mycophilic more studies need to be done to understand the biology and ecology of this species.

Ramularia collo-cygni B. Sutton & J.M. Waller, Trans. Brit. Mycol. Soc. 90: 57. 1988.
≡ *Ophiocladium hordei* Cav., Z. Pflanzenkr. 3: 26. 1893.
≡ *Ovularia hordei* (Cav.) R. Sprague, Mycologia 38: 63. 1946.
≡ *Ramularia hordeicola* U. Braun, Int. J. Mycol. Lichenol. 3 (2–3): 281. 1988.
For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 202).

Specimens examined: **Austria**, Reichersberg am Inn, on *Hordeum vulgare*, unknown date, Züchtungsfirma Saatbau Linz (neotype designated here: CBS H-22641, MBT371836, culture ex-neotype CBS 101180). **Germany**, Bavaria, Aspachhof, Uffenheim, on *Hordeum vulgare*, 1998, E. Sachs, CBS H-17711, cultures CBS 101181, CBS 101182. **Norway**, Central Norway, on *Hordeum vulgare*, unknown date, S. Salamati, cultures CBS 119439 = CPC 12693, CBS 119440 = CPC 12692, CBS 119441 = CPC 12690, CBS 119442 = CPC 12688.

Substrate and distribution: On *Bromus*, *Festuca*, *Glyceria*, *Leucopoa*, *Lolium*, *Phalaris*, and *Triticale* (*Poaceae*) and *Cannabis* (*Cannabaceae*); Europe, N. America (Canada, Mexico, USA), S. America (Chile, Colombia), Asia (Japan, Russia), Australia and New Zealand.

Notes: *Ramularia collo-cygni* was originally isolated from the host *Hordeum vulgare* collected in Italy, but the type specimen is presumed missing (Braun 1998). The strains used in this study cluster together in a highly supported clade (Fig. 2, clade 38, 1/100/100) and a strain isolated from the same host that was collected in Austria is designated as neotype. *Ramularia collo-cygni* is the causal agent of Ramularia leaf spot disease on barley, a disease that has been known for more than 100 years but of which the importance has only been recognised in the last 30 years. The disease has been reported worldwide and on various cereals and grasses. On barley, the symptoms appear late in the season as reddish brown necrotic spots that lead to premature leaf senescence and subsequent grain yield loss. Environmental conditions such as temperature and humidity are key factors in activating the production of rubellin, a non-host specific toxin, by the fungus. The development of molecular diagnostic tools has improved the detection of the pathogen in plant tissue and seeds before symptom development. Vertical transmission of the fungus in barley has been confirmed (Havis *et al.* 2015) and further evidence points to the existence of an endophytic life-style that shifts towards necrotrophy depending on plant

health. Population studies using simple-sequence repeat markers and sequence analyses of housekeeping genes revealed a high genetic diversity in *R. collo-cygni* isolates (Piotrowska 2014, Havis *et al.* 2015). A high level of genotypic diversity is usually indicative of sexual recombination, but the sexual morph of *R. collo-cygni* is yet to be identified. Control of the disease can be accomplished by timely fungicide application between the Zadoks growth stages (ZGS) 30 and ZGS 49, well before the symptoms develop that usually happens at stage ZGS 70. *Ramularia collo-cygni* has lost sensitivity to strobilurin-based fungicides due to the development of the G143A point mutation in the cytochrome b gene, which is now prevalent in most populations. The introduction of a new generation of SDHI fungicide has brought some leverage in disease control, but the rapid evolutionary potential displayed by this fungus suggests it can adapt to new control strategies quickly. Despite all the research performed so far several questions still need to be addressed to fully understand the biology of this species in order to develop appropriate control measures (Havis *et al.* 2015). *Ramularia collo-cygni* also causes Tan Leaf Spot on turfgrass. Turfgrasses are used to control water and wind erosion of soil, and are used as ornamental plants and as ground cover of playing fields in many sports. The disease has been reported from Australia, Japan, New Zealand and North America (Smiley *et al.* 1983).

Ramularia coryli Chevassut, in Braun, Monograph *Cercosporella*, *Ramularia* Allied Genera (Phytopath. Hyphom.) 2: 140. 1998.

Description in vivo: See Braun (1998: 140).

Specimen examined: **Netherlands**, Utrecht, Rhijnauwen, on dead leaves of *Corylus avellana*, G. Verkley, 25 Apr. 2005, culture CBS 117800 = CPC 12090.

Substrate and distribution: On *Corylus avellana*; Europe (France, Netherlands).

Notes: *Ramularia coryli* was originally described on *Coryllus avellana* from France, and is currently the only *Ramularia* species known to infect this host (Braun 1998). The strain used in this study forms a single lineage (Fig. 2, clade 83), and is positioned on a very long branch, which supports this species as unique. Unfortunately, this strain proved to be sterile, and thus we could not compare it morphologically. This clade is for now maintained as representative of *R. coryli* until fresh material is collected and more information becomes available.

Ramularia cupulariae Pass., Hedwigia 15: 107. 1876.
= *Ovularia inulae* Sacc., Fungi ital., Tab. 971. 1881.
≡ *Ramularia inulae* (Sacc.) Höhn., in Kab. & Bub., Fungi Imperf. Exs. no. 389. 1906.
= *Ovularia inulae* f. *major* Brunaud, Actes Soc. Linn. Bordeaux 1890: 46. 1890.
= *Ramularia inulae-britannicae* Allesch., in Jaap, Abh. Bot. Ver. Prov. Brandenb. 47: 98. 1905.
= *R. codonocephali* Annaliev, Novosti Sist. Nizsh. Rast. 15: 74. 1978.

Description in vivo: See Braun (1998: 81).

Specimens examined: **Former Czechoslovakia**, on *Inula* sp., unknown date, L. Marvanová, culture CBS 235.73. **Italy**, Vigheffio near Parma, Oct. 1874, Passerini [Rahenh., Fungi Eur. Exs. 2065; lectotype, designated in Braun (1998), HAL].

Substrate and distribution: On *Carpesium*, *Codonocephalum*, *Inula*, and *Pulicaria* (*Asteraceae*); Asia, Caucasus, Europe.

Notes: Two varieties are known for this species, *R. cupulariae* var. *cupulariae* (lectotype on *Inula viscosa*, Italy, in HAL) and *R. cupulariae* var. *britannicae* (holotype on *Inula britannica*, Germany, in HBG). Specimens of var. *britannicae* have very long and filiform conidiophores (20–100 × 2.5–5 µm) when compared to var. *cupulariae* (5–30 × 2–5 µm). This species has been reported from four different host genera within the family *Asteraceae* (*Carpesium*, *Codonocephalum*, *Inula* and *Pulicaria*) from Asia, Caucasus and Europe. The strain used in this study forms a single lineage (Fig. 2, clade 6).

Ramularia cyclaminicola Trel., Trans. Illinois Acad. Sci. 9: 145. 1916.
= *Cladosporium cyclaminis* Massey & Tilford, Phytopathology 22(1): 19. 1932.

Description in vivo: See Braun (1998: 226).

Specimen examined: **USA**, on stunted *Cyclamen persicum*, unknown collector and date, isolated and deposited by K.F. Baker, 1951, culture CBS 399.51; Illinois, Urbana, University, north greenhouse, 14 Jan. 1914, Trelease (holotype ILL 14246).

Substrate and distribution: On *Cyclamen* (*Primulaceae*); N. America.

Notes: *Ramularia cyclaminicola* causes both a leaf spot disease and a stunt or wilt through systemic invasion of vascular tissue in *Cyclamen persicum*. Cyclamen plants, grown for their flowers, were imported into America from Germany and the Netherlands. No disease was reported from these countries and it is likely that *R. cyclaminicola* is native to North America, perhaps infecting other members of the *Primulaceae* (Baker *et al.* 1950). The disease may be confused with a physiological problem or with Fusarium wilt or Phialophora wilt, and was more common in the first half of the 20th century than it is today (Daughtrey *et al.* 1995). *Ramularia cyclaminicola* was originally described on *Cyclamen persicum* from Illinois, USA (holotype in ILL). In the present study, *Ramularia cyclaminicola* is represented by a single lineage (Fig. 2, clade 18). Strain CBS 399.51 was isolated by Baker and deposited at CBS in 1951, which means this is likely an authentic strain of this species.

Ramularia cynarae Sacc., Michelia 1: 536. 1879.
= *R. cardui* P. Karst, Meddeland. Soc. Fauna Fl. Fenn. 14: 109. 1888.
= *R. cirsii* Allesch., Ber. Bayr. Bot. Ges. 2: 18. 1892.
= *R. jurineae* Holl'os, Ann. Hist.-Nat. Mus. Natl. Hung. 5: 467. 1907.
= *R. carthami* Zaprom., Bolez. Rast. 15(3): 142. 1926, and Mater. Mikofl. Sredn. Azii I: 32. 1926.
For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 101).

Specimens examined: **France**, Saintes, Brunaud, herb. Saccardo (holotype PAD). **Netherlands**, Gelderland Prov., Hoge Veluwe Nat. Park, on *Carduus* sp., 2012, S.I.R. Videira culture CPC

25897; Nijmegen, on *Carex acutiformis*, Jul. 2012, S.I.R. Videira, culture CPC 25896. **Sweden**, Uppland, Haga, Årtopet, on *Cirsium arvense*, 4 Oct. 1989, E. Gunnerbeck, culture CBS 114728; Uppland, Dalby, on leaves of *Carduus crispus*, 29 Aug. 1989, E. Gunnerbeck, culture CBS 114729. **USA**, California, Monterey County, Castrovill, on leaves of *Cynara cardunculus*, 10 Aug. 2010, S.T. Koike (epitype CBS H-20514, culture ex-epitype CBS 128912 = CPC 18426); *idem*. CPC 18427; California Santa Clara County, Morgan Hill, on leaves of *Carthamus tinctorius*, 19 Oct. 2010, S.T. Koike, cultures CBS 128779 = CPC 18725, CPC 18726.

Substrate and distribution: On *Carduus*, *Carthamus*, *Cirsium*, *Cousinia*, *Cynara*, *Echinops*, *Jurinea*, *Onopordum*, *Saussurea*, and *Silybum* (*Asteraceae*); worldwide.

Notes: *Ramularia cynarae* was originally described on *Cynara scolymus* from France (holotype in PAD), but the species has a wide host range within the *Asteraceae* (Braun 1998). This species was epitypified by Koike *et al.* (2011), who reported the pathogen *R. cynarae* as the causal agent of leaf spot symptoms on *Carthamus tinctorius* (spineless safflower) in California, USA. Spineless safflower is grown as commercial cut flower crops in coastal California. The isolates collected from both *Cynara* and *Carthamus* were identical in morphology and ITS sequences (GenBank HQ728117, HQ728118). This supports the hypothesis that *R. cynarae* has a broad host range on *Asteraceae* hosts instead of being a species complex. *Ramularia carthami* was previously reported from agronomic safflower grown for oil production in Northern California (Hostert *et al.* 2006). The ITS sequence of this isolate (DQ466083) is 100 % similar to the ITS sequence of the *R. cynarae* ex-epitype culture (CBS 128912), indicating that these are likely the same species. In this study, strains of *R. cynarae* clustered in a highly supported clade (Fig. 2, clade 9, 1/100/100). Some internal variation was observed and the transition from concordance to conflict determined the phylogenetic limit of this species (Taylor *et al.* 2000). This intraspecific variation may be the reason that this species is able to colonise a broad host range or indicate that it is undergoing sexual reproduction, as can be observed with *R. vizellae* (Videira *et al.* 2015b).

Ramularia deusta (Fuckel) Karak. **var. *deusta***, Fungi Imperfecti Parasitici. I. Hyphomycetes: 116. 1937.
Basionym: *Scolicotrichum deustum* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 357. 1870

Description in vivo: See Braun (1998: 156).

Specimens examined: **Germany**, near Eberbach, on *Lathyrus linifolius* [Fuckel, Fungi Rhen. Exs. 2206; lectotype, designated in Braun (1998), HAL]. **Guadeloupe**, on *Lathyrus latifolius*, unknown collector and date, dep. K.F. Baker & W.C. Snyder, Oct. 1950, culture CBS 473.50.

Host and distribution: On *Lathyrus* (*Fabaceae*); Asia, Europe, N. and S. America, New Zealand.

Notes: *Ramularia deusta* is distributed worldwide in temperate and subtropical climates on nine species of *Lathyrus*, including the cultivated sweet pea (*L. odoratus*) and perennial pea (*L. latifolius*). The first pathological study was conducted in England on sweet pea (Dowson 1924), and since then it has been reported from several countries around the world. The economical impact of this disease was considered minor on this crop (Baker *et al.* 1950). Two physiological

forms were recognised by Baker *et al.* (1950) from collections in California, *R. deusta* f. *odorati* as pathogenic on the host *Lathyrus odoratus*, and *R. deusta* f. *latifolii* as pathogenic on the host *L. latifolius*. Braun (1998) divided *Ramularia deusta* into three varieties. *Ramularia deusta* var. *alba* (on *Lathyrus odoratus*, Denmark, holotype in B) has whitish caespituli while *R. deusta* var. *deusta* (on *Lathyrus linifolius*, Germany, lectotype in HAL) has yellowish ochraceous or pink to reddish caespituli. *Ramularia deusta* var. *lathyrimaritimi* (on *Lathyrus maritimus*, Sweden, holotype in BPI) has longer and mostly septate conidia (15–30 × 2.5–5 µm), while *R. deusta* var. *deusta* has shorter and mostly aseptate conidia, (5–)8–20(–23) × 2.5–5 µm. Although *R. deusta* f. *odorati* was synonymised under *R. deusta* var. *alba* (Braun 1998), *R. deusta* f. *latifolii* does not appear as synonym of any of the other varieties and should, therefore, be considered as a synonym of *R. deusta* var. *deusta*. The strain used in this study (CBS 473,50; Fig. 2, clade 62) was previously identified as *R. deusta* f. *latifolii* and was deposited by Baker and Snyder in 1950, which makes it an authentic strain and a reliable representative of the species *Ramularia deusta* var. *deusta* until fresh material from the same location and host as the type material is recollected.

Ramularia didyma Unger **var. *didyma***, Exanth. Pfl.: 169. 1833.
≡ *Didymaria ungeri* Corda, Icon. fung. (Prague) 1: 32. 1837.
≡ *D. didyma* (Unger) Pond, Amer. Naturalist 23: 163. 1889.
= *Fusisporium aequivocum* Ces., Bot. Zeitung (Berlin) 15: 43. 1857.
≡ *Ramularia aequivoca* (Ces.) Sacc., Fungi ital. Del., Tab.: 994. 1881.
= *Ramularia ovularioides* H.C. Greene, Trans. Wisconsin Acad. Sci. 38: 246. 1946 (1947).
For additional synonyms see Braun (1998).

Description in vivo: See Braun (1998: 239).

Specimens examined: **Luxembourg**, Kantenbach, on leaf spot on *Ranunculus repens*, unknown collector and date, isol. L. Marvanová, 25 Sep. 1967, dep. L. Marvanová, Oct. 1967, culture CBS 431.67. **Sweden**, Uppland, Haga par., Årtopet, on *Ranunculus repens*, 23 Oct. 1988, E. Gunnerbeck, culture CBS 114299 = UPSC 2746. **UK**, South West England, Exeter, on leaf spot from *Ranunculus repens*, unknown collector and date, isol. S.A.J. Tarr, 30 Apr. 1967, dep. S.A.J. Tarr, Sep. 1967, culture CBS 420.67.

Substrate and distribution: On *Anemone* and *Ranunculus* (*Ranunculaceae*); Asia, Caucasus, Europe, N. and S. America, New Zealand.

Notes: There are three varieties of this species, namely *R. didyma* var. *didyma* [neotype on *Ranunculus nemorosus*, Switzerland, designated in von Arx (1983), in ZT], *R. didyma* var. *exigua* (holotype on *Ranunculus uncinatus*, USA, Oregon, WSP) and *R. didyma* var. *pulsatillae* [neotype on *Pulsatilla pratensis*, Denmark, designated in Braun (1998), in C]. While *R. didyma* var. *didyma* conidiophores emerge through stromata and form catenate conidia, *R. didyma* var. *exigua* exhibits conidiophores erumpent through the cuticle, and *R. didyma* var. *pulsatillae* frequently forms solitary conidia. *Ramularia didyma* var. *didyma* has a wider distribution than the other two varieties (Braun 1998). *Ramularia didyma* was identified as the causal agent of leaf spotting symptoms on Persian buttercups (*Ranunculus asiaticus*) in USA, California. These are colourful, cool-season perennials or annuals grown for the flowers and bulbs. Introduction of this pathogen into commercial production fields could cause significant economic loss (Blomquist

& Warfield 2011). The ITS sequence (GenBank HQ442297) generated at that time is 100 % similar to the ITS sequence of the strains in this clade. Based on phylogenetic analyses in this study, this species forms a highly supported clade (Fig. 2, clade 72, 1/100/100). The morphology could not be observed since the cultures were sterile and no herbarium materials corresponding to the strains were preserved. This clade is tentatively maintained as a representative of this species until fresh material from the type host and location is recollected.

Ramularia diervillae Peck, Rep. (Annual) New York State Mus. Nat. Hist. 38: 99. 1885. Fig. 42.
= *Ramularia umbrosa* Davis, Trans. Brit. Mycol. Soc. 19: 714. 1919.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–2-septate, cylindrical-oblong, straight to sinuous, unbranched, (10–)26.5–35(–54) × (1–)1.5–2(–3) µm, or reduced to conidiogenous cells, terminal on conidiophores or intermediate in the mycelium, cylindrical-oblong, narrower at the top, (5.5–)14.5–19(–29) × 1.5–2(–3) µm, with one or two conidiogenous loci almost flat to protuberant; *conidiogenous loci* thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong, sometimes sinuous or curved, (9.5–)14–17(–26.5) × (1.5–)2–2.5(–3) µm, 0–1-septate, with 2 apical hila. *Intercalary conidia* cylindrical-oblong, fusoid, sometimes curved, aseptate, (8–)11–13(–19.5) × (1.5–)2(–3) µm, in branched chains of up to seven conidia. *Terminal conidia* cylindrical-oblong to obovoid, aseptate, (5–)7–8(–11) × (1.5–)2(–2.5) µm. Sporulating on SNA.

Culture characteristics: On MEA, 11 mm diam, surface raised, folded, with sparse aerial mycelium, smooth, rosy buff, with margins crenate and convex, colony reverse cinnamon with

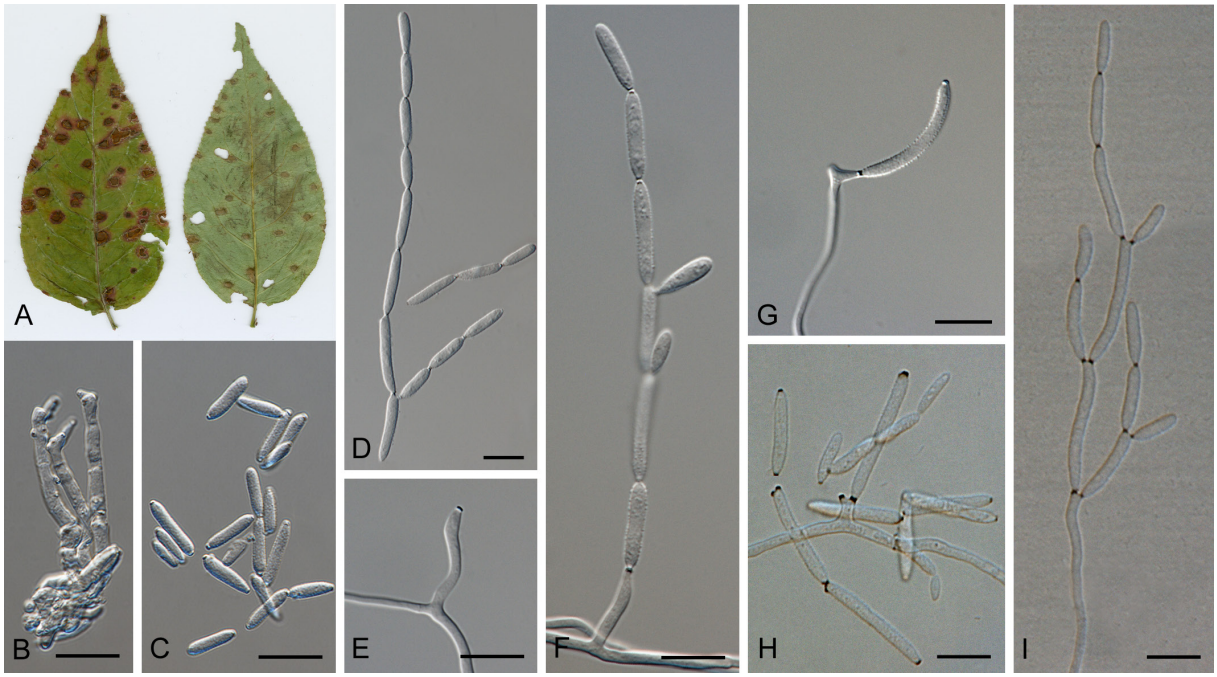


Fig. 42. *Ramularia diervillae* (CPC 16859). A–C. Observations from herbarium material. D–I. Structures formed in culture. A. Leaf spot symptoms on the host. B, E. Conidiophores. C, D. Conidia. F–I. Conidiophores and conidia. Scale bars = 10 µm.

olivaceous grey patches; on OA, 9 mm diam, surface smooth, low convex, white with pale olivaceous grey tinge, with margins undulate, colony reverse fawn; on PDA, 10 mm diam, surface low convex, pale olivaceous grey, smooth, producing tiny transparent exudate droplets, with margins lobate, colony reverse olivaceous grey with a buff margin.

Description in vivo: See Braun (1998: 130).

Specimens examined: **Canada**, Quebec, La Peche, Lac Bernard, on *Diervilla lonicera*, 5 Jul. 2009, K.A. Seifert, cultures CPC 16859, CPC 16860, CPC 16863, CPC 16864. **USA**, New York, Adirondack Mt., on *Diervilla lonicera*, Peck (holotype NYS).

Substrate and distribution: On *Diervilla* (*Caprifoliaceae*); N. America (Canada, USA).

Notes: *Ramularia diervilla* was originally described on *Diervilla lonicera* from New York, USA (holotype in NYS), and is the only species of *Ramularia* known to infect this host. Although it has been previously reported from North America, this is the first report from Canada. This species formed a highly supported clade (Fig. 2, clade 41, 1/100/100). Braun (1998) reported that when associated with its host, *R. diervilla* produces simple, straight to geniculate-sinuous conidiophores, 5–25 × 1.5–3.5 µm, and catenate, cylindrical-fusiform conidia, 5–25(–30) × 1.5–4 µm. The conidiophores described in culture are longer and the conidia are slightly narrower than what is described *in vivo* (Fig. 42). In the herbarium specimen corresponding to the isolate CPC 16859, the conidiophores are shorter than in culture [(25–)28–30(–33) × (1.5–)2(–3) µm] but more similar to the description provided by Braun (1998), while the conidial dimensions [(4–)8–9(–12) × (1.5–)2(–3) µm] are smaller than in culture, but still narrower than in Braun (1998). The cultures and specimens represented in this clade are considered here as representative material of the species until collections from the type location are examined.

Ramularia digitalis-ambiguae Arx, Sydowia 3: 93. 1949.
= *Mycosphaerella digitalis-ambiguae* Arx, Sydowia 3: 92. 1949.
= *Asteromella digitalis-ambiguae* Arx, Sydowia 3: 94. 1949.

Specimens examined: **Luxembourg**, Kantenbach, on leaf spot on *Digitalis purpurea*, unknown collector and date, isol. L. Marvanová, 25 Sep. 1967, dep. L. Marvanová, Oct. 1967, culture CBS 434.67. **Netherlands**, on *Digitalis* sp., unknown collector and date, isol. F. Hespe, dep. Jul. 1937, culture ex-type CBS 297.37.

Notes: Although these isolates were originally identified as *R. variabilis*, the latter species clusters in clade 50 (Fig. 2; 1/100/ 100), in contrast to the *Digitalis* isolates (Fig. 2, clade 58, 1/100/100), which clearly represents a different species. Since collections of *Ramularia* on *Digitalis* and *Verbascum* spp. are *in vivo* morphologically barely distinguishable, Braun (1998) assigned them to a single species, *R. variabilis*, and reduced *Mycosphaerella digitalis-ambiguae* and *Ramularia digitalis-ambiguae* to synonym under *R. variabilis*. Although not yet phylogenetically proven, *R. digitalis-ambiguae* is available for the *Digitalis Ramularia* and can at least tentatively be used for this taxon until sporulating cultures retrieved from *Ramularia* lesions on *Digitalis ambigua* and *D. purpurea* are available for comparison. The connection of *Mycosphaerella digitalis-ambiguae* and the two syn-asexual morphs, *Ramularia digitalis-*

ambiguae and *Asteromella digitalis-ambiguae*, has only been observed *in vivo* (Arx 1949), but not yet verified *in vitro* or by means of molecular methods. Aptroot (2006) referred to the strong morphological similarity between *M. digitalis-ambiguae* and the saprobic *M. subradians* (Fr.: Fr.) J. Schröt. *Mycosphaerella digitalis* (Ferraris) Tomilin (≡ *Sphaerella digitalis* Ferraris; Ferraris 1902: 451, and plate X, fig. II), on dry stems of *Digitalis lutea*, described from North Italy, is quite distinct from *M. digitalis-ambiguae*, differing in having much larger asci, 60 × 20–21 µm, and longer, wider ascospores, 18–10 × 5–6 µm without constrictions at the septa (*vs.* asci 32–42 × 7–9 µm, ascospores 11–15 × 3.5–4.5 µm, constricted at the septa in *M. digitalis-ambiguae*).

Ramularia endophylla Verkley & U. Braun, Mycol. Res. 108: 1276. 2004.
= *Sphaeria punctiformis* Pers., Ann. Bot. (Usteri) 11: 26. 1794, non *Ramularia punctiformis* Sacc., 1904.
≡ *Mycosphaerella punctiformis* (Pers.) Starbäck, Bih. Kongl. Svenska Vetensk.-Akad. Handl., Afd. 3, 15(no. 9): 163. 1889.
For additional synonyms see Verkley *et al.* (2004).

Specimens examined: **Netherlands**, Utrecht Prov., Baarn, Groeneveld, on dead leaves of *Castanea sativa*, 23 Feb. 1999, A. Aptroot, culture CBS 101680; De Stompert, Soest, on fallen leaves of *Quercus robur*, G. Verkley, culture CBS 113871; same location, on dead fallen leaves of *Quercus robur*, Apr. 2003, G. Verkley (holotype CBS H-7949, culture ex-epitype CBS 113265, previously *Mycosphaerella punctiformis*); same location, on green leaf (endophytic) of *Quercus robur*, unknown collector and date, isol. G. Verkley, Aug. 2002, CBS 115302, CBS 115303; same location, on living leaves (endophytic) of *Quercus robur*, G. Verkley, CBS 113869.

Substrate and distribution: On *Quercus* and *Castanea* (*Fagaceae*); Europe (Belgium, Netherlands), Asia (South Korea).

Notes: See Verkley *et al.* (2004) and Videira *et al.* (2015b). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 87, 1/100/100). The host range and distribution of this species is insufficiently known and only those of existing strains were considered above.

Ramularia eucalypti Crous, Fungal Diversity 26: 174. 2007.

Specimens examined: **Australia**, Queensland, Cairns, Kuranda, Karoomba River Walk, on leaves of *Eucalyptus* sp., 19 Aug. 2006, P.W. Crous, culture CBS 120728 = CPC 13304. **Italy**, Norcia, on *Corymbia grandifolia*, 10 May 2006, W. Gams (holotype CBS H-19832, ex-type culture CBS 120726 = CPC 13043). **Netherlands**, Gelderland, Wageningen, *Phragmites* sp., 19 Feb. 2011, P.W. Crous, culture CPC 19188.

Substrate and distribution: On *Carex* (*Cyperaceae*), *Corymbia and Eucalyptus* (*Myrtaceae*), *Geranium* (*Geraniaceae*), *Malus* (*Rosaceae*), *Phragmites* (*Poaceae*), and *Pinus* spp. (*Pinaceae*); Australia and Europe.

Notes: See Crous *et al.* (2007c), Videira *et al.* (2015a). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 31, 1/100/100).

Ramularia euonymicola Videira, H.D. Shin, U. Braun & Crous, **sp. nov.** MycoBank MB816848. Fig. 43.

Etymology: Named after the host genus from which it was isolated, *Euonymus* (inhabitant of *Euonymus*).

In planta: Leaf spots subcircular to irregular, white to ochraceous. *Caespituli* emerging through stomata, hyaline to buff. *Conidiophores* hyaline, thin-walled, slightly verruculose, erect, fasciculate, septate, cylindrical-oblong, straight to sinuous, unbranched, (31–)48.5–56(–73) × (2.5–)3–3.5(–4.5) µm. *Conidiogenous cells* hyaline, slightly verruculose, terminal or intermediate in the conidiophore, cylindrical-oblong or geniculate-sinuous, (8–)13–16(–27) × 2–3(–4.5) µm, with one or two conidiogenous loci almost flat to protuberant; *conidiogenous loci* thickened, darkened and refractive. *Conidia* hyaline, thin-walled, slightly verruculose, solitary or in short chains, rarely branched, cylindrical-oblong to obovate, (1–)3–4-septate, (20.5–)30–35.5(–51) × (3–)3.5–4(–5) µm with hila thickened, darkened and refractive.

Specimen examined: **South Korea**, Hongcheon, on *Euonymus alatus*, 16 May 2003, H.D. Shin, (holotype KUS-F19467, isotypes HAL 1869 F and CBS H-22520, culture ex-type CBS 113308).

Substrate and distribution: On *Euonymus alatus* (*Celastraceae*); Asia (South Korea).

Notes: Presently only *Ramularia celastri* has been described from *Euonymus alatus* (USA). It was described as having simple and straight to geniculate-sinuous conidiophores measuring 10–40(–60) × 1.5–4.5(–5.5) µm, and catenate conidia that are fusiform to subcylindrical,

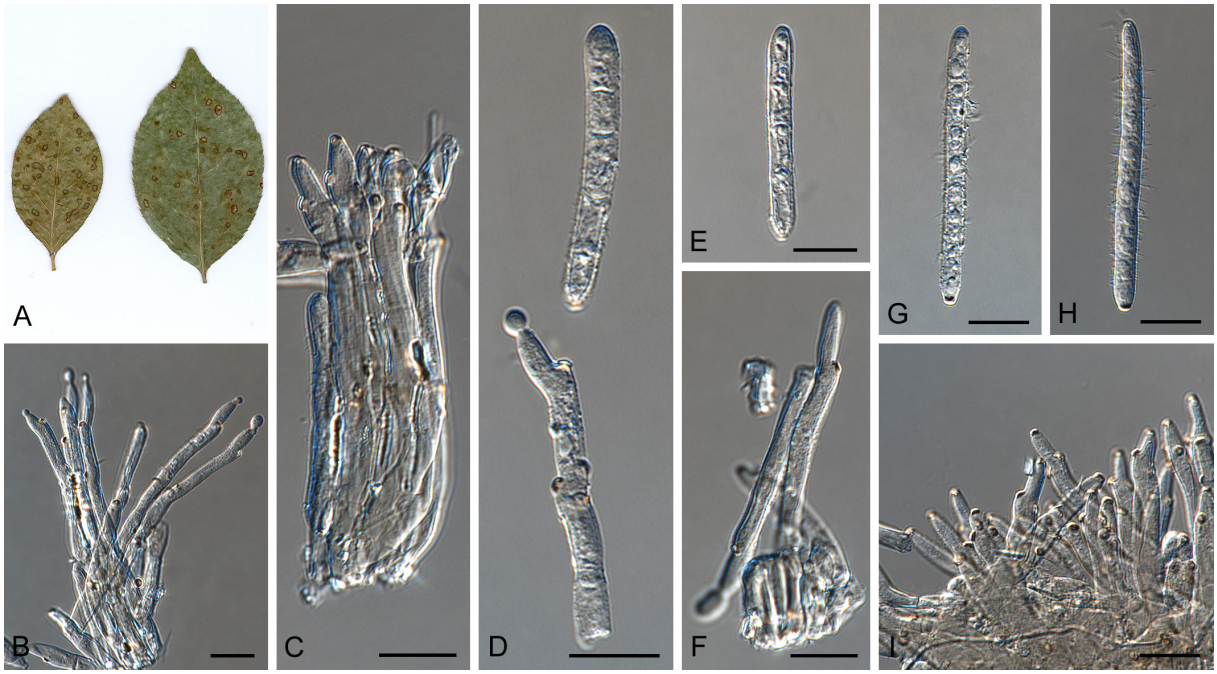


Fig. 43. *Ramularia euonymicola* (CBS 113308). A–I. Observations from herbarium material. A. Leaf spot symptoms on the host. B, C, F, I. Conidiophores and conidiogenous cells. D. Conidiogenous cell and conidia. E, G, H. Conidia. Scale bars = 10 µm.

0–2(–3)-septate, 8–35 × 2–4.5 µm (Braun 1998). *Ramularia euonymicola* was collected in South Korea and differs from *R. celastri* by producing slightly longer conidiophores and much longer conidia that are often 3–4-septate (Fig. 43). This species is represented by a single lineage in the phylogenetic analyses (Fig. 2, clade 73).

Ramularia gaultheriae Videira & Crous, **sp. nov.** MycoBank MB817158. Fig. 44.

Etymology: Named after the host genus from which it was isolated, *Gaultheria*.

Mycelium hyaline, septate, branched. Conidiophores and conidiogenous cells scarce and insufficient for complete description. *Conidia* hyaline, smooth to slightly verruculose, catenate, consistently aseptate, ellipsoid-ovoid, subcylindrical, obovoid (4–)5.5–6.5(–11) × (1.5–)2–2.5(–3.5) µm.

Sterile in culture/*in vitro*. *Ramularia gaultheriae* (Fig. 2, clade 88), differs from its closest phylogenetic neighbour, *R. endophylla* (Fig. 2, clade 87), by unique allelles in five loci based on alignments of the separate loci deposited in TreeBASE as Study S19315: *rpb2* positions 3(C), 15(C), 24(G), 33(C), 48(T), 69(C), 78(C), 87(T), 96(T), 99(C), 102(A), 108(G), 138(T), 157(T), 195(C), 196(C), 198(C), 204(C), 219(T), 234(C), 240(A), 249(C), 252(T), 261(A), 291(T), 297(G), 318(A), 324(T), 330(A), 333(C), 336(A), 339(A), 342(T), 345(C), 346(C), 366(C), 369(T), 372(A), 393(A), 402(T), 409(C), 420(C), 429(T), 453(A), 468(C), 471(T), 472(T), 474(C), 475(G), 477(T), 480(C), 483(C), 487(G), 495(C), 498(C), 500(A), 504(A), 511(A), 516(A), 522(T), 525(A), 531(T), 537(A), 541(T), 543(A), 549(C), 552(C), 555(C), 558(T), 559(A), 564(C), 570(G), 573(G), 577(A), 578(A), 583(C), 585(A), 606(C), 607(T), 613(G), 614(G), 627(C), 630(A), 639(T), 642(C), 645(A), 654(A); ITS positions 33(T), 45(A), 46(G), 48(A), 49(A), 50(T), 76(G), 81(A), 421(C), 422(T), 423(T), 425(A), 427(T), 428 insertion (C), 429(A), 430(A), 431(T), 465(A), 466(A), 478(A), 479(A), 480(A); *actA* positions 31(T), 34(C), 47(G), 49(C), 50(T), 62(C), 63(T), 68(C), 69(T), 71(C), 72(G), 73(G), 82(G), 83(C), 87(C), 88(A), 95(G), 98(T), 101(A), 104(G), 105(C), 107(T), 115(C), 118(A), 138(C), 165(T), 166(A), 168(T), 175(T), 177(T), 178(C), 179(A), 180(T), 182(T), 185(A), 186(C), 187 insertion (T), 209(A), 210(C), 212(G), 214(G), 218(C), 220(A), 245(A); *gapdh* positions 17(C), 18(T), 19(C), 21(T), 54–58 insertion (ATGTG), 59(G), 61(T), 64(G), 65(A), 93(T), 94(G), 99(T), 101(G), 107(A), 108(C), 109(A), 111(A), 119(A), 120(C), 121(A), 122(G), 124(A), 156(C), 158(C), 161(T), 207(C), 208(A), 209(G), 210(C), 212(T), 257(C), 259(T), 263(A), 269(G), 271(A), 272(T), 282(C), 284(T), 287(A), 288(C), 289(C), 290(T), 297(C), 298(A), 301(G), 303(C), 304(C), 308(C), 309(A), 310 insertion (A), 311(T), 312(C), 313(C), 353(T), 389(C), 404(C), 405(A), 411(G), 442(A), 449(A), 461(T), 521(C), 557(C), 566(C), 569(C), 575(T), 587(C), 593(T), 617(T); *tef1*-α positions 15(C), 16(T), 22(G), 23(C), 24(T), 25–26 insertion (CC), 59(T), 69(C), 72(G), 78(C), 95(C), 96(A), 107(G), 183(T), 196(C), 205(C), 223(T), 225(A), 233(T), 243(T), 275(C), 277(A), 284(T), 286(T), 294(G), 296(C), 303–304 insertion (GC), 305(G), 313(A), 315(G), 316(T), 399(C), 401(G), 402(C), 404(G), 405(A), 408(A), 410(G), 412(T), 413 insertion (T), 423(A), 424(A), 425(A), 427(T), 429(T), 430(G), 431(C), 444(C).

Specimen examined: **Italy**, on healthy leaf of *Gaultheria shallon*, unknown collector and date, isol. and dep. O. Petrini, May 1980, (holotype CBS H-17765, ex-type culture CBS 299.80).

Substrate and distribution: On *Gaultheria shallon* (*Ericaceae*); Europe (Italy).

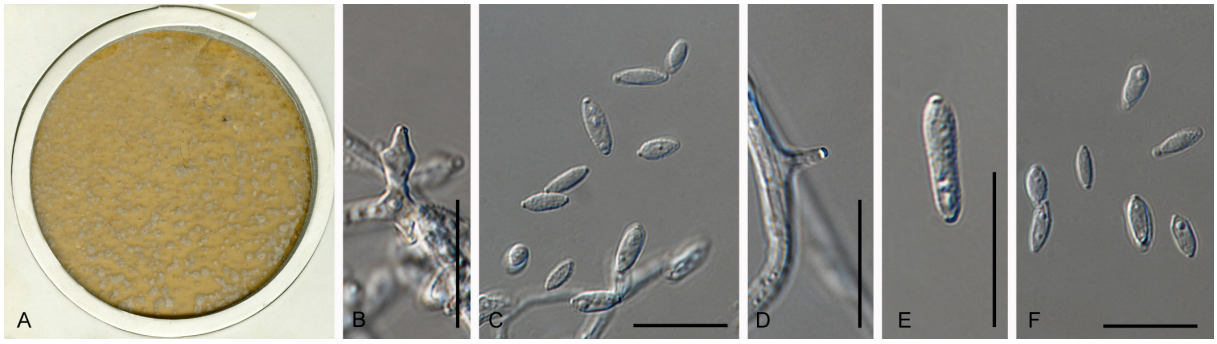


Fig. 44. *Ramularia gaultheriae* (CBS 299.80). A–F. Observations from herbarium material. B, D. Conidiophore reduced to conidiogenous cell. C, E, F. Conidia. Scale bars = 10 µm.

Notes: The strain used in this study forms a single lineage (Fig. 2, clade 88), basal to *R. endophylla*, and is positioned on a very long branch, which supports this species as unique. No *Ramularia* species is currently known from *Gaultheria*. Unfortunately, the culture was sterile and the herbarium material is an old dried culture on which some conidiophores and conidiogenous cells could be observed but were not sufficient to warrant a full description. (Fig. 44), so the molecular differences based on the sequence data are also provided.

Ramularia gei (A.G. Eliasson) Lindr., Acta Soc. Fauna Fl. Fenn. 23: 26. 1902.
Basionym: *Ovularia gei* A.G. Eliasson, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 22(12): 19. 1897.
≡ *Ramularia gei* (A.G. Eliasson) Höhn., Ann. Mycol. 2: 57. 1904, homonym!
= *Ramularia gei* (Fuckel) Lindau, in Rabenh., Krypt.-Fl., 2. Aufl., 1 Bd., Pilze IX. Abt., Fungi Imperfecti, Hyphomycetes: 766. 1920, homonym!
≡ *Pseudocercospora gei* (Fuckel) Y.-L. Guo & X.-J. Liu, Acta Mycol. Sin.: 344. 1986.
= *Acrotheca gei* Fuckel, Jahrb. Nassauischen Vereins Naturk. 15: 43. 1860.
For additional synonyms see Braun (1998).

Description in vivo: See Braun (1998: 246).

Specimens examined: **Netherlands**, Baarn, Loenen, Overholland, on *Geum urbanum*, 12 Apr. 1969, J.A. von Arx, CBS H-4927, culture CBS 344.49. **Sweden**, Uppland, Danmark par., Bergsbrunna, on *Geum* sp., 25 Sep. 1986, E. Gunnerbeck, culture CBS 113977; near Uppsala, on *Geum urbanum*, 4 Sep. 1895, Eliasson (holotype S-F-58091).

Substrate and distribution: On *Geum* (*Rosaceae*); Asia, Caucasus, Europe, Iceland, N. America.

Notes: *Ramularia gei* was originally described on *Geum urbanum* from Sweden (holotype in S). The similarities between *Acrotheca gei* and *Ramularia gei* were discussed by Hughes (1953b) and those between *R. gei* and *R. submodesta* were pointed out by Höhnel (1904). The strains included here form a highly supported clade (Fig. 2, clade 74, 1/100/100), but were sterile in culture and the herbarium specimen is depauperate.

Ramularia geranii Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 361. 1870. Fig. 45.

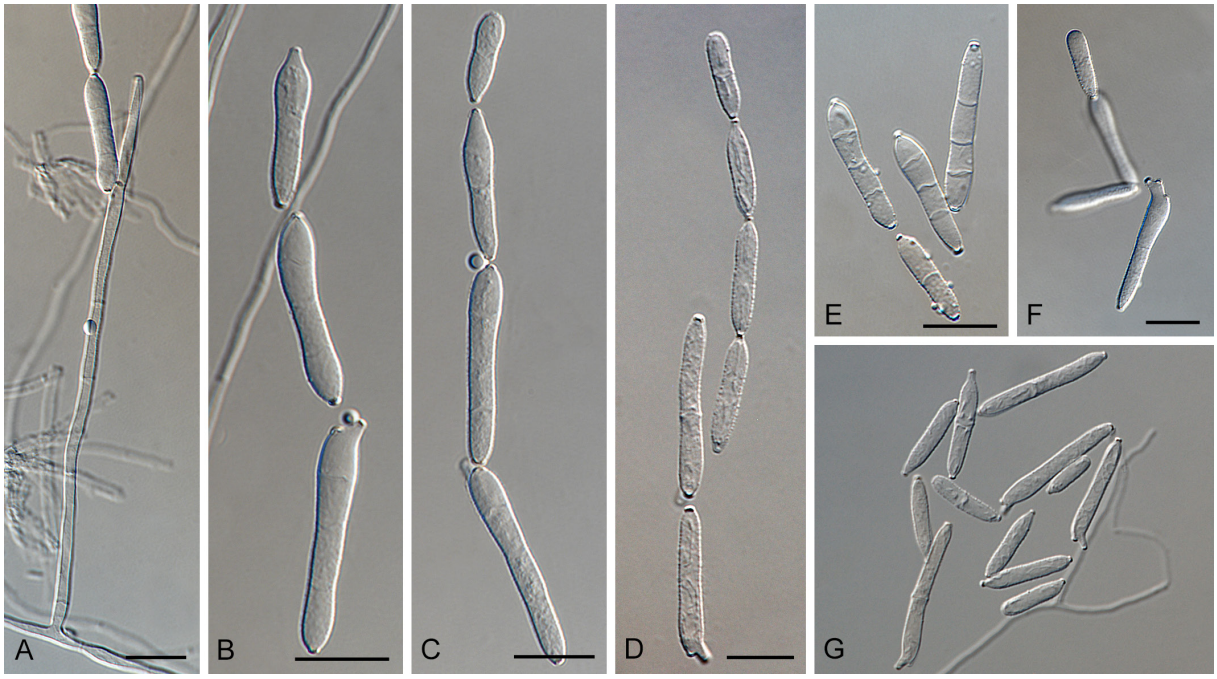


Fig. 45. *Ramularia geranii* (CBS 160.24). A–G. Structures formed in culture. A. Conidiophore, conidiogenous cell and conidia. B–G. Conidia. Scale bars = 10 µm.

= *Fusidium geranii* Westend., Bull. Acad. Belg. 18: 413. 1851.
≡ *Cylindrospora geranii* (Westend.) J. Schröt., Krypt.-Fl. Schlesien 3.2(4): 486. 1897.
For additional synonyms see Braun (1998) or MycoBank.

Mycelium consisting of hyaline, septate, branched, smooth, 1.5–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, erect, septate, straight to geniculate-sinuous, cylindrical-oblong, unbranched, (65–)82–100(–150) × 2–2.5(–3) µm or reduced to conidiogenous cells, hyaline, smooth, integrated in mycelium or terminal in conidiophores, cylindrical-oblong, (14.5–)19–22(–28) × 2–3 µm, with one apical *conidiogenous locus*, thickened and darkened. *Conidia* hyaline, thin-walled, smooth, with hila thickened and darkened. *Ramoconidia* subcylindrical to clavate, 1–4-septate, (23–)28–30(–35) × (3–)4–4.5(–5) µm, with 2–3 conidiogenous apical hila. *Intercalary conidia*, 0–3-septate, subcylindrical to clavate, straight or slightly curved, narrower at the centre and broader at the apices, (17–)22–25(–30) × (2.5–)3.5–4(–5) µm, in chains of up to five conidia. *Terminal conidia* 0–1-septate, obovoid, clavate, phalangoid, (11–)15.5–18(–25) × (3–)4(–5) µm.

Culture characteristics: On MEA, 11 mm diam, surface rosy vinaceous to pale vinaceous grey, strongly folded, raised with margins crenate, colony reverse cinamon with iron grey patches. On OA, 10 mm diam, surface rosy buff, flat, sparse aerial mycelium with margins undulate and sparse aerial mycelium, colony reverse rosy buff with brown vinaceous patches. On PDA, 11 mm diam, surface folded, rosy buff to pale olivaceous grey, raised, with margins undulate, concave, colony reverse olivaceous.

Description in vivo: See Braun (1998: 164).

Specimens examined: **France**, on *Geranium pyrenaicum*, collector and date unknown, isol. and

dep. C. Killian, Jun. 1924, culture CBS 159.24; on *Geranium sylvaticum*, unknown date, C. Killian (epitype designated here CBS H-17726, MBT371838, culture ex-epitype CBS 160.24). **Poland**, on *Geranium pusillum* [Schneider, Herb. Schles. Pilze 898; neotype, designated in Braun (1998), HAL].

Substrate and distribution: On *Erodium* and *Geranium* (*Geraniaceae*); Asia, Caucasus, Europe, N. America.

Notes: Two varieties are known for *Ramularia geranii*, *R. geranii* var. *geranii* (on *Geranium pusillum*, Poland, neotype in HAL) and *R. geranii* var. *erodii* (on *Erodium cicutarium*, Germany, neotype in B). The latter differs from the first by having long slender conidia with up to four septa. They are distributed in the northern hemisphere and *R. gerani* var. *gerani* has also been reported from *Erodium*. The strains representing *Ramularia geranii* in this study clustered separately with CBS 259.24 and CBS 160.20 forming one clade (Fig. 2, clade 3) and CBS 114566 forming a single lineage on a long branch (Fig. 2, clade 4). The strains CBS 159.24 and CBS 160.24 produce very large conidia fitting with the original description and were isolated from the same host genus, but from a different species and country. Strain CBS 114566 was isolated from the same host as the type but from a different European country. Unfortunately it was sterile and morphological comparison with the original description was not possible. Strains CBS 159.24 and CBS 160.24 (Fig. 2, in clade 3, 1/100/100; Fig. 45) are considered good representatives of *R. geranii* both morphologically and phylogenetically, and CBS 160.24 is therefore chosen as ex-epitype. The strain CBS 114566 appears as *R. geranii* in the CBS database but it is not conspecific with the species in this clade and will be treated as a *Ramularia* sp. A for the time being.

Ramularia geraniicola Videira & Crous, **sp. nov.** MycoBank MB816849. Fig. 46.

Etymology: Named after the host genus, *Geranium*, from which it was collected.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2.5 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, emerging from hyphae or dark hyphal spherical aggregates, erect, 1–2(–4)-septate, straight to sinuous, cylindrical-oblong, unbranched (22.5–)35.5–44(–66.5) × (1.5–)2–3(–4) µm or reduced to conidiogenous cells. *Conidiogenous cells*, integrated, cylindrical-oblong and narrower at the top, geniculate-sinuous, (12–)18–22(–33) × 2–2.5(–3) µm, with 1–4 apical conidiogenous loci, almost flat or protuberant; *conidiogenous loci* thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, (10–)13.5–16(–22.5) × (2–)3(–4) µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, fusoid, 0–1-septate, (8.5–)12.5–14.5(–21.5) × (2.5–)3(–4) µm, in branched chains of up to eight conidia. *Terminal conidia* subcylindrical to obovoid, aseptate, (3–)6.5–8.5(–13) × (2–)2.5–3(–3.5) µm (on SNA).

Culture characteristics: On MEA, 15 mm diam, raised, folded, smooth, radially striated, olivaceous grey, with margins pale olivaceous grey and lobate, colony reverse olivaceous grey; on OA, 13 mm diam, flat, sparse aerial mycelium, smooth, olivaceous grey with some tufts pale olivaceous grey, with margins with sparse aerial mycelium and entire edge, colony reverse olivaceous grey; on PDA, 16 mm diam, flat, olivaceous grey, fluffy aerial mycelium,

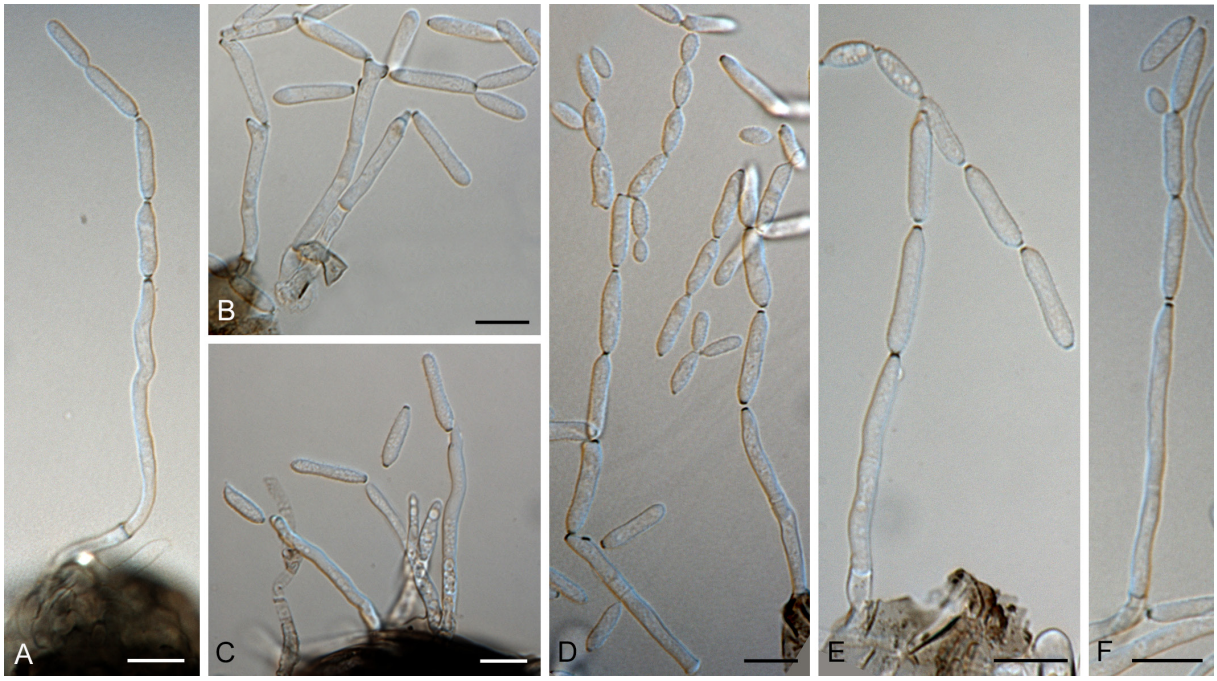


Fig. 46. *Ramularia geraniicola* (CBS 141110). A–F. Conidiophores, conidiogenous cells and conidia formed in culture. Scale bars = 10 µm.

pale olivaceous grey, with margins undulate, colony reverse olivaceous grey and buff margin.

Specimen examined: **Netherlands**, Utrecht, Rhijnauwen, on *Geranium* sp., May 2013, U. Damm (holotype CBS H-22521, culture ex-type CBS 141110 = CPC 25912).

Substrate and distribution: On *Geranium* sp. (*Geraniaceae*); Europe (Netherlands).

Notes: Two *Ramularia* species (*R. geranii* var. *geranii*, *R. pseudogeranii*) and two ramularia-like species (*Phacellium geranii* and *Pseudocercosporella magnusiana*) have thus far been described from *Geranium* (Braun 1998). *Ramularia geranii* var. *geranii* produces conidia that are smooth to verruculose, ellipsoid-ovoid to fusiform, 0–3-septate and 10–40(–55) × (2–)2.5–6(–7) µm. *Ramularia pseudogeranii* produces solitary obovoid conidia, 14–25 × 6–12 µm. The synnematous *Phacellium geranii* produces catenate conidia, ellipsoid-ovoid to fusoid, 12–28 × 4–7 µm. *Pseudocercosporella magnusiana* produces solitary conidia, subcylindrical-filiform to acicular (30–)40–100(–120) µm, 2–8-septate, with hyaline, unthickened hilum. The morphological characters of *R. geraniicola* (Fig. 46) are also distinct from the closest species, *R. variabilis* that produces shorter conidiophores and narrower fusiform to obovoid conidia (Fig. 2, clade 50). *Ramularia geraniicola* has unique morphological characters and forms a single lineage in the phylogenetic analysis (Fig. 2, clade 51).

Ramularia glechomatis U. Braun, Nova Hedwigia 56: 426. 1993. Fig. 47.
= *Fusisporium calceum* Desm., Ann. Sci. Nat., Bot., 2 Sér., 17: 95. 1842.
≡ *Cylindrospora calcea* (Desm.) J. Schröt., in Cohn, Krypt.-Fl. Schles. 3.2(4): 491. 1897.
For additional synonyms see Braun (1998) or MycoBank.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores*

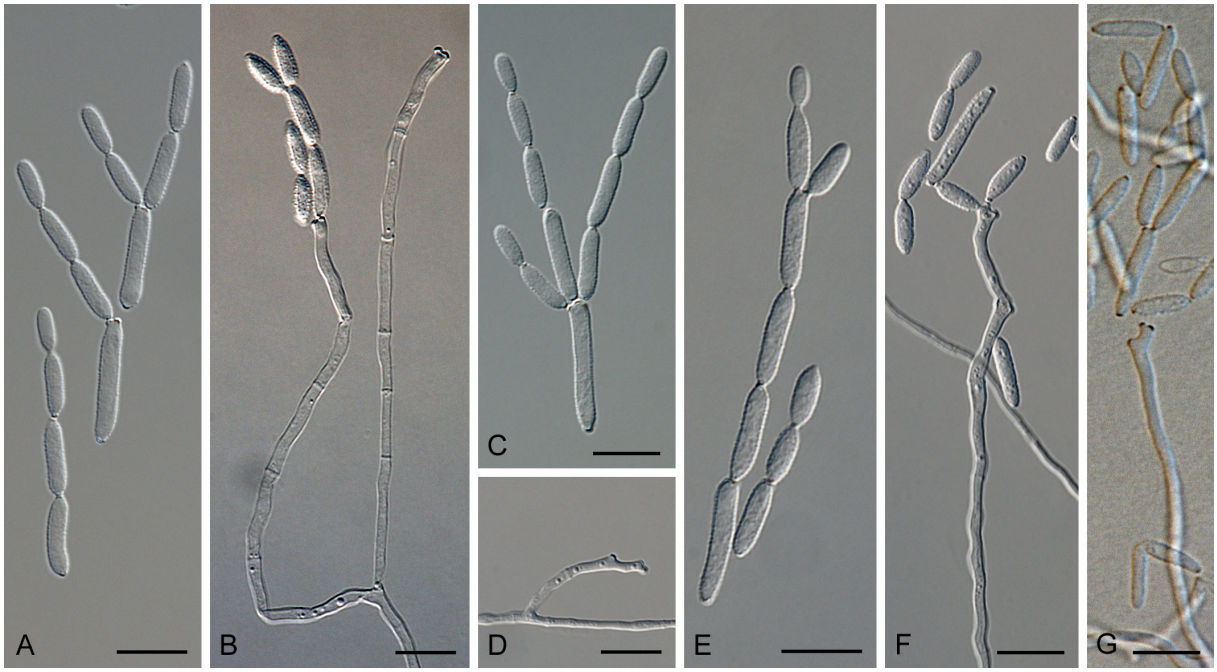


Fig. 47. *Ramularia glechomatis* (CBS 108980). A–G. Structures formed in culture. A, C, E. Conidia. B, F, G. Conidiophores, conidiogenous cells and conidia. D. Conidiophore. Scale bars = 10 µm.

hyaline, smooth, thin-walled, erect, septate, cylindrical-oblong, straight to sinuous, unbranched (15–)28–36(–61) × (1.5–)2 µm, or reduced to conidiogenous cells, terminal in conidiophores or intermediate in the mycelium, cylindrical-oblong to geniculate-sinuous, (4–)11–13(–18) × 1.5–2(–3) µm, with up to three protuberant conidiogenous loci; *conidiogenious loci* thickened, darkened and refractive. *Conidia* hyaline, thin-walled, slightly verruculose, catenate, with hila thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong, (8–)11–13(–17) × 2(–3) µm, 0–1-septate, with two apical hila. *Intercalary conidia* cylindrical-oblong, fusoid, aseptate, (6.5–)8.5–10(–14) × 2(–3) µm, in branched chains of up to seven conidia. *Terminal conidia* cylindrical-oblong to obovoid, aseptate, (3–)5–6.5(–9) × (1–)2(–3) µm (on SNA).

Culture characteristics: On MEA, 10 mm diam, surface raised, smooth, white with a greyish tinge, with margins lobate, colony reverse iron-grey; on OA, 12 mm diam, surface flat, smooth, pale grey, with margins entire, colony reverse iron-grey; on PDA, 11 mm diam, surface flat, smooth, white with greyish patches, with margins entire, colony reverse iron-grey.

Description in vivo: See Braun (1998: 180).

Specimens examined: **Germany**, Brandenburg, Nedlitz near Potsdam, on *Glechoma hederacea*, 7 Sep. 1919 [Sydow, Mycoth. Germ. 1757] (holotype JE). **Netherlands**, Utrecht Prov., Baarn, de Hooge Vuursche, on leaf spot on *G. hederacea*, 22 Jun. 2000, G. Verkley, cultures CBS 108979, CBS 108980; Utrecht Prov., Nieuwersluis, Overholland, on leaf spot on *Glechoma hederacea*, unknown collector and date, isol. and dep. J.A. von Arx, Nov. 1949, culture CBS 343.49.

Substrate and distribution: On *Glechoma hederacea* (*Lamiaceae*); Asia, Caucasus, Europe.

Notes: *Ramularia glechomatis* was originally described on *Glechoma hederaceae* from Germany (holotype in JE) but it has been reported on this host from almost all countries in Europe including the Netherlands (Braun 1998). The strains used in this study cluster in a highly supported clade (Fig. 2, clade 45, 1/100/100). Morphologically, they are similar to the description available in literature (Braun 1998) except for producing narrower conidia, but our observations are based on cultures on SNA (Fig. 47).

Ramularia glennii Videira & Crous, Persoonia 34: 55. 2015.

Specimens examined: **Iraq**, Al-Kora, Basrah, on leaves of *Eucalyptus camaldulensis*, 1 Mar. 2009, A. Saadoon, cultures CPC 16560, CPC 16565. **Italy**, Viterbo, on leaves of *Corymbia grandifolia*, 1 Apr. 2006, W. Gams, culture CBS 120727 = CPC 13047. **Netherlands**, on human bronchial alveolar lavage, Rotterdam, Maasstad Ziekenhuis (Clara), on human bronchial alveolar lavage, 2011, unknown collector, dep. A. van Duin (holotype CBS H-21617, ex-type culture CBS 129441); Rotterdam Maasstad Ziekenhuis (Clara), on human skin tissue, 29 April 2008, unknown collector, dep. H. Naaktgeboren, culture CBS 122989. **USA**, Athens, on rubber of refrigerator, Sep. 2010, A. Glenn, culture CPC 18468.

Substrate and distribution: On *Corymbia grandifolia* and *Eucalyptus camaldulensis* (*Myrtaceae*), human and environmental samples; Western Asia (Iraq), Europe, USA.

Notes: See Videira *et al.* (2015a). The phylogenetic analyses provide good support for this species clade (Fig. 2, clade 32, 1/ 100/96).

Ramularia grevilleana (Oudem.) Jørst., Meld. Stat. Plantepatol. Inst. 1: 17. 1945, emend. U. Braun, A monograph of *Cercosporella*, *Ramularia* and allied genera (Phytopathogenic Hyphomycetes) 2: 68. 1998.
Basionym: *Cylindrosporium grevilleanum* Oudem., Arch. Néerl. Sci. Exact. Nat. 8: 392. 1873.
= *Cylindrosporium* sp., in Tul. & C. Tul., Select. fung. carpol. 2: 288. 1863.
= *Mycosphaerella fragariae* (Tul. & C. Tul.) Lindau, in Engler & Prantl, Nat. Pflanzenfam., ed.1, Sphaeriales, 1(1): 424. 1897.
= *Ramularia tulasnei* Sacc., Michelia 1: 536. 1879, nom. superfl.!
= *Ramularia fragariae* Peck, Annual Rep. (Annual) New York State Mus. Nat. Hist. 32: 43. 1879.
= *R. modesta* Sacc., Fungi ital. Del., Tab. 999. 1881.
For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 248).

Specimens examined: **Netherlands**, unknown host, date and collector, isol. Moll, dep. Oct. 1934, cultures CBS 298.34; unknown host, date and collector, isol. van Egmond, dep. Aug. 1936, CBS 259.36; Heemstede, on *Fragaria vesca*, Jul. 1872, Oudemans [lectotype, designated by Braun & Pennycook (2003), L 371868]. **New Zealand**, Auckland, on *Fragaria* sp., unknown date and collector, isol. and dep. W.F. Hartill, Dec. 1983, culture CBS 719.84. **Sweden**, Uppland, Alsike, on *Fragaria ananassa*, 4 Oct. 1989, E. Gunnerbeck, culture CBS 114732.

Substrate and distribution: On *Duchesnea*, *Fragaria*, *Horkelia*, *Potentilla*, and *Waldsteinia*

(*Rosaceae*); almost circumglobal.
Notes: The valid publication of *Cylindrosporium grevilleanum*, the basionym of *Ramularia grevilleana*, dates back to Oudemans (1873b). A detailed discussion of the complicated nomenclature of this species and its lectotypification has been published by Braun & Pennycook (2003). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 28, 1/100/100). *Ramularia grevilleana* causes Ramularia leaf spot disease of strawberry and other hosts of the *Rosaceae*. The most conspicuous symptoms are leaf lesions but symptoms can also develop on fruits, calyxes, fruit trusses, petioles and stolons. It occurs worldwide on cultivated varieties as well as wild strawberry species. In earlier years, the economic impact of the disease was so great that Ramularia leaf spot was considered the most important strawberry disease. With increased emphasis on the development and use of resistant cultivars, Ramularia leaf spot disease, although still an important foliar disease is now of less concern (Maas 1984). The link between the sexual morph *Mycosphaerella fragariae* and the asexual morph *R. grevilleana* has been experimentally proven (Dudley 1889).

Ramularia haroldporteri Videira & Crous, Persoonia 34: 58. 2015.

Specimen examined: **South Africa**, unidentified bulb plant, 14 Jan. 2009, P.W. Crous (holotype CBS H-21616, ex-type cultures CBS 137272 = CPC 16296, CPC16297).

Substrate and distribution: Thus far only known from South Africa.

Notes: See Videira *et al.* (2015a). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 30, 1/ 100/100).

Ramularia helminthiae Bremer & Petr., Sydowia 1: 259. 1947. Fig. 48
= *Ramularia helminthiae* T.M. Achundov, Novosti Sist. Nizsh. Rast. 20: 59. 1983, nom. illeg.

Mycelium consisting of hyaline, septate, branched, smooth, 1–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–3-septate, straight to flexuous, cylindrical-oblong, unbranched (19–)41–53(–82) × (1.5–)2–2.5(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal on conidiophores, cylindrical-oblong, (15–)21.5–25.5(–36) × 2.0–2.5(–3) µm, with 1–2 apical conidiogenous loci almost flat to short cylindrical, thickened, darkened, refractive. *Conidia* hyaline, thin-walled, smooth to slightly verruculose, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, (14–)21–27(–44) × (2.5–)3–3.5(–4) µm, 0–3-septate, with 2–3 apical hila. *Intercalary conidia* hyaline, smooth, 0–3-septate, subcylindrical with apices rounded and broader, (14–)19–25(–50) × (2.5–)3–4(–4.5) µm, in branched chains of up to four conidia. *Terminal conidia* aseptate, subcylindrical to obovoid, (5.5–)13–16.5(–25.5) × (2–)3–3.5(–4.5) µm.

Culture characteristics: On MEA, 15 mm diam, surface raised, folded, smooth mycelium, smoke-grey with olivaceous tinge, with small buff droplets, with margins lobate, convex, feathery, colony reverse olivaceous grey and ochraceous patches; on OA, 15 mm diam, surface low convex, smooth mycelium, white, with margins buff, naked, undulate, colony reverse rosy-buff; on PDA, 20 mm diam, surface low convex, smooth mycelium, white with greyish tinge with margins undulate, feathery, colony reverse rosy-buff and iron-grey patches.

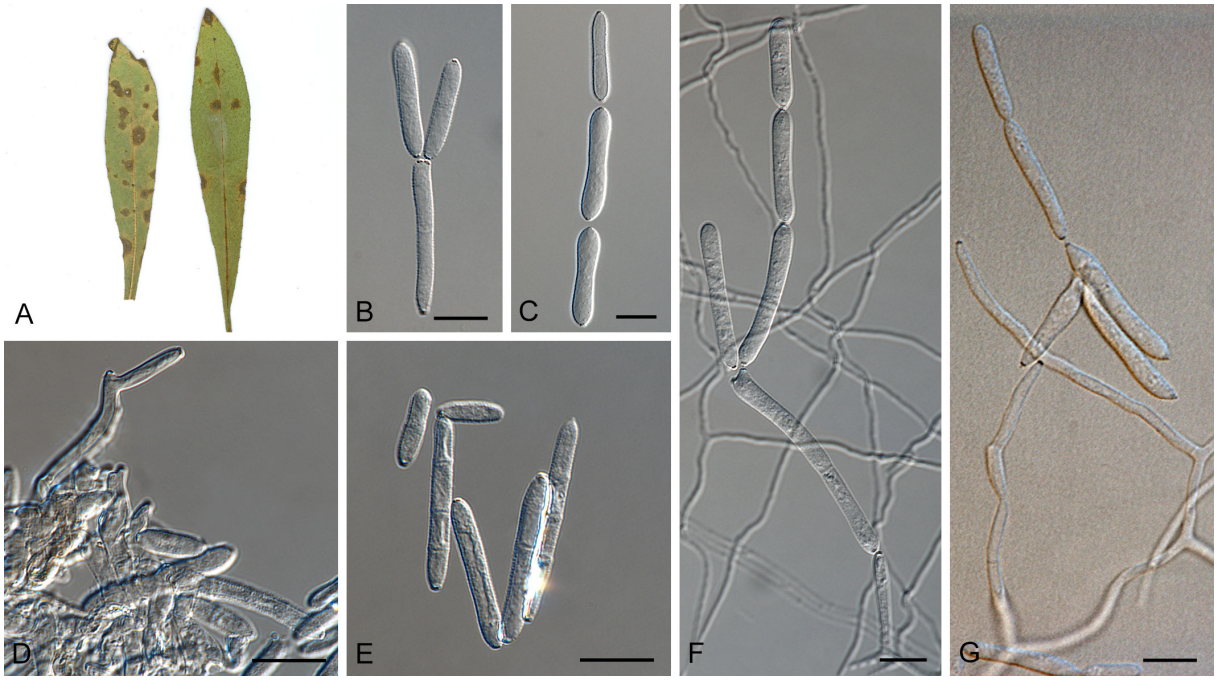


Fig. 48. *Ramularia helminthiae* (CPC 11504). A, D, E. Observations from herbarium material. B, C, F, G. Structures formed in culture. A. Leaf spots on the host. D, F, G. Conidiophores and conidia. B, C, E. Conidia. Scale bars = 10 µm.

Specimens examined: **Azerbaijan**, Talysh, district Massalli, Kyzylagadzh, on *Helminthotheca echioides* (≡ *Picris echioides*), 2 Jun. 1974, T.M. Achundov (isotype of *R. helminthiae* T.M. Achundov LE 41974). **South Korea**, Hongcheon, on *Picris hieracioides* var. *glabrescens*, 9 Jul. 2004, H.D. Shin, KUS-F20442, culture CPC 11502, CPC 11504. **New Zealand**, Auckland, Mt. Albert, on *H. echioides*, unknown collector and date, isol. C.F. Hill, Jul. 2005, det. C.F. Hill, culture CBS 118418. **Turkey**, Adana, Terliksiz, on *H. echioides*, 8 Jun. 1943, G. Karel [lectotype of *R. helminthiae* Bremer & Petr., designated in Braun (1998),W 15449].

Notes: These strains were initially identified as *R. inaequalis*, but this species clusters in clade 40 (Fig. 2). Several names have been synonymised with *R. inaequalis* that refer to species isolated from different hosts and locations. These need to be recollected and re-examined since it appears that *R. inaequalis* is a species complex. *Helminthotheca echioides* is of Mediterranean origin, but now with a widespread, almost cosmopolitan neophytic distribution. The descriptions of both species named *R. helminthiae* are from the neophytic area of the host, but the origin of the species concerned is probably Mediterranean as well. A sporulating culture based on material collected on *H. echioides* in Turkey or adjacent countries should serve as epitype for this species, but is not yet available. Therefore, the name *R. helminthiae* is only tentatively used for the present strains until appropriate cultures will be available. *Ramularia helminthiae* (Fig. 48) is supported as distinct from other included species by the phylogenetic analyses (Fig. 2, clade 5, 1/100/100). The strain CBS 118418 did not sporulate in culture.

Ramularia heraclei (Oudem.) Sacc., Fungi ital. Del., Tab. 1008. 1881, emend. U. Braun, A monograph of *Cercosporella*, *Ramularia* and allied genera (Phytopathogenic Hyphomycetes) 2: 68. 1998. Fig. 49.

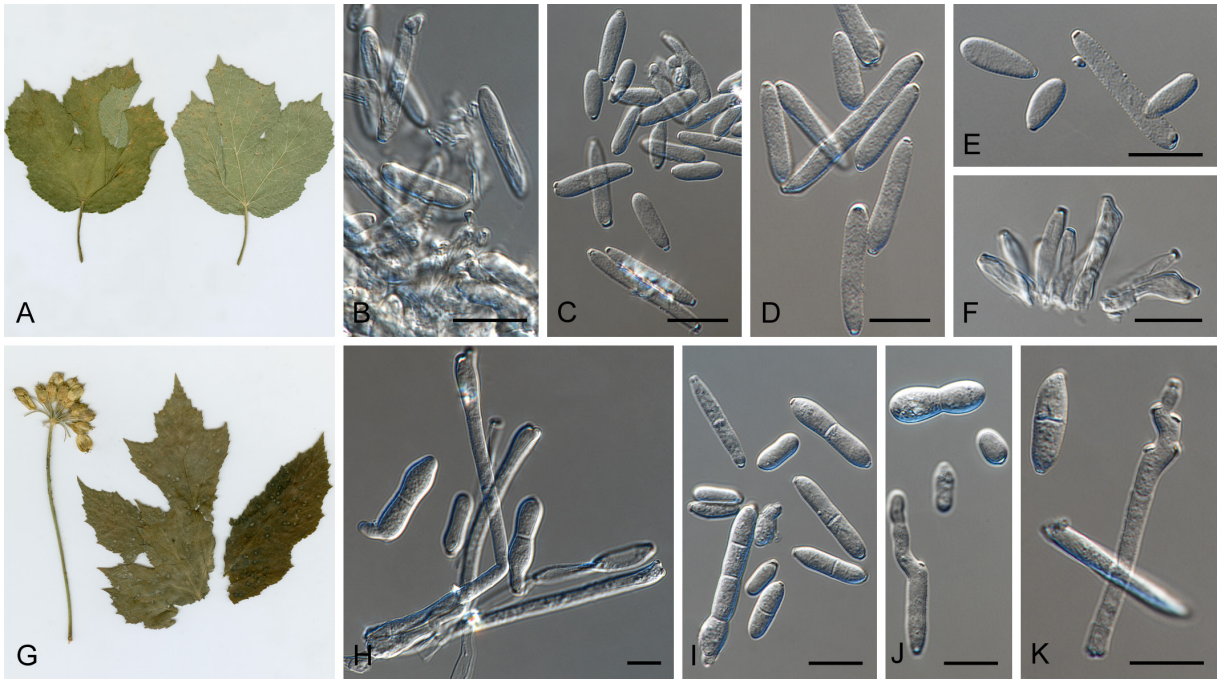


Fig. 49. *Ramularia heraclei* (CBS 108972, CBS 108988). A–K. Observations from herbarium material A–F. CBS 108972. G–K. CBS 108988. A, G. Leaf spot symptoms on the host. B, H. Conidiophores, conidiogenous cells and conidia. F, K. Conidiogenous cells. C–E, I–J. Conidia. Scale bars = 10 µm.

Basionym: *Cylindrosporium heraclei* Oudem., Arch. Néerl. Sci. Exact. Nat. 8: 383. 1873.
= *Ramularia cicutae* P. Karst., Hedwigia 23: 7. 1884.
= *R. levistici* Oudem., Ned. Kruidk. Arch., 2 ser., IV: 540. 1886.
= *R. pastinacae* Bubák, Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-nat. Kl., 1903: 19. 1903.
= *R. coriandri* Moesz & Smarods, Magyar Bot. Lapok 1/12: 37. 1930.
For additional synonymies see Braun (1998).

Description in vivo: See Braun (1998: 58).

Specimens examined: **Austria**, Ötztal, Ötz near Habichen, on leaf spot of *Heracleum* sp., 24 Jul. 2000, G. Verkley, cultures CBS 108987, CBS 108988. **Netherlands**, Bloemendaal, on *Heracleum sphondylium*, Aug. 1871, Oudemans [lectotype, designated in Braun (1998), in L]; Limburg Prov., Gerendal, on leaf spot of *Heracleum sphondylium*, 28 Jun. 2000, G. Verkley (epitype designated here CBS H-22638, MBT371839, culture ex-epitype CBS 108969); *idem*. CBS 108972. **South Korea**, Yangpyeong, on *Heracleum moellendorffii*, 24 Jun. 2004, H.D. Shin, cultures CPC 11505–11507. **Sweden**, Uppland, Danemora par., Andersby, on *Heracleum sphondylium*, 31 Aug. 1987, E. Gunnerbeck, culture CBS 113976 = UPSC 2344. **Unknown country**, on *Pastinaca sativa*, unknown collector and date, isol. and dep. J.E.V. Smith, Apr. 1923, culture CBS 194.25.

Substrate and distribution: On *Apium*, *Cicuta*, *Conium*, *Coriandrum*, *Hansenia*, *Heracleum*, *Levisticum*, *Malabaila*, and *Pastinaca* (*Apiaceae*); Asia, Africa, Caucasus, Europe, New Zealand, N. America and West Indies.

Notes: *Ramularia heraclei* was originally described on *Heracleum sphondylium* from the

Netherlands (lectotype in L). Strains of *Ramularia heraclei* used in this study formed two sister clades that are both highly supported in the multigene phylogeny (Fig. 2, clade 78, 1/100/100). In literature (Braun 1998), the description of this species is quite broad including conidiophores in fascicles or forming crustose-like layers, erect and simple, cylindrical to geniculate-sinuous and variable in length, 5–80(–110) × 2–6 µm and conidia which are catenate, 0–3-septate, smooth to verruculose, (8–)10–35(–45) × 2–6 µm. The herbarium material corresponding to strain CBS 108972 has short conidiophores, (5–)12–17(–20) × 2–3 µm and conidia which are catenate, verruculose, 0–1-septate, (6–)11–14(–25) × (2–)3(–6) µm. The herbarium material corresponding to the strain CBS 108988 has longer conidiophores, (29–)49–59(–82) × 2–3 µm and longer conidia, catenate, smooth to slightly verruculose, (0–)1–3-septate and (6.5–)15.5–20(–36) × (2.5–)3.5–4(–6) µm. They both fit the morphological description in literature and strain CBS 108969, which was collected from the Netherlands and isolated from *Heracleum sphondylium*, the same location and host as the type species, and is herewith designated as epitype (Fig. 49). The morphology of *Ramularia* collections from hosts of *Apiaceae* that are preserved in herbaria are difficult to distinguish and several names were synonymised with *R. heraclei* (Braun 1998). The variation in morphology and the phylogeny indicate that this may be a species complex that needs further study and comparison with collections from other apiaceous hosts.

Ramularia hieracii-umbellati A.G. Eliasson, Svensk. Bot. Tidskr. 9: 412. 1915. Fig. 50.

In planta: *Leaf spots* rectangular, following the leaf nerves, yellowish to brown. *Caespituli* emerging through stomata, hyaline to buff. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, cylindrical-oblong, straight to geniculate-sinuous, rarely branched, (14–)27–32(–41.5) × (2–)3(–4) µm. *Conidiogenous cells* terminal or intermediate in the conidiophore, cylindrical-oblong or geniculate-sinuous, (7–)10–13(–22) × (2–)3(–4) µm, with multiple *conidiogenous loci* almost flat to protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, solitary or in short chains unbranched, cylindrical-oblong to obovate, (0–)1–2-septate, (8–)15–20(–25) × (2–)2.5–3 µm with hila thickened, darkened and refractive.

Culture characteristics: On MEA, 13 mm diam, surface raised, olivaceous grey fluffy aerial mycelium, droplets of iron-grey, margins undulate, convex, feathery, colony reverse undulate, convex, feathery, iron-grey; on OA, 15 mm diam, surface low convex, smooth, pale olivaceous grey, with margins with entire edge, colony reverse olivaceous grey; on PDA, 14 mm diam, surface raised, greenish grey, with olivaceous grey droplets exudate, radially striated, with margins lobate, convex, feathery, colony reverse iron-grey.

Specimens examined: **South Korea**, Pocheon, on *Hieracium umbellatum*, 2 Sep. 2003, H.D. Shin, KUS-F19596, cultures CPC 10690–10692; Pyeongchang, on *Hieracium umbellatum*, 4 Sep. 2003, H.D. Shin, KUS-F19601, cultures CPC 10788, CPC 10789; **Sweden**, Smolandiae, Lofthammer, on *Hieracium umbellatum*, 12 Jul. 1912, A.G. Eliasson (holotype UPS).

Substrate and distribution: On *Hieracium umbellatum* (*Asteraceae*); Asia (South Korea), Europe (Sweden).

Notes: Previously identified as *Ramularia inaequalis* these strains in fact represent a separate species (Fig. 50), since they do not cluster together with the type of *R. inaequalis* (Fig. 2, clade

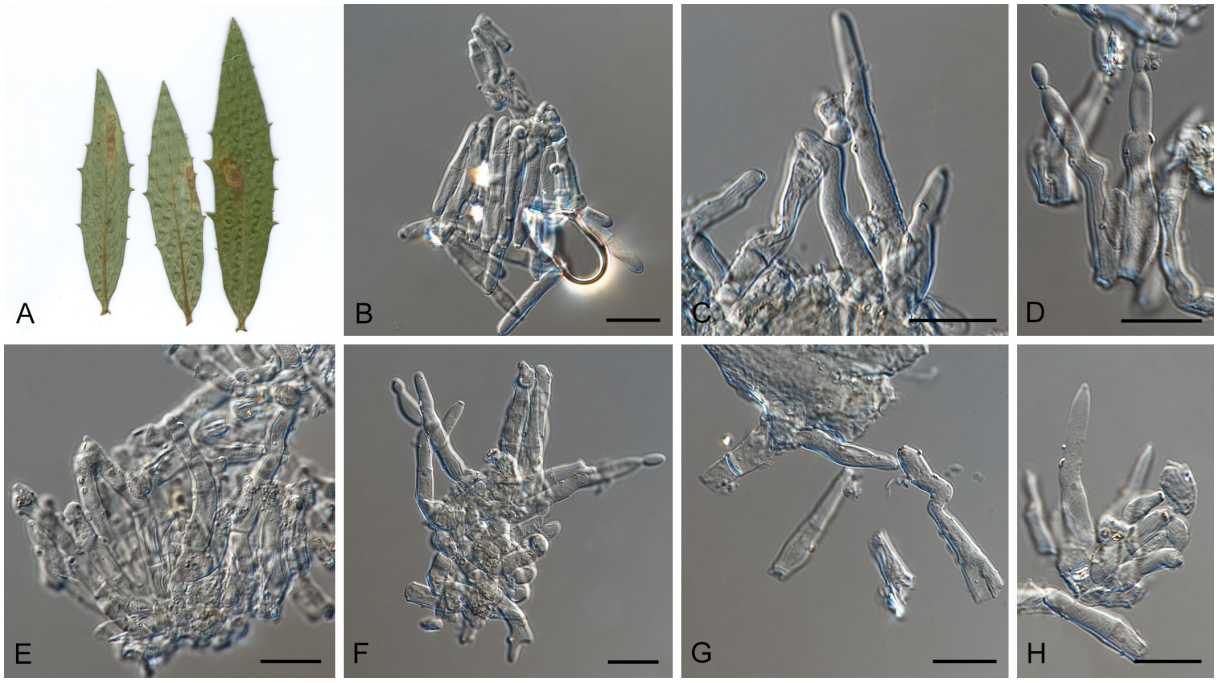


Fig. 50. *Ramularia hieracii-umbelati* (CPC 10690). A–H. Observations from herbarium material. A. Leaf spot symptoms on the host. B. Conidia. C–H. Conidiophores and conidiogenous cells. Scale bars = 10 µm.

40). The morphology agrees well with *R. hieracii-umbellati* described on *Hieracium umbellatum* from Sweden. Cultures and sequences based on collections from Sweden are not available for comparison, but since the Korean material might belong to this species, we prefer to apply the latter name, at least tentatively. *Hieracium umbellatum* is a widespread circumpolar species. Strains of *R. hieracii-umbellati* form a highly supported clade (Fig. 2, clade 56, 1/100/100). *Ramularia hieracii-umbellati* formed a sister clade to *R. rhabdospora*, but the latter produces wider conidiophores [10–50(–115) × 2–8 µm] and larger catenate conidia [(10–)15–40(–50) × 3–7 µm], echinulate, ellipsoid-ovoid to cylindrical, and 0–3(–4)-septate (Braun 1998).

Ramularia hydrangeae-macrophyllae U. Braun & C.F. Hill, Australas. Mycol. 27: 53. 2008. Fig. 51.

In planta: Leaf spots variable, from angular-irregular speckles to large brown leaf blotches. *Mycelium* internal and external but lacking stromata. *Conidiophores* arising from internal hyphae, emerging through stomata or from superficial hyphae, straight, simple, thin-walled, smooth, subcylindrical to moderately geniculous-sinuous, 4–35 × 1.5–3.5 µm, 0–1-septate, or reduced to conidiogenous cells, 4–20 µm long; *conidiogenous loci* conspicuous, thickened and darkened. *Conidia* catenate, sometimes in branched chains, ellipsoid-ovoid to fusiform-subcylindrical, 4–18 × 1.5–2.5 µm, 0–1-septate, hyaline, thin-walled, smooth to verruculose, hila thickened and darkened. Description adapted from Braun & Hill (2008). *Ascomata* pseudothecial, single, brown, immersed, becoming erumpent, globose, apical ostiole. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid to narrowly ellipsoid. *Ascospores*, straight to fusoid-ellipsoid, hyaline, thin-walled, with subobtuse ends, medianly 1-septate, symmetrical or with one side slightly larger than the other, sometimes slightly constricted at the septa, (4.5–)5–6(–7.5) × (1–)1.5–2(–2.5) µm.

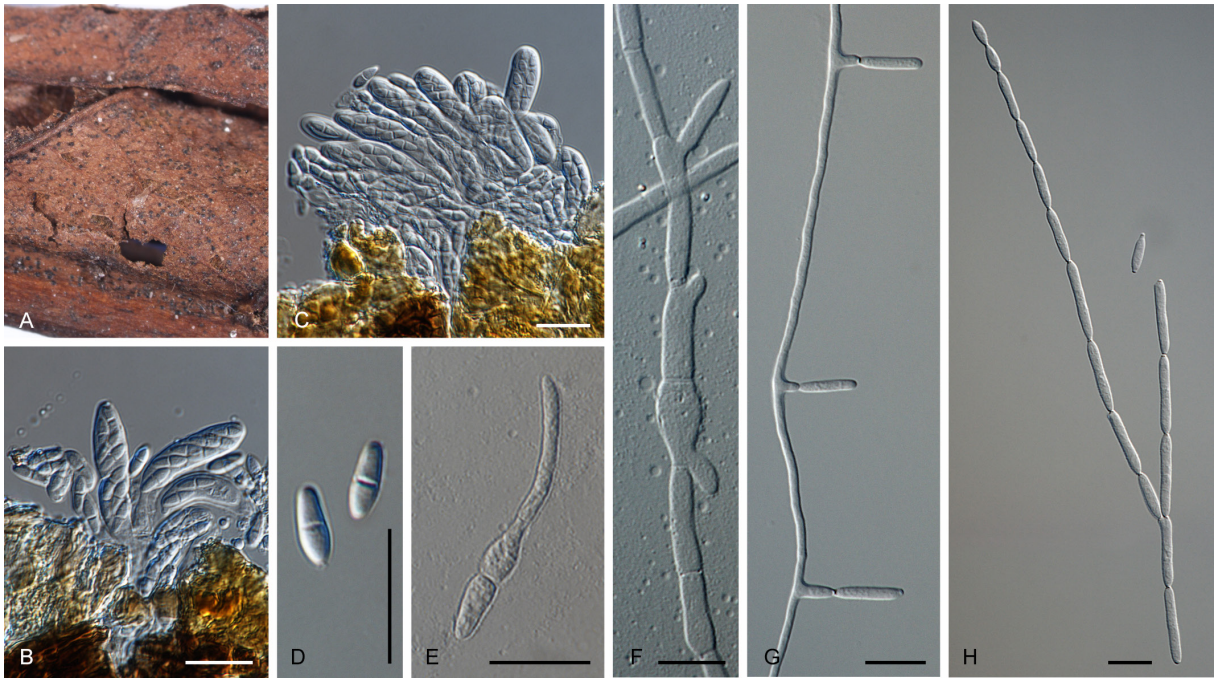


Fig. 51. *Ramularia hydrangeae-macrophyllae* (CPC 25902). A–D. Observations from herbarium material. E–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, C. Asci and ascospores. D. Ascospores. E, F. Germinating ascospores. G, H. Conidia. Scale bars = 10 µm.

Specimens examined: **Italy**, Grancarlo, on *Feijoa sellowiana*, unknown date, G. Polizzi, culture CPC 19854. **Netherlands**, Flevoland Prov., Lelystad, Hollandse Hout, on *Platanus* sp., Apr. 2012, S.I.R. Videira, culture CPC 25901; same prov., Kortenhoefse Plassen, on a dead leaf of *Sparganium ramosum*, Jan. 1982, W. Gams, culture CBS 159.82; Utrecht prov., Bilthoven, on *Phragmites* sp., 6 Jan. 2011, P.W. Crous, cultures CPC 19026, CPC 19027; Breukelen, on *Sparganium ramosum*, unknown collector and date, isol. W. Gams, Sep. 2003, culture CBS 113614; Houten, on *Typha* sp., Jul. 2012, S.I.R. Videira, cultures CPC 25903; Nieuwersluis, Overholland, from leaf spot on *Angelica sylvestris*, unknown collector and date, dep. Nov. 1949, culture CBS 341.49; Utrecht, Botanical Garden, on *Aesculus hippocastanum*, Apr. 2012, S.I.R. Videira, cultures CPC 25902; Utrecht, Botanical Garden, on *Iris foetidissima*, collector and date unknown, culture CPC 20484; Utrecht, on *Juncus* sp., May 2013 U. Damm, culture CPC 25907; Utrecht, on *Potentilla* sp., Oct. 2012, U. Damm, cultures CPC 25904; Utrecht, on *Laurus* sp., May 2013, W. Quaedvlieg, culture CPC 25908; Veenendaal, on *Carex* sp., May 2013, W. Quaedvlieg, cultures CPC 25905, CPC 25906; **New Zealand**, Auckland, Grey Lynn, on *Helleborus niger*, 1 May 2005, C.F. Hill, culture CBS 118408; Mt. Albert, Rurangi Road, on the underside of the leaf of *Hydrangea macrophylla*, 2 Jul. 2007, C.F. Hill (holotype HAL 2103 F, culture ex-type CBS 122273); Grafton, Park Road, The Auckland Domain, on dead leaves of *Iris* ×*hollandica* hybrid, 28 Oct. 2007, C.F. Hill, culture CBS 122625 = CPC 14811; Grey Lynn, Great North Road, Western Springs, on leaf lesion from *Iris* sp., 23 Sep. 2007, C.F. Hill, culture CBS 122272; Grey Lynn, on *Ligularia clivorum*, unknown collector and date, isol. C.F. Hill, 13 Jun. 2005, dep. C.F. Hill, culture CBS 118410. **Sweden**, Uppland, Dalby par., Jerusalem, on *Filipendula vulgaris*, 12 Jul. 1988, E. Gunnerbeck, culture CBS 114117. **UK**, England, Basingstoke, Upton Grey, Weston Road, on *Iris* sp., 25 Dec. 2010, P.W. Crous, culture

CPC 19030; Exeter, endophyte on *Ulex europaeus*, unknown collector and date, isol. and dep. J. Fisher, Nov. 1984, culture CBS 766.84. **USA**, California, Walnut Creek, Ruth Bancroft Botanical Garden, on *Eucalyptus caesia*, 20 Mar. 2012, P.W. Crous, culture CPC 20406.

Substrate and distribution: *Aesculus* (*Sapindaceae*), *Angelica* (*Apiaceae*), *Carex* (*Cyperaceae*), *Eucalyptus*, *Feijoa* (*Myrtaceae*), *Filipendula*, *Potentilla* (*Rosaceae*), *Helleborus* (*Ranunculaceae*), *Hydrangea* (*Hydrangeaceae*), *Iris* (*Iridaceae*), *Laurus* (*Lauraceae*), *Ligularia* (*Asteraceae*), *Phragmites* (*Poaceae*), *Platanus* (*Platanaceae*), *Sparganium*, *Typha* (*Typhaceae*), and *Ulex* spp. (*Fabaceae*); Europe, N. America, New Zealand.

Notes: The species epithet of *Ramularia hydrangeae-macrophyllae* reflects the name of the host on which it was first observed, *Hydrangea macrophylla*, from New Zealand (holotype in HAL). Within this clade the phylogenetic structure was not resolved consistently in all gene trees (data not shown; Fig. 2, clade 21) and, in accordance with the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) concept, the transition from concordance to conflict determined the limit of these species (Taylor *et al.* 2000). *Ramularia sparganii* was described from *Sparganium emersum* from Sweden (holotype in C) and has not been reported from the Netherlands (Braun 1998). The species produces conidiophores that are subcylindrical to geniculate-sinuous, 5–40(–60) × 1–3 µm, catenate conidia, smooth, ellipsoid-fusoid, 0–1-septate, 8–30(–33) × 1.5–3 µm and with minute hila. The strain CBS 159.82 was possibly misidentified based on the host but was sterile in culture and morphological characters were not observed. *Ramularia hellebori* was described from *Helleborus foetidus* from Germany (lectotype in HAL), and was firstly reported from New Zealand on *Helleborus orientalis* (Braun & Hill 2002) and later on *Helleborus niger* (CBS 118408) (Braun *et al.* 2006), but no ex-type culture was designated. This species description includes conidiophores that are subcylindrical to geniculate sinuous, 10–45 × 1.5–5 µm, conidia catenate, ellipsoid-ovoid to fusiform, verruculose, 0–1-septate, 6–20(–30) × 2–4 µm and minute hila. *Ramularia rollandii* was described from *Iris pseudacorus* from France (lectotype in PC) and the species was reported from New Zealand on an *Iris* × *hollandica* hybrid (CBS 122625) (Braun & Hill 2008), but no ex-type culture is known. This species produces conidiophores that are cylindrical to geniculate-sinuous, apically minutely subdenticulate, 5–15(–20) × 2–3 µm, conidia solitary or in short chains, smooth to faintly verruculose, filiform to acicular, 15–40(–60) × 1–2 µm, 1–4-septate, with minute hila. *Ramularia butomi* is mycophilic and was originally described overgrowing ascomycetous stromata on dead leaves of *Butomus umbellatus* in Sweden (lectotype in B), but the strain CBS 114117 is not documented as hyperparasite in the database. This species produces conidiophores that are simple, subcylindrical to geniculate-sinuous, 8–60 × 1–4 µm, conidia catenate, narrowly ellipsoid-ovoid to subcylindrical-fusiform, (5–)8–16(–24) × (1.5–)2–3(–4) µm, 0–1(–2)-septate, verruculose and with minute hila. *Ramularia deusta* var. *alba* is not reported from *Ulex* and the representative clade for this species has been designated in this study (Fig. 2, clade 62). All the species mentioned above have in common that the conidia are catenate and slightly verruculose to verruculose, with minute hila, but size and septation vary among them. It is necessary to collect fresh material from the type location and host for further observations. The only ex-type culture present in this clade is that of *Ramularia hydrangeae-macrophyllae* (CBS 122273) (Braun & Hill 2008), and in accordance with the GCPST concept, we accept that name for this clade. This species, now with a broad host range and wide geographical distribution, forms a highly supported clade (Fig. 2, clade 21, 1/100/100). Similar intraspecific variation, wide host range and geographical distribution have

been observed before for *Ramularia vizellae* (Videira *et al.* 2015b; Fig. 2, clade 85). Strains CPC 25901 and CPC 25902 were isolated using the method developed for single ascospore isolation for *Mycosphaerella* (Crous *et al.* 1991, Crous 1998), which means this species has a sexual morph (Fig. 51).

Ramularia hydrangeicola J.H. Park & H.D. Shin, Mycotaxon 131: 97. 2016

Specimens examined: **South Korea**, Yangpyeong, on *Hydrangea serrata*, 18 Oct. 2007, H.D. Shin, holotype KUS-F23039, ex-type culture KACC43597; *idem*. cultures CPC 14767–14769; Jeju, on *Hydrangea serrata*, 2 Nov., H.D. Shin, KUS-F23141, cultures CPC 14832–14834.

Substrate and distribution: Only known from South Korea.

Notes: This species has been recently described (Park & Shin 2016) and is only known from South Korea. Until now, only two *Ramularia* species were known to infect *Hydrangea* hosts, *R. hydrangeae* Y.L. Guo & U. Braun (on *Hydrangea bretschneideri*, China, holotype in HMAS) and *Ramularia hydrangeae-macrophyllae* U. Braun & C.F. Hill (on *Hydrangea-macrophylla*, New Zealand, holotype in HAL). The isolates of *Ramularia hydrangeicola* cluster in a highly supported clade (Fig. 2, clade 70, 1/100/100) and are not conspecific with *R. hydrangeae-macrophyllae* (Fig. 2, clade 21).

Ramularia inaequalis (Preuss) U. Braun, Monogr. Cercosporella, Ramularia and Allied Genera (Phytopath. Hyphom.) 2: 68. 1998. Fig. 52.
Basionym: *Fusoma inaequale* Preuss, Linnaea 26: 706. 1855. 1853.
= *Ramularia lineola* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 32: 43. 1879.
= *R. traxaci* P. Karst., Hedwigia 23: 7. 1884.
For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–2-septate, cylindrical-oblong, straight to sinuous, unbranched (25–)40–50(–70) × (1.5–)2–2.5(–3) µm, or reduced to conidiogenous cells. *Conidiogenous cells* terminal on conidiophores or intermediate in the mycelium, cylindrical-oblong, (7.5–)16.5–20(–28) × (1.5–)2(–2.5) µm, with one conidiogenous locus almost flat to protuberant, thickened, darkened and refractive. *Conidia* catenate, hyaline, thin-walled, smooth with hila thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong, sometimes with the apices broader than the centre, (14.5–)18–20.5(–27) × (1.5–)2–2.5(–3) µm, 0–1(–3)-septate, with two apical hila. *Intercalary conidia* cylindrical-oblong, fusoid or clavate, 0–1-septate, slightly narrower at the septa, (10.5–)14–16.5(–26.5) × (1.5–)2(–2.5) µm, in branched chains of up to five conidia. *Terminal conidia* cylindrical-oblong to obovoid, aseptate, (5.5–)10.5–13(–19) × (1–)1.5–2(–3) µm.

Culture characteristics: On MEA, 25 mm diam, surface with convex centre, smooth, with rosy-buff centre turning buff and white towards the raised margin, undulate and feathery, colony reverse olivaceous grey in the centre and ochreous margin; on OA, 25 mm diam, surface flat, smooth, white with a greyish tinge, with margins undulate, naked, buff, colony reverse olivaceous grey centre and cinnamon towards the margin; on PDA, 22 mm diam, surface flat, short and uniform aerial mycelium, pale olivaceous grey, margins naked, entire, buff, colony

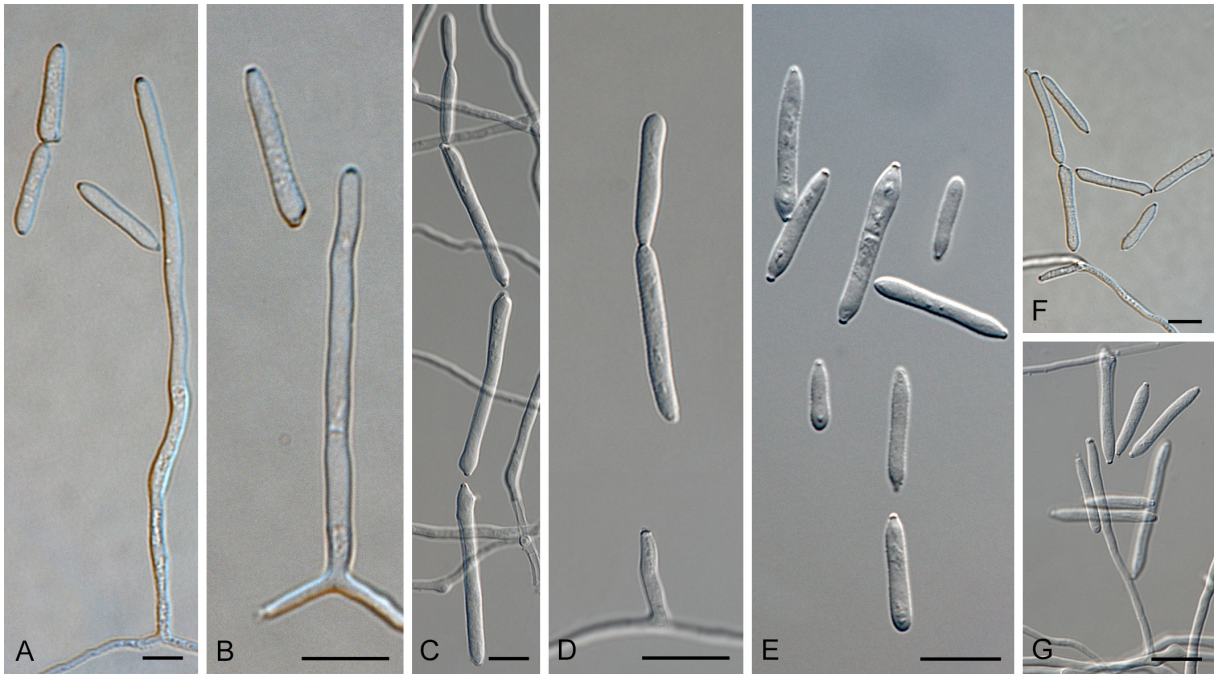


Fig. 52. *Ramularia inaequalis* (CPC 15752). A–G. Structures formed in culture. A, B, D, F, G. Conidiophores and conidia. C, E. Conidia. Scale bars = 10 µm.

reverse olivaceous grey centre and buff margin.

Specimens examined: **Austria**, Krems, on *Taraxacum officinale*, 1870 [Thüm, Fungi Austr. Exs. 888; neotype, designated in Braun (1998), in HAL]. **Canada**, Nova Scotia, Truro, on *Taraxacum officinale*, unknown date, S. Green, culture CBS 250.96. **Mexico**, Montecillo, on *Taraxacum* sp., 1 Oct. 2008, M. de Jesús Yáñez-Morales, culture CPC 15815; Montecillo, on *Taraxacum* sp., 22 Sep. 2008, M. de Jesús Yáñez-Morales, cultures CPC 15752, CPC 15753. **Netherlands**, Utrecht, Rhijnauwen, on *Taraxacum officinale*, May 2013, U. Damm, (epitype designated here: CBS H-22544, MBT204826, culture ex-epitype CBS 141111 = CPC 25741); *idem*. CPC 25742.

Substrate and distribution: On *Andryala*, *Cichorium*, *Crepis*, *Hedypnois*, *Hieracium*, *Hyoseris*, *Hypochoeris*, ?*Lactuca*, *Leontodon*, *Picris*, *Reichardia*, *Rhagadiolus*, *Scorzonera*, *Sonchus*, *Taraxacum*, and *Tolpis* (*Asteraceae*); circumglobal.

Notes: Braun (1998) synonymised several names with *R. inaequalis* since the specimens available on numerous hosts belonging to the *Asteraceae* were morphologically very uniform. *Ramularia inaequalis* was originally described on *Taraxacum officinale* from Austria (neotype in HAL) but it is a commonly reported species worldwide and in a wide range of hosts. The strains originally identified as *R. inaequalis* used in this study fell in three different clades (Fig. 2, clades 5, 40 and 56). Only in clade 40 (Fig. 2) are strains collected from Europe that were suitable for epitypification (Fig. 52); the other strains are tentatively considered as *R. hieracii-umbellati* (Fig. 2, clade 56) and as *R. helminthiae* (Fig. 2, clade 5). The clade representing *R. inaequalis* is highly supported (Fig. 2, clade 40, 1/100/100). *Ramularia inaequalis* has a very wide host range and distribution.

Ramularia interstitialis (Berk. & Broome) Gunnerb. & Constant., Thunbergia 15: 50. 1991. Fig. 53.
Basionym: *Peronospora interstitialis* Berk. & Broome, Ann. Mag. Nat. Hist. 15: 34. 1875.
≡ *Ovularia interstitialis* (Berk. & Broome) Massee, British Fungus-Flora 3: 322. 1893.
= *Ramularia primulana* P. Karst., Hedwigia 23 (1): 7. 1884.
= *Ovularia corcellensis* Sacc. & Berl., Atti Ist. Veneto Sci. Lett. Arti 3: 731. 1885.

Mycelium hyaline, septate, branched. *Conidiophores* and *conidiogenous cells* scarce and insufficient for complete description. *Conidia* hyaline, smooth to slightly verruculose, catenate, branching chains, consistently aseptate, ellipsoid-ovoid, occasionally subcylindrical, obovoid (3.5–)6–8(–20) × (2.5–)3.5–4(–5) µm.

Description in vivo: See Braun (1998: 225).

Specimen examined: **UK**, Southwestern England, Exeter, on *Primula vulgaris* × *vernalis*, S.A.J. Tarr, CBS H-17746, culture CBS 120.68.

Substrate and distribution: On *Primula* (*Primulaceae*); Europe.

Notes: Two species have been described from hosts of the genus *Primula*, *Ramularia primulae* and *R. interstitialis*, that have a broad distribution in Europe. *Ramularia primulae* produces catenate conidia, (8–)10–35(–40) × 3–6 µm, that are 0–2(–3)-septate. *Ramularia interstitialis* produces very distinctive conidiophores, erect or decumbent to repent, long and strongly geniculate-sinuous, the conidia are produced singly, occasionally in short chains, are aseptate and (6–)8–16(–21) × (4–)5–8(–10) µm. In the observed specimen (Fig. 53), the conidiogenous structures observed were too scarce for a proper analysis and the conidia were slightly narrower than in the description of *R. interstitialis* found in literature (Braun 1998). However, the name is tentatively used for this isolate pending the collection of fresh material since *in vitro* measurement can vary when compared to *in vivo*. The strain used in this study originated from the UK and falls in the *Ramularia* clade (Fig. 1, clade XIV), but was not used in the multigene phylogeny because it was not possible to amplify the partial genes of *gapdh* and *rpb2*.

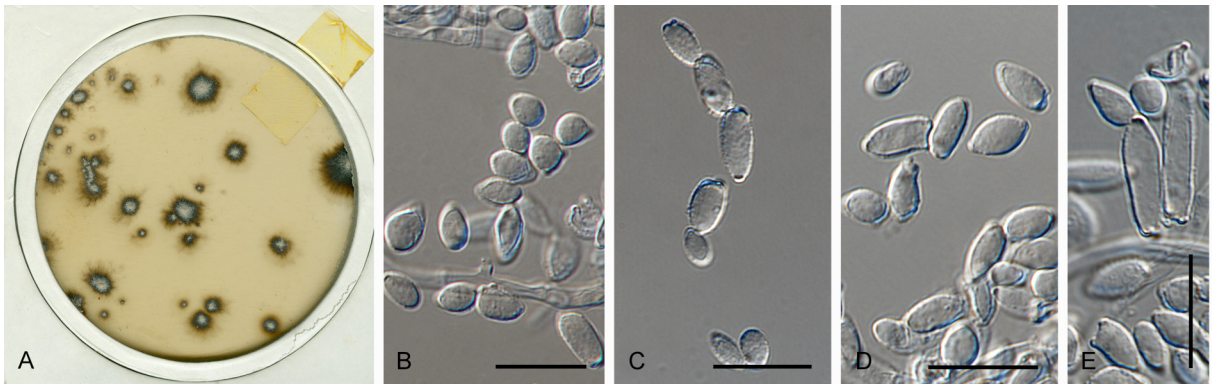


Fig. 53. *Ramularia interstitialis* (CBS 120.68). A–F. Observations from herbarium material. B–F. Conidia. Scale bars = 10 µm.

Ramularia kriegeriana Bres., Hedwigia 39: 328. 1900.
= *Ramularia plantaginis* Ellis & G. Martin, Amer. Naturalist 16: 1003. 1882, nom. illeg., non *R. plantaginis* Peck, 1880.

Specimens examined: **Germany**, Saxony, Königstein, Pfaffendorf, on *Plantago major*, 17 Jul. 1895 [Krieger, Fungi Saxon Exs. 1630; lectotype of *R. kriegeriana*, designated in Braun (1998), in JE]. **South Korea**, Hoengseong, on *Plantago asiatica*, 10 Oct. 2003, H.D. Shin, KUS-F19845, culture CPC 10825–10827. **USA**, Kentucky, Lexington, on *Plantago major*, Jul. 1882, Kellerman s.n.; type of *R. plantaginis* Ellis & G. Martin, in BPI 418612.

Substrate and distribution: On *Plantago* spp. (*Plantaginaceae*); Asia, Europe, N. America.

Notes: Braun (1998) used the name *Ramularia plantaginis* Ellis & G. Martin for *Ramularia* on *Plantago major* and other species characterised by verruculose conidia. This was based on the wrong assumption that *R. plantaginis* Peck was also published in 1882, which is, however, not correct since the latter name was published in 1880, which makes *R. plantaginis* Ellis & G. Martin an illegitimate homonym. Thus, *R. kriegeriana* is the oldest valid name for this fungus. This species has previously been reported from South Korea on *Plantago asiatica*, and is known from several *Plantago* species in Asia, Europe and N. America, including *P. asiatica* from China (Braun 1998). The strains in this study cluster together in a highly supported clade (Fig. 2, clade 65, 1/100/100) although a collection from Germany is required to fix the application of this name. *Plantago asiatica* is phylogenetically close to *P. major*, the principal host of *Ramularia kriegeriana*. The two species belong in *Plantago* subgen. *Plantago*, in contrast to *P. lanceolata*, the principal host of *R. rhabdospora*, which belongs in subgen. *Psyllium* (Rønsted *et al.* 2002).

Ramularia lamii Fuckel var. *lamii*, Jahrb. Nassauischen Vereins Naturk. 23–24: 361. 1870. Fig. 54.
≡ *Ovularia lamii* (Fuckel) Sacc., Syll. ung. 6: 144. 1886.
For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth, 1–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, straight to geniculate-sinuous, cylindrical-oblong, unbranched, (8–)10–50(–80) × 1.5–2(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal on conidiophores, cylindrical-oblong, (7.5–)18.5–24.5(–33) × 1.5–2(–2.5) µm, with 1–3 apical conidiogenous loci almost flat, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical to clavate, sometimes with broader apexes and narrower at the centre, (9–)14–18(–28) × (2.5–)3–3.5(–4) µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, sometimes slightly curved, ovoid, (8.5–)11.5–13(–19) × (2.5–)3(–4) µm, in branched chains of up to six conidia. *Terminal conidia* obovoid, aseptate, (4.5–)7–8(–11.5) × (2–)2.5–3(–5) µm (on SNA, CBS 108971).

Culture characteristics: On MEA surface strongly folded, rosy-buff with smoke-grey areas, low convex with margins concave and crenate, colony reverse fawn to cinnamon, folded, grows 1.7 mm after 2 wk at 25 °C. On OA surface flat, aerial mycelium white with a rose tinge raised in the centre, produces a transparent exudate, with margins undulate, sparse aerial mycelium,

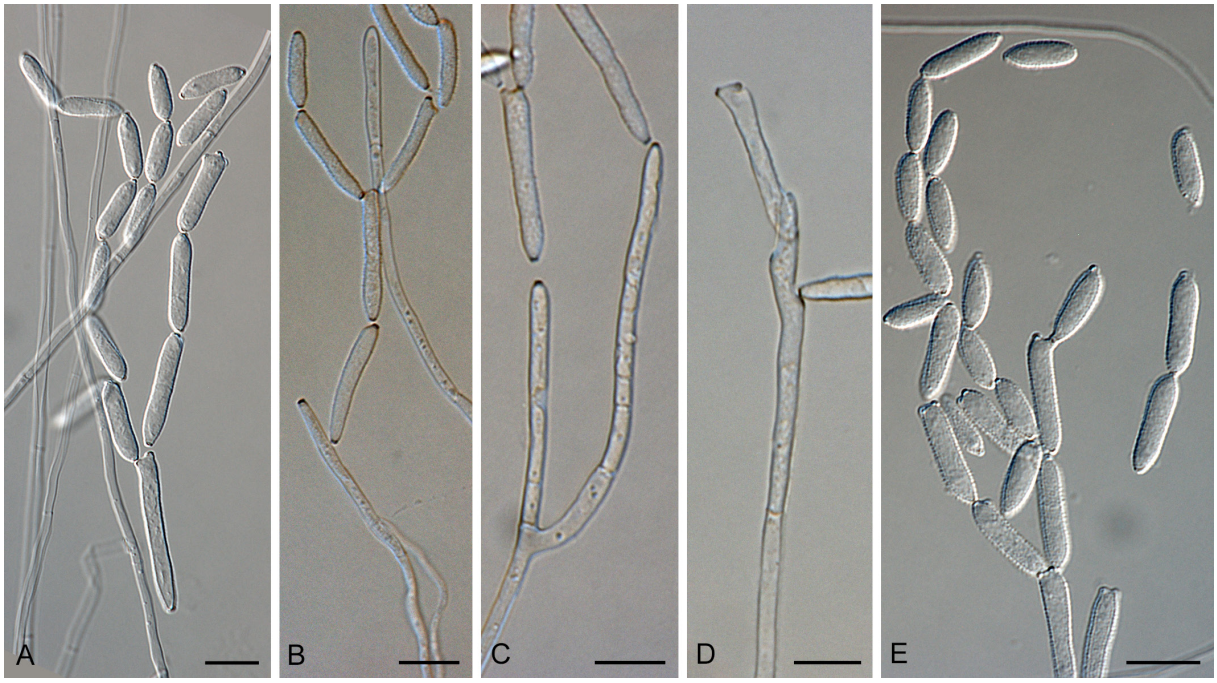


Fig. 54. *Ramularia lamii* var. *lamii* (CBS 108971). A–E. Structures formed in culture. A, E. Conidia. B–D. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

rosy-buff, colony reverse saffron, grows 1.8 mm after 2 wk at 25 °C. On PDA, surface low convex, white with a light grey tinge, fluffy, with margins slightly undulate, colony reverse salmon with olivaceous grey patches, grows 1.8 mm after 2 wk at 25 °C.

Specimens examined: **Germany**, on *Lamium album* [Fuckel, Fungi Rhen. Exs. 136; lectotype, designated in Braun (1998), in HAL]. **Netherlands**, Utrecht Prov., Baarn, de Hooge Vuursche, leaf spot of *Lamium album*, 22 Jun. 2000, G. Verkley (epitype designated here CBS H-22639, MBT371840, culture ex-epitype CBS 108970); *idem*. CBS 108971.

Description in vivo: See Braun (1998: 183).

Substrate and distribution: on *Lamium* (*Lamiaceae*); Asia, Caucasus, Europe, N. Africa, N. America.

Notes: There are two varieties of *R. lamii*, namely *R lamii* var. *lamii* (on *Lamium album*, Germany, lectotype in HAL), and *R. lamii* var. *minor* (on *Prunella vulgaris*, USA, Winsconsin, holotype in NY). The latter variety has smaller conidiophores and smaller and narrower conidia. Strains originally identified as *R. lamii* appeared in three distinct clades in the phylogeny (Fig. 2, clades 1, 46 and 67) showing that more than one species is present in this complex. The strains in clade 67 (Fig. 2) were collected in the Netherlands and are morphologically good representatives of *R. lamii* (Fig. 54), and are therefore designated as ex-epitype strains, whereas the other strains are assigned to *R. leonuri* and *R. agastaches*, respectively. All three phylogenetic analyses provided high support to this species clade (Fig. 2, clade 67, 1/100/100).

Ramularia leonuri Sorokīn, Trudy Obshch. Estestvoisp. Imp. Kazansk. Univ. 2: 30. 1872. Fig.

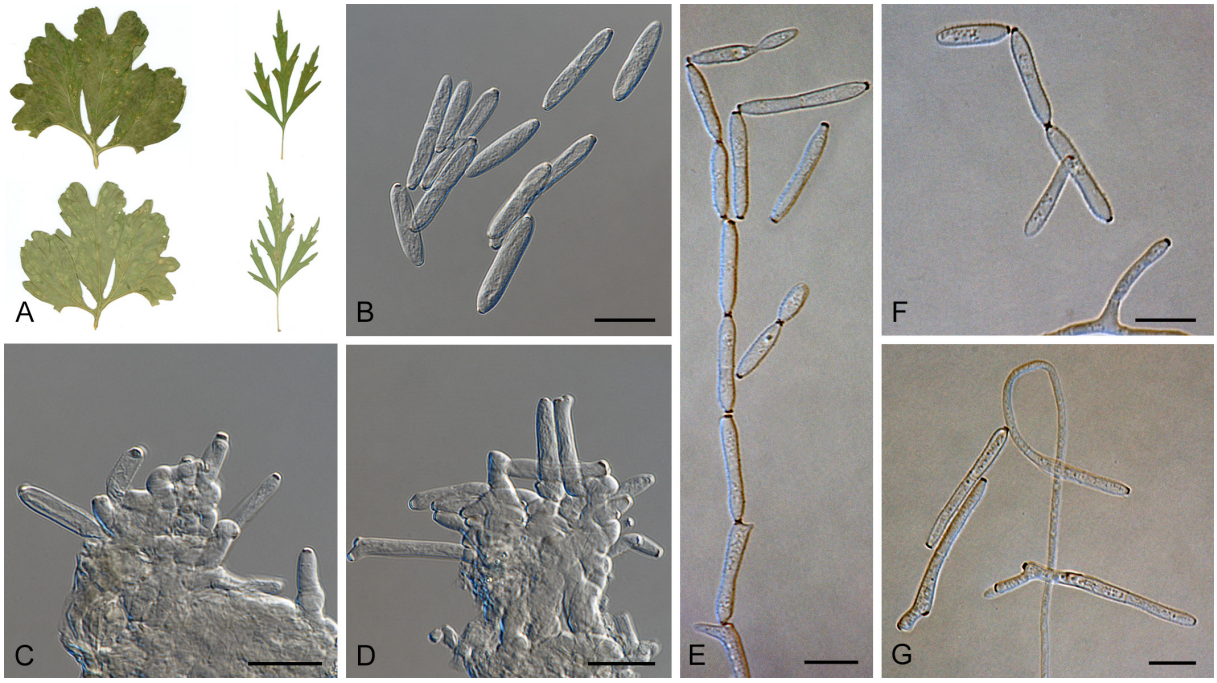


Fig. 55. *Ramularia leonuri* (CPC 11314). A–D. Observations from herbarium material. E–G. Structures formed in culture. A. Leaf spot symptoms on the host. B, E. Conidia. C, D. Conidiophores and conidiogenous cells. F, G. Conidiophores and conidia. Scale bars = 10 µm.

55.
≡ *Ramularia sorokinii* Sacc. & Syd., Syll. fung. 14: 1065. 1899, nom. illeg. (superfl.).
= *Ramularia leonuri* Sacc. & Penz., Michelia 2: 638. 1882.

Mycelium consisting of hyaline, septate, branched, smooth, 1–1.5 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–3-septate, straight, cylindrical-oblong, unbranched, (11.5–)20–25.5(–28) × 1.5–2 µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium, cylindrical-oblong, (4–)11–15(–19) × 1–2(–3) µm, with one conidiogenous locus, thickened and darkened. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened and darkened. *Ramoconidia* subcylindrical to clavate, aseptate to 1-septate and narrower at the septa, (18–)21–23.5(–28) × (2–)2.5–3 µm, with two conidiogenous apical hila. *Intercalary conidia*, aseptate to 1-septate, subcylindrical, sometimes curved, (14.5–)18.5–21(–28) × (1.5–)2.5–3(–3.5) µm, in chains of up to five conidia. *Terminal conidia*, aseptate, subcylindrical to obovoid, (6.5–)13–15(–25) × (2–)2.5–3(–4) µm.

Culture characteristics: On MEA, 27 mm diam, surface smooth, low convex, radially striated, cracking in the centre, with entire margins, convex and feathery, colony reverse iron-grey with ochreous margin; on OA, 20 mm diam, surface flat, fluffy uniform, white with buff tinge, with margins buff and with no aerial mycelium, undulate, colony reverse buff; on PDA, 25 mm diam, surface concave, smooth and white, margins entire, feathery and low convex, colony reverse olivaceous grey and buff.

Specimens examined: **France**, Rouen, on *Leonurus cardiaca*, Letendre, herb. Saccardo (holotype of *R. leonuri* Sacc. & Syd. PAD); **Russia**, Jaroslavl, Bernichino, on *Leonurus cardiaca*, 22

Aug. 1909, Serebrianikov [Tranz. & Serebr., Mycoth. Ross. 48; neotype of *R. leonuri* Sorokīn, designated in Braun (1998), in LE 200619]; **South Korea**, Hongcheon, on *Leonurus sibiricus*, 9 Oct. 2007, H.D. Shin, KUS-F22992, CBS H-22522, culture CBS 141112 = CPC 14570; *idem*. CPC 14571, CPC 14572; Jinju, on *Leonurus sibiricus*, 14 May 2004, H.D. Shin, KUS-F20195, cultures CPC 11312–11314; Yangpyeong, on *Leonurus sibiricus*, 23 Jul. 2004, H.D. Shin, KUS-F20502, cultures CPC 11411–11413.

Notes: *Ramularia leonuri* on *Leonurus cardiaca*, reduced to synonymy under *R. lamii* var. *lamii* by Braun (1998), is morphologically indistinguishable from the Korean material on *L. sibirica*. Therefore, we prefer to apply this name to this collection, at least tentatively, although cultures of *R. leonuri* from France and Russia are not yet available for comparison. The *R. leonuri* clade was highly supported by phylogenetic analyses (Fig. 2, Clade 1, 1/100/100) and is currently known only from South Korea. These strains were previously identified as *R. lamii* var. *lamii* but the type of *R. lamii* clusters in a different clade (Fig. 2, clade 67). *Ramularia leonuri* and *Ramularia lamii* var. *lamii* are morphologically very similar but *R. leonuri* produces shorter conidiophores, smaller conidiogenous cells and longer terminal conidia (Fig. 55).

Ramularia lethalis Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 43: 86. 1891. Fig. 56.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, thin-walled, smooth, integrated in mycelium, cylindrical-oblong to geniculate-sinuous, (6–)10–12(–15) × 1–2 µm, with 1–3 apical conidiogenous loci almost flat to protuberant, thickened and darkened. *Conidia* hyaline, thin-walled, smooth to verruculose, catenate, mostly aseptate and rarely 1-septate, with hila thickened and darkened. *Ramoconidia* subcylindrical to ellipsoid, (4–)6–7(–12) × (1.5–)2.5–3

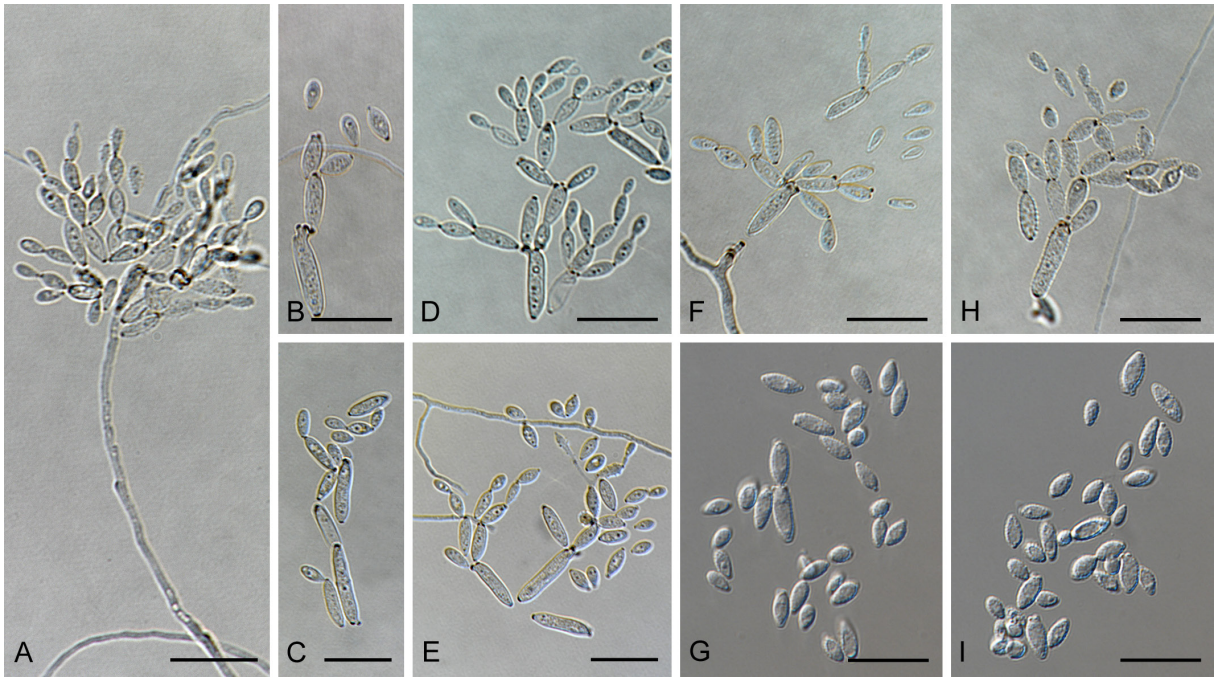


Fig. 56. *Ramularia lethalis* (CBS 141113). A–I. Structures formed in culture. A, F. Conidiophores reduced to conidiogenous cells and conidia. B–E, G, H, I. Conidia. Scale bars = 10 µm.

µm, with 2–3 conidiogenous apical hila. *Intercalary conidia*, fusoid-ellipsoid, (4–)5(–6.5) × (1.5–)2–3µm, in chains of up to three conidia. *Terminal conidia*, aseptate, ellipsoid-obovoid, (2–)3–4 × (1–)2–2.5 µm.

Culture characteristics: On MEA, 8 mm diam, surface raised, irregular, mycelium smooth and white, with entire margin, convex and feathery, colony reverse ochraceous; on OA, 10 mm diam, surface raised, irregular, mycelium smooth, white with buff tinge, margins undulate, colony reverse buff; on PDA, 9 mm diam, surface smooth, mycelium flat and white, entire margins, colony reverse buff with olivaceous patches.

Description in vivo: See Braun (1998: 46).

Specimens examined: **Netherlands**, Utrecht, Hollandse Hout, on leaves of *Acer pseudoplatanus*, 5 Apr. 2012, S.I.R. Videira, cultures CBS 141113 = CPC 25910. **Canada**, Ontario, London, on *Acer rubrum*, Oct. 1890, Dearness [Ellis & Everh., N. Amer. Fungi 2596; lectotype, designated in Braun (1998), in NY 830534].

Substrate and distribution: On *Acer*; Caucasus, Europe (the Netherlands) and North America.

Notes: Three species of *Ramularia* are known from *Acer*, namely *R. lethalis*, *R. unterseheri* and *R. vizellae*. *Ramularia lethalis* (Fig. 56) was originally described on *Acer rubrum* from Canada (lectotype in NY). The strain used in this study forms a single lineage and is positioned in a very long branch, which supports this species as unique (Fig. 2, clade 84). Morphological characters of the isolate used in this study agree with the description of *R. lethalis* from literature (Braun 1998). This is a first report of this pathogen in Europe and on *Acer pseudoplatanus*.

Ramularia ligustrina Maubl., Bull. Trimestriel Soc. Mycol. France 22: 70. 1906.

Specimen examined: **Italy**, Torino, on living leaf of *Ligustrum vulgare*, unknown collector and date, isol. and dep. M. Ribaldi, Oct. 1952, culture CBS 379.52.

Substrate and distribution: On *Ligustrum vulgare*; Caucasus (Armenia), Europe (Bulgaria, France, Germany, Italy and Moldova).

Notes: *Ramularia ligustrina* was described as a pathogen on *Ligustrum vulgare* in France, but was considered doubtful by Braun (1998) since type material or other collections agreeing with the description could not be traced. The species is insufficiently known but the name is tentatively accepted here given its distinct phylogeny (Fig. 2, clade 69), pending further collections.

Ramularia macrospora Fresen., Beitr. Mykol. 3: 88. 1863.
≡ *Cylindrosporium macrosporum* (Fresen.) J. Schröt., Krypt.-Fl. Schlesien 3.2(4): 490. 1897.
= *Scolicotrichum ochraceum* Fuckel, Fungi Rhen. Exs., Cent. 22: no. 2108. 1868.
= *Ramularia prismatocarpi* Oudem., Ned. Kruidk. Arch. 3: 155. 1877.
= *Cercospora phyteumatis* A.B. Frank, Krankh. Pfl., 1. Aufl.: 601. 1880.
= *Ramularia adenophorae* Moesz, Bot. Közlem. 35 (1–2): 67. 1938.
= *Ramularia rapunculoidis* Nannf., in Lundell & Nannfeldt, Fungi Exs. Suec. 39–40: 31. 1950.
For additional synonyms see (Braun 1998)

Description in vivo: See Braun (1998: 125).

Specimen examined: **Austria**, Ötztal, Sölden, Hoch-Sölden, alt. 1800 m., on leafspots of *Phyteuma betonicifolium*, 25 Jul. 2000, G. Verkley, No. 1011.1, cultures CBS 109015, 109016.

Substrate and distribution: On *Adenophora*, *Asyneuma*, *Campanula*, *Gadellia*, *Legousia*, and *Phyteuma* (*Campanulaceae*), *Aristolochia punjabensis* (*Aristolochiaceae*); Asia, Caucasus, Europe, N. America, Pakistan.

Notes: *Ramularia macrospora* was described as a pathogen on *Campanula pyramidalis* from Germany (iconotype Pl. XI, figs 29–32). The strains used in this study cluster in the *Ramularia* clade (Fig. 1, clade XIV) but were not used in the multigene analysis because it was not possible to amplify and sequence the *tef1*-α partial gene. Although *R. macrospora* is usually associated with members of the *Campanulaceae* (Braun 1998), it was recently observed infecting a host from the *Aristolociaceae* (Mukhtar *et al.* 2012).

Ramularia major (Unger) U. Braun, Nova Hedwigia 47: 340. 1988.
Basionym: *Cylindrospora major* Unger, Exanth. Pfl.: 168: 1833.
= *Fusidium petasitidis* Pass., in Thüm., Mycoth. Univ. 1473. 1879.
= *Ramularia cervina* Speg., Dec. Mycol. Ital.: 107. 1879.
≡ *Cylindrospora cervina* (Speg.) J. Schöt., in Cohn, Krypt.-Fl. Schlesien 3.2(4): 488. 1897.
= *R. variegata* Ellis & Holw., in Arth., Rep. Bot. Minnesota: 34. 1886.
= *R. petasitis-tomentosae* Săvul. & Sandu, Hedwigia 73: 121. 1933.
For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 86).

Specimens examined: **Germany**, Thuringia, Erfurt, on *Petasites hybridus*, 7 Oct. 1910, Diedicke [neotype, designated in Braun (1998), in JE]. **South Korea**, Chuncheon, on *Petasites japonicus*, 25 Oct. 2005, H.D. Shin, KUS-F21578, CBS H-22523, cultures CBS 141114 = CPC 12542; *idem*. CPC 12543, CPC 12544.

Substrate and distribution: On *Adenostyles*, *Homogyne*, and *Petasites* (*Asteraceae*); Asia, Caucasus, Europe, N. America.

Notes: *Ramularia major* was originally described on *Petasites hybridus* from Germany (neotype in JE) and is a common pathogen associated with a few related hosts of the family *Asteraceae* worldwide (Braun 1998). The strains used in this study form a highly supported clade (Fig. 2, clade 10, 1/100/100), which is tentatively maintained as representative of the species until material from the type host and location are recollected and examined.

Ramularia mali Videira & Crous, Persoonia 34: 58. 2015.

Specimen examined: **Italy**, Piemont, on *Malus domestica* fruit in cold storage, May 2011, unknown collector, dep. R. Piemonte & G. Michelatti (holotype CBS H-21618, culture ex-type CBS 129581).

Substrate and distribution: Thus far only known from the type collection.

Notes: See Videira *et al.* (2015a). This species formed a single lineage (Fig. 2, clade 33) basal to the *R. glenii* clade (Fig. 2, clade 32). In a single lineage next to *R. mali* we can observe *Ramularia* sp. B, which is sterile in culture and could not be described.

Ramularia malicola Videira & Crous, **sp. nov.** MycoBank MB816850. Fig. 57.

Etymology: Named after the host it was isolated from, *Malus*.

Mycelium consisting of hyaline, septate, branched, smooth, 2–4 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, multiseptate, straight, cylindrical-oblong, unbranched, (45–) 100–120(–158) × (2.5–)4–5(–6) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium, cylindrical-oblong, (16.5–)25–32(–42) × (3–)4(–5) µm, with one apical conidiogenous locus, thickened and darkened. *Conidia* formed singly, hyaline, thin-walled, smooth, aseptate, ellipsoid, obovoid, (11–)21–27(–40) × (4.5–)6–7(–8) µm, with hila thickened and darkened.

Culture characteristics: On MEA, 15 mm diam, surface raised and strongly folded, rosy-vinaceous with erumpent white mycelium, with small ochreous droplets, with margins crenate, colony reverse ochreous; on OA, 10 mm diam, surface raised, folded, rosy-vinaceous with erumpent white mycelium, with margins crenate, feathery, colony reverse brick; on PDA, 15 mm diam, surface raised and strongly folded, rosy-vinaceous with erumpent white mycelium, with small buff droplets, with margins crenate, colony reverse ochreous.

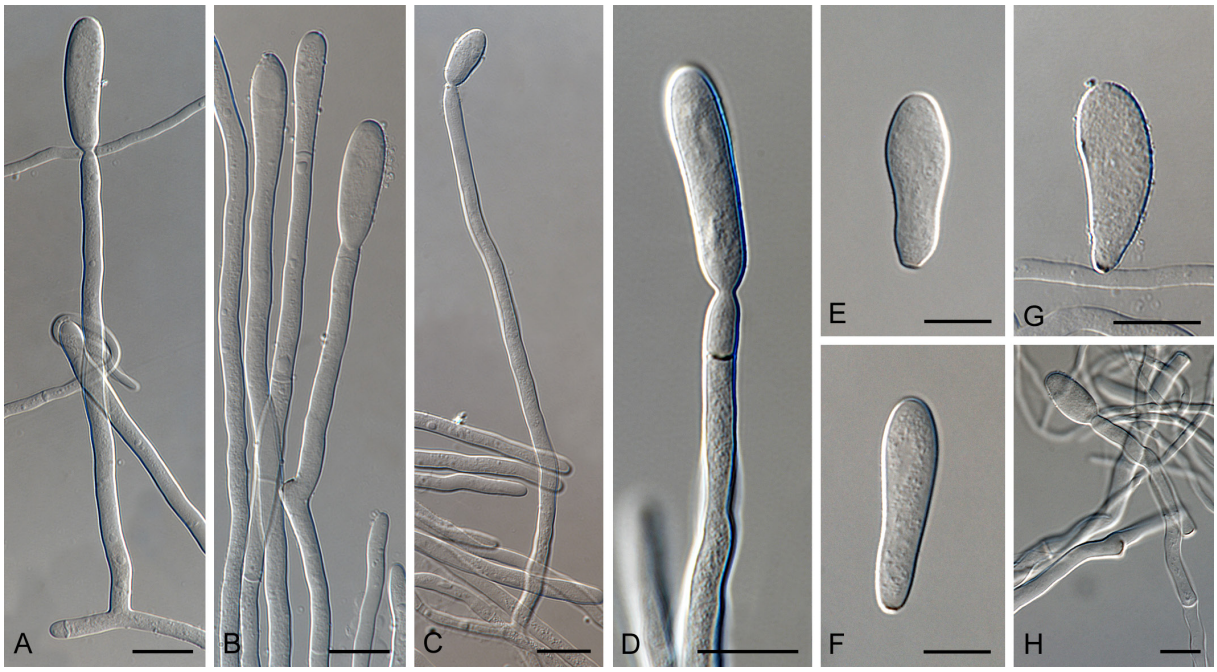


Fig. 57. *Ramularia maliicola* (CBS 119227). A–H. Structures formed in culture. A–D. Conidiophores and conidia. E–G. Conidia. H. Conidiogenous cells. Scale bars = 10 µm.

Specimen examined: **USA**, Missouri, New Franklin, on *Malus* sp., Sep. 2000, J. Batzer (holotype CBS H-22524, ex-type culture CBS 119227).

Note: *Ramularia malicola* formed a single lineage (Fig. 2, clade 80) that is sister to *R. rubella* (Fig. 2, clade 79). This species is morphologically similar to *R. rubella* but differs by forming wider conidia (Fig. 57). *Ramularia malicola* was first isolated in a study related to sooty blotch and flyspeck on apple in the USA (Batzer *et al.* 2005). It was present in samples collected from two orchards and caused punctate symptoms on the fruit. It was described as *Ramularia* sp. P5 based on the morphological characteristics that included hyaline, single-celled, ovularia-type conidia, irregular in shape, 5.2–14.5 × 1.5–7 µm (CLA media), produced on brown conidiophores that had dendritic branches with a single central basal cell. In this study, the conidiophores observed were always hyaline but a different culture medium was used to that of Batzer *et al.* (2005).

Ramularia miae Crous, Fungal Planet No. 3. 2006.

Specimens examined: **South Africa**, on *Wachendorfia thyrsiflora*, 4 Jan. 2006, M.K. Crous & P.W. Crous (holotype CBS H-19763, ex-type culture CBS 120121 = CPC 12736), *idem*. cultures CPC 12737, CPC 12738; on *Gazania rigens* var. *uniflora*, 9 Aug. 2011, P.W. Crous, culture CPC 19835; on *Leonotis leonurus*, 30 Jul. 2011, P.W. Crous, culture CPC 19770; on *Wachendorfia thyrsiflora*, 28 Oct. 2012, M.J. Wingfield, culture CPC 21692.

Substrate and distribution: On *Gazania rigens* var. *uniflora* (*Asteraceae*), *Leonotis leonurus* (*Lamiaceae*) and *Wachendorfia thyrsiflora* (*Haemodoraceae*); South Africa.

Notes: See Crous and Groenewald (2006) and Videira *et al.* (2015a). The phylogenetic analyses provide high support for this species clade (Fig. 2, clade 29, 1/100/100).

Ramularia neodeusta Videira & Crous, **sp. nov.** MycoBank MB817159.

Etymology: Named after its morphological similarity to *Ramularia deusta*.

Cultures sterile. *Ramularia neodeusta* (Fig. 2, clade 15), differs from its closest phylogenetic neighbour, *R. vallisumbrosae* (Fig. 2, clade 16), by unique allelles in five loci based on alignments of the separate loci deposited in TreeBASE as Study S19315: *rpb2* positions 12(C), 15(A), 27(G), 39(A), 45(G), 54(C), 63(G), 75(A), 87(A), 99(C), 120(G), 135(C), 150(C), 151(T), 165(C), 168(T), 171(T), 186(G), 189(C), 195(T), 201(G), 204(T), 234(C), 240(G), 246(C), 252(C), 253(T), 264(A), 285(T), 297(G), 303(G), 318(C), 321(G), 324(C), 327(A), 330(G), 333(A), 336(A), 354(A), 357(A), 363(G), 375(G), 378(C), 387(T), 405(G), 411(T), 420(T), 441(G), 447(G), 456(T), 468(T), 478(G), 480(G), 483(C), 489(C), 492(T), 499(T), 504(C), 505(A), 507(T), 511(G), 519(G), 524(A), 532(C), 540(C), 546(A), 570(A), 576(T), 582(G), 591(C), 597(A), 630(A), 639(T), 642(A), 651(A); ITS positions 77(A), 81(T), 82(C), 108(G), 109(A), 110–111 deletion (TC), 342(A), 419(A), 420(G), 472(G), 500(C); *actA* positions 19(T), 31(G), 34(T), 49(C), 59(C), 61(A), 62(T), 63–67 insertion (GAGCA), 68(G), 69(C), 73(C), 82–83 deletion (AC), 86–88 deletion (CGA) 95(A), 96(G), 98(A), 99(A), 101(C), 108(T), 115(T), 116(T), 121(A), 122(T), 153(C), 164(C), 167(T), 182(T), 186(T), 208(C), 210(A), 211(T), 233(A), 238(C); *gapdh* positions 13(G), 18(A), 30(C), 39(A), 41(A), 42(C), 44(G), 47(G),

49(C), 60(G), 65(A), 66(G), 68(C), 101(G), 106(A), 113 deletion (C), 114(C), 116(G), 131(C), 140(C), 167(C), 200(C), 206(T), 207(C), 208(G), 210(T), 258(T), 259(C), 260(C), 262–263 insertion (TA), 264(C), 265 insertion (A), 267 insertion (G), 268(A), 269(A), 270(T), 271(A), 281(G), 282(G), 284(C), 286(C), 287(C), 288(G), 290(T), 292(C), 298(T), 299(T), 305(T), 307(T), 308(C), 313 deletion (G), 314(C), 315(C), 374(C), 389(C), 431(T), 449(A), 455(C), 506(T), 548(C), 554(C), 566(T), 584(T), 593(T), 614(C), 623(T), 626(T); *tef1-α* positions 14(T), 15(T), 16(T), 20(T), 22(C), 23(C), 24(T), 26 deletion (C), 27(T), 29 deletion (T), 45 deletion (CTC), 48(A), 49(C), 52(A), 57(G), 58(C), 86(C), 95(A), 99(T), 107(A), 129(T), 145(T), 178 deletion (T), 195(C), 212(T), 226–228 insertion (TAA), 232(A), 241(A), 242(A), 247(T), 255(C), 256(C), 257(A), 269(A), 271(T), 291(C), 292(C), 294(A), 304(T), 307–310 insertion (CTAT), 311(G), 313(A), 316(C), 398(T), 400(C), 401(T), 404(A), 406(C), 407(A), 409(A), 410(C), 411–424 insertion (TTCTCAACAAACTT), 427(T), 431(A), 432(A), 434(T), 447(C), 448(A), 450(T), 455(C), 578(T).

Specimens examined: **New Zealand**, on leaf of *Vicia faba*, 25 Oct. 2005, C.F. Hill (holotype CBS H-22525, culture ex-type CBS 141115 = CPC 13567); on leaf of *Lathyrus odoratus*, 23 Oct. 2005, C.F. Hill, culture CPC 13568.

Notes: This strain was initially identified as *R. deusta* var. *alba*, a species that was previously reported from New Zealand on *Lathyrus pratensis* and *L. latifolius*. However, an authentic strain of *R. deusta* can be found in clade 62 (Fig. 2). Therefore, the strains in this clade represent a new species that is highly supported (Fig. 2, clade 15, 1/100/100). Unfortunately the strains were sterile and therefore a molecular description is provided.

Ramularia nyssicola (Cooke) Videira & Crous, Persoonia 34: 60. 2015.
Basionym: *Sphaerella nyssicola* Cooke, Hedwigia 17: 40. 1878.
≡ *Mycosphaerella nyssicola* (Cooke) F.A. Wolf, Mycologia 32: 333. 1940.

Description: See Minnis *et al.* (2011b).

Specimens examined: **USA**, Maryland, Prince George's County, Glen Dale, on overwintered leaves *Nyssa ogeche* × *sylvatica* hybrid, R.T. Olsen, culture CBS 127664; same location, substrate and collector, 18 Jun. 2009 (epitype BPI 880897, AR 4656, culture ex-epitype CBS 127665).

Substrate and distribution: On *Nyssa* (*Cornaceae*); N. America (eastern USA).

Notes: See Minnis *et al.* (2011b), who designated an epitype for the species, and Videira *et al.* (2015a) who reassigned the species to the genus *Ramularia*. The phylogenetic analyses provide high support to this species clade (Fig. 2, clade 81, 1/100/100).

Ramularia osterici Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816851. Fig. 58.

Etymology: Named after the host genus on which it occurs, *Ostericum*.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2.5 µm diam hyphae. *Conidiophores* hyaline, erect, 1–3(–5)-septate, straight, cylindrical-oblong, unbranched (13–)

Fig. 58. *Ramularia osterici* (CPC 10751). A, B. Observations from herbarium material. C–G. Structures formed in culture. A. Leaf spot symptoms on the host. B–D, F, G. Conidiophores, conidiogenous cells and conidia. E. Conidia. Scale bars = 10 µm.

34–51(–140) × (1.5–)2–2.5(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, integrated in mycelium or terminal in conidiophores, cylindrical-oblong, (10–) 17.5–21(–30) × (2–)2.5–3(–4) µm, with one apical conidiogenous locus, almost flat, thickened, darkened, refractive. *Conidia* hyaline, smooth, catenate, with hila thickened, darkened, refractive. *Ramoconidia* subcylindrical, clavate, with broader apices and narrower centre, (10–)14.5–17.5(–30) × (2–)3(–4) µm, 0–1-septate, with two apical hila. *Intercalary conidia* subcylindrical, fusoid, sometimes curved, 0–1-septate, (9.5–)12.5–14(–18) × (2.5–)3(–4) µm, in branched chains of up to eight conidia. *Terminal conidia* subcylindrical to obovoid, (4.5–)8–9.5(–14.5) × (2–)2.5–3(–3.5) µm.

Culture characteristics: On MEA, 10 mm diam, surface raised, strongly folded, smooth, pale smoke-grey with margins undulate, colony reverse iron-grey; on OA, 13 mm diam, surface convex, fluffy aerial mycelium, white to buff, with margins undulate, colony reverse buff; on PDA, 14 mm diam, surface raised, folded, with fluffy aerial mycelium white to buff, with margins undulate, colony reverse buff with iron-grey patches.

Specimens examined: **South Korea**, Pyeongchang, on *Ostericum grosseserratum* (≡ *Angelica grosseserrata*, = *Ostericum koreanum*), 20 Sep. 2003, H.D. Shin (holotype KUS-F19687, isotype CBS H-22545, culture ex-type CBS 141116 = CPC 10750); *idem*. CPC 10751, CPC 10752.

Substrate and distribution: On *Ostericum* (*Apiaceae*); Asia (South Korea).

Notes: *Ramularia osterici* is morphologically similar to *R. archangelicae*, but with shorter and broader ramoconidia, intercalary and terminal conidia (Fig. 58), and it does not produce any

pigment in culture. Strains CBS 108991 (*R. archangelicae*) and CPC 10751 (*R. osterici*) are identical based on their ITS sequences but differ in several nucleotides in the other six genes amplified: 1 (LSU), 24 (*actA*), 32 (*gapdh*), 45 (*tef1*-α), 25 (*his3*), 26 (*cmdA*). The *R. osterici* clade is highly supported (Fig. 2, clade 20, 1/100/100). This is the first *Ramularia* species described on *Ostericum* (*Apiaceae*).

Ramularia parietariae Pass., in Rabenh., Fungi Eur. Exs., Ed. nov., Ser. sec., Cent. 2 (resp. Cent. 21), no. 2066: 1876.
≡ *Cylindrospora parietariae* (Pass.) J. Schröt., in Cohn, Krypt.-Fl. Schlesien 3.2(4): 493: 1897.
= *Ramularia parietariae* var. *minor* Bub ak, Bull. Herb. Boiss., 2 S er., 6: 486. 1906.

Description in vivo: See Braun (1998: 274).

Specimens examined: **Czech Republic**, Moravia, Pavlov, forest around the ruin, on leaf spot on *Parietaria officinalis*, 18 Sep. 2008, G. Verkley, cultures CBS 123730, CBS 123731. **Italy**, Parma, Gajone, on *Parietaria officinalis*, Oct. 1874, Passerini [Rabenh., Fungi Eur. Exs. 2066; lectotype, designated in Braun (1998), in HAL].

Substrate and distribution: On *Parietaria* (*Urticaceae*); Central Asia, Caucasus, Europe, Israel, N. Africa, N. America.

Notes: *Ramularia parietariae* was originally described on *Parietaria officinalis* from Italy (lectotype in HAL), but it is also pathogenic to other species of the genus *Parietaria*. Phylogenetic analyses showed that these strains cluster together in a highly supported clade (Fig. 2, clade 47, 1/100/100).

Ramularia phacae-frigidae (E. Müll. & Wehm.) Videira & Crous, Fungal Biol. 119: 836. 2015.
Basionym: *Mycosphaerella phacae-frigidae* E. Müll. & Wehm., Sydowia 8: 190. 1954.

Specimen examined: **Switzerland**, Corveglia, above St. Moritz, on dead leaves of *Phaca frigida*, 20 Jul. 1953, E. Müller (holotype in ZT, ex-type culture CBS 234.55).

Substrate and distribution: On *Phaca frigida* (*Fabaceae*), Europe (Switzerland).

Notes: *Ramularia phacae-frigidae* was originally described as *Mycosphaerella phacae-frigidae*, a pathogen infecting *Phaca frigida* from Helvetia (holotype in ZT). Although Müller & Wehmeyer (1954) mentioned the presence of *Ramularia* and *Asteromella* morphs in his description of *Mycosphaerella phacae-frigidae*, he refrained from naming them. The allocation to *Ramularia* was based on the phylogenetic position of the ex-type culture (Videira *et al.* 2015b), which in this study is located in clade 63 (Fig. 2).

Ramularia plurivora Videira & Crous, Persoonia 34: 60. 2015.

Description: Videira *et al.* (2015a).

Specimens examined: **Netherlands**, Den Haag, Laboratory of Medical Microbiology, Hospital Leyenburg, from human bone marrow, 2005 (holotype CBS H-21619, culture ex-type CBS

118743 = CPC 12207); Hilversum, Central Biological and Serological Laboratory, on human skin from neck, 20 May 2005, culture CBS 118693 = CPC 12206; on melon in storage, 1 Jan. 2008, J.H. Houbraken, culture CPC 16123, CPC 16124. **South Korea**, on *Coleosporium plectranthi* on *Plectranthus excisus*, 2004, H.D. Shin, CPC 11517.

Substrate and distribution: On human samples, on *Cucumis* sp., on *Coleosporium plectranthi on Plectranthus excisus*; in Europe (Netherlands) and East Asia (South Korea).

Notes: See Videira *et al.* (2015a). Phylogenetic analyses provided high support for this species clade (Fig. 2, clade 35, 1/100/100).

Ramularia pratensis Sacc. var. ***pratensis***, Fungi ital. Del., Tab. 998. 1881, and Michelia 2: 550. 1882 emend. U. Braun, 1998. Fig. 59.
= *Ramularia rhei* Allesch., Hedwigia 35: 34. 1896.
= *Ovularia rumicis* A. G. Eliasson, Bih. Kungl. Svenska Vetenskapsakad. Handl. 22, Afd. 3, 12: 18. 1897.
= *Ramularia rumicis-crispi* Sawada, Rep. Dept. Agric. Gov. Res. Inst. Formosa 85: 89. 1943.
= *Ramularia oxyriae-digynae* Gjaerum, Norweg. J. Bot. 18: 110. 1971.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* reduced to *conidiogenous cells*, hyaline, thin-walled, smooth, integrated in mycelium or terminal in conidiophores, cylindrical-oblong and narrower at the top, (5.5–)12–15(–27) × (1.5–)2(–3) µm, with 1–2 apical conidiogenous loci almost flat to short cylindrical; *conidiogenous loci* thickened, darkened, refractive, 1 µm diam. *Ramoconidia* hyaline, thin-walled, smooth, subcylindrical to

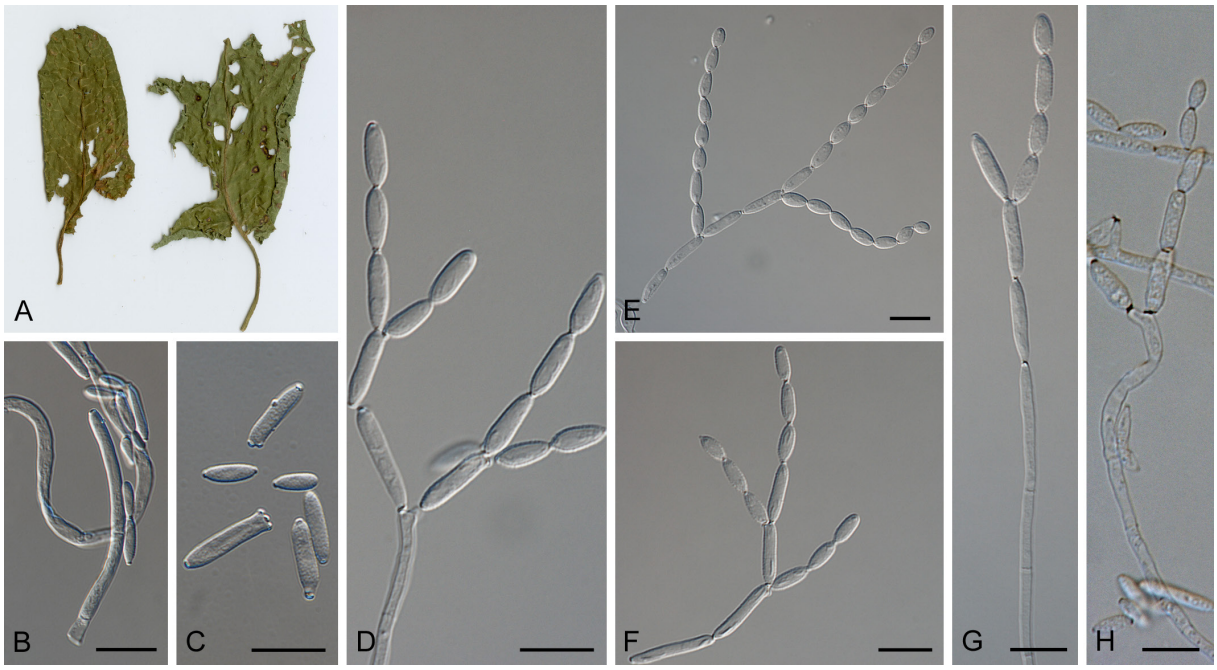


Fig. 59. *Ramularia pratensis* var. *pratensis* (CBS 122105). A–C. Observations from herbarium material. D–H. Structures formed in culture. A. Leaf spot symptoms on the host. B. Conidiogenous cells and conidia. D, G, H. Conidiophores, conidiogenous cells and conidia. C, E, F. Conidia. Scale bars = 10 µm.

obclavate, (5–)8.5–11(–19) × (2–)2.5–3(–4) µm, aseptate to 1–3-septate, with 2–3 apical hila. *Intercalary conidia* hyaline, smooth, aseptate or 1–3-septate, subcylindrical with apices rounded and broader, (5–)7–8(–11.5) × 2–2.5(–3) µm, in branched chains of up to seven conidia. *Terminal conidia*, hyaline, smooth, aseptate, obovoid, (3–)4.5–5(–6) × 2–2.5(–3) µm, *hila* thickened, darkened, refractive, 1 µm diam.

Culture characteristics: On MEA, 18 mm diam, surface low convex, folded, fluffy aerial mycelium, pale olivaceous grey and dirty white, with margins undulate, convex, feathery, colony reverse iron-grey and buff margin; on OA, 30 mm diam, surface flat, smooth aerial mycelium, dirty white, transparent exudate small droplets, margins with entire edge with no aerial mycelium, colony reverse violet slate; on PDA, 30 mm diam, surface flat, fluffy aerial mycelium, pale olivaceous grey and olivaceous grey, with margins crenate, with sparse aerial mycelium, colony reverse slate blue with buff margin.

Description in vivo: See Braun (1998: 123).

Specimens examined: **Canada**, Stittsville, Ontario, on *Verbascum* sp., 12 Jul. 2009, K.A. Seifert, culture CPC 16868. **Italy**, Padova, on *Rumex acetosa*, herb. Saccardo (holotype PAD); **Taiwan**, Hualian County, Hehuanshan, on living leaves of *Rumex* sp., 3 Apr. 2007, R. Kirschner & C.-J. Chen, culture CBS 122105. **Unknown country**, unknown collection details, culture CPC 19448.

Substrate and distribution: On *Oxyria*, *Rheum*, and *Rumex* (*Polygonaceae*), and *Verbascum* (*Scrophulariaceae*); Asia, Caucasus, Europe, N. and S. America.

Notes: Two varieties of *Ramularia pratensis* have been described, *R. pratensis* var. *pratensis* (on numerous *Rumex* species) with broader conidia, (6–)8–25(–35) × (1.5–)2–4(–5) µm), and *R. pratensis* var. *angustiformis* (*Rumex acetosella*, USA, holotype in NY) with very narrow conidia, 10–35 × 1.5–2 µm. It is the first time *R. pratensis* var. *pratensis* is reported from the host *Verbascum* (*Scrophulariaceae*). *Ramularia rhei*, currently a synonym of *R. pratensis* var. *pratensis*, has been reported as the causal agent of rhubarb leaf and petiole spot disease in the UK (Zhao *et al.* 2002). Rhubarb (*Rheum rhaponticum*) is a perennial crop that that is largely grown in northern Europe, the USA and Canada. Rhubarb petioles are mainly used in domestic food and in processed products such as jams, syrups and wine (Foust & Marshall 1991). Since the disease is not yet a problem of economic importance to rhubarb production in Europe, little research and investigation have been conducted on its biology and epidemiology, besides the work of Zhao *et al.* (2006) comparing the effect of temperature on conidial germination. This species clade is highly supported by the phylogenetic analyses (Fig. 2, clade 23, 1/100/100), and the strain CBS 122105 is considered a good representative of the species based on its morphological characters (Fig. 59).

Ramularia proteae Crous & Summerell, Austral. Pl. Pathol. 29: 277. 2000.

Specimen examined: **Australia**, Tasmania, on *Protea longifolia*, Aug. 1999, A. Macfadyen (holotype DAR 74883, culture ex-type CBS 112161 = CPC 3075).

Substrate and distribution: Thus far only known from the type location.

Notes: *Ramularia proteae* was the first *Ramularia* species reported from a *Protea* host. It was observed causing a leaf spot disease on *P. longifolia* in Tasmania (Crous *et al.* 2000). *Ramularia proteae* is morphologically similar to *R. stellenboschensis*, described from South Africa but with smaller and fusoid conidia. This species clusters very close to *R. stellenbochensis* in the phylogenetic analyses (Fig. 1, clade XIV) and was not included in the multigene phylogeny because it was not possible to amplify the *tef1*-α partial gene.

Ramularia pusilla Unger, Exanth. Pfl.: 169. 1833. Fig. 60.
≡ *Caeoma pusilla* (Unger) Bonord., Handb. Mykol.: 41. 1851.
≡ *Ovularia pusilla* (Unger) Sacc., Syll. Fung. 4: 140. 1886.
= *Ramularia pulchella* Ces., Bot. Zeitung (Berlin) 11: 238. 1853.
For additional synonyms see Braun (1998) or MycoBank.

Mycelium consisting of hyaline, septate, branched, smooth, 0.5–1 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–3-septate, cylindrical-oblong, straight and apically geniculate-sinuous, unbranched (7.5–)37–50(–96) × (1–)2(–3) µm. *Conidiogenous cells* terminal on conidiophores, cylindrical-oblong to geniculate-sinuous, narrower at the top, (6.0–)19–23(–37) × (1–)2(–3) µm, with multiple conidiogenous loci almost flat to protuberant and in a terminal or lateral position, thickened, darkened, refractive. *Conidia* formed singly, hyaline, thin-walled, smooth to verruculose, aseptate, ellipsoidal to obovoid, (5–)8–10(–15) × (3–)5–6(–8) µm, hila thickened, darkened, refractive. Sporulating on SNA.

Culture characteristics: On MEA, 12 mm diam, surface raised, with white fluffy mycelium with a rosy-buff tinge, margins lobate, feathery and convex, colony reverse buff; on OA, 15 mm diam, surface wavy, smooth, with white to buff aerial mycelium, margins entire, colony

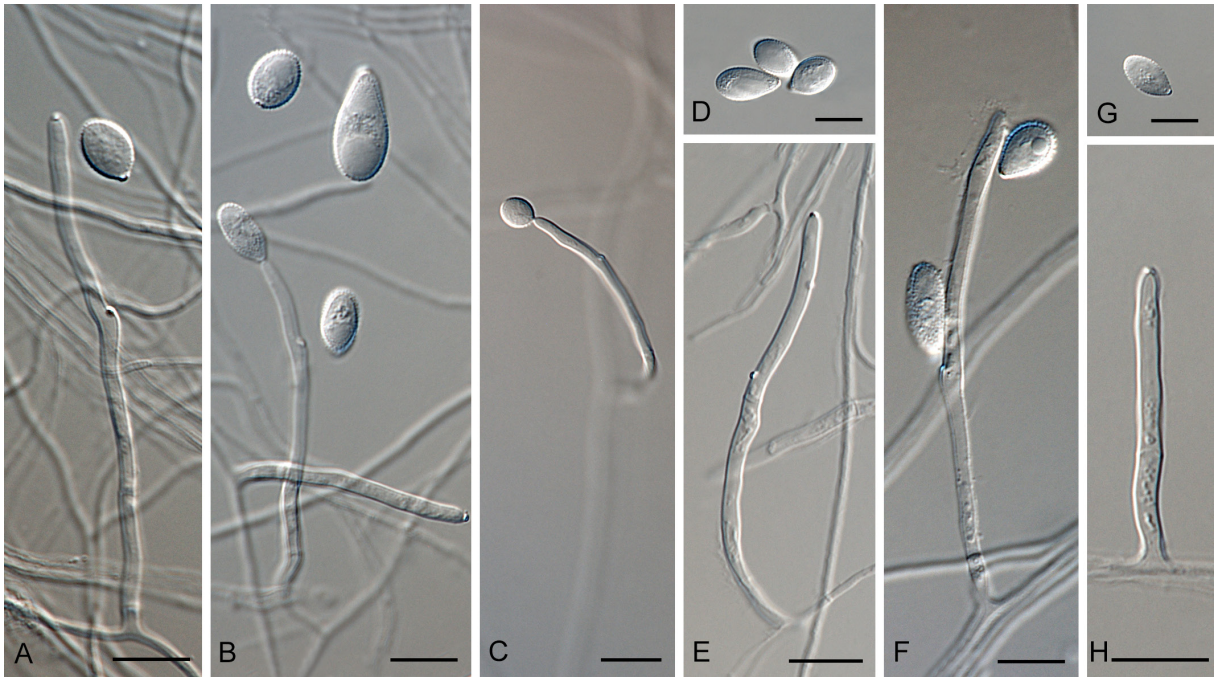


Fig. 60. *Ramularia pusilla* (CBS 124973). A–H. Structures formed in culture. A–C, F. Conidiophores and conidia. D, G. Conidia. E, H. Conidiophores. Scale bars = 10 µm.

reverse fawn; on PDA, 12 mm diam, surface flat, smooth, with fluffy white to buff mycelium, with margins entire, colony reverse buff.

Description in vivo: See Braun (1998: 205).

Specimens examined: **Austria**, on *Poa nemoralis*, Unger, Exanth. Pfl., Pl. II, fig. 12, lectotype (iconotype, see Braun 1998). **Germany**, Frankfurt am Main, Botanical Garden, on leaves of *Poa annua*, 25 Feb. 2008, R. Kirschner (epitype designated here CBS H-22527, MBT204832, culture ex-epitype CBS 124973).

Substrate and distribution: *Agropyrum*, *Agrostis*, *Alopecurus*, *Anthoxanthum*, *Arctagrostis*, *Arrhenatherum*, *Bromus*, *Calamagrostis*, *Cinna*, *Cynosurus*, *Dactylis*, *Deschampsia*, *Elymus*, *Eremopyrum*, *Festuca*, *Glyceria*, *Helictotrichon*, *Hierochlöe*, *Hordeum*, *Lolium*, *Melica*, *Muhlenbergia*, *Phalaris*, *Phleum*, *Poa*, *Puccinellia*, *Trisetum*, *Triticum*, *Vulpia*, and other undetermined grasses (*Poaceae*), almost circumglobal.

Notes: *Ramularia pusilla* is the type species of the genus *Ramularia* and has a broad host range within the family *Poaceae* and a worldwide distribution (Braun 1998). Two varieties of *Ramularia pusilla* are known, *R. pusilla* var. *pusilla* (on *Poa nemoralis*, Austria, iconotype) with conidiophores in small fascicles of 2–6, and *R. pusilla* var. *baldingerae* (on *Phalaris arundinacea*, Sweden, holotype in UPS), forming large tufts of conidiophores of 5–20. Strain CBS 124973 was examined by means of morphology and LSU sequence data in a previous study (Kirschner 2009), and was considered to be a good representative of the type species of the genus. In this study this strain forms a single lineage (Fig. 1, clade XIV; Fig. 2, clade 39) and is closely related to *R. collo-cygni*. The existing type material of this species consists of the original illustration (iconotype) since the original type material was not preserved and appropriate material for a neotypification could not be traced (Braun 1998). We hereby designate the strain CBS 124973 as ex-epitype culture of *R. pusilla* (Fig. 60).

Ramularia rhabdospora (Berk. & Broome) Nannf., Fungi Exs. Suec. Fasc. 39–40, Sched.: 32. 1950.
Basionym: *Cylindrosporium rhabdosporum* Berk. & Broome, Ann. Mag. Nat. Hist. 15: 34. 1875.
= *Ramularia plantaginis* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 32: 43. 1879 (1880).
≡ *Ramularia peckii* Sacc. & P. Syd., Syll. Fung. 14: 1065. 1899, nom. illeg. (superfl.).
For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 197).

Specimens examined: **Germany**, on unknown host, unknown date, S. Petzoldt, culture CBS 312.92. **New Zealand**, Auckland, Grey Lynn, on *Plantago lanceolata*, unknown collector and date, isol. C.F. Hill, Jul. 2005, dep. C.F. Hill, culture CBS 118415. **UK**, Glamis, on *Plantago lanceolata*, Berkeley (holotype K).

Substrate and distribution: On *Plantago* (*Plantaginaceae*); Asia, Caucasus, Europe, N. and S. America, New Zealand.

Notes: *Ramularia rhabdospora* was originally described on *Plantago lanceolata* from England (holotype in K) but has since been reported from several other countries (Braun 1998). Two species have been described from the host *Plantago*, *R. rhabdospora* and *R. kriegeriana*. Traditionally, these species are distinguished by the ornamentation of the conidia that is echinulate in *R. rhabdospora* and verruculose in *R. kriegeriana*, which is correlated with the phylogenetic affinity of the host species. *Plantago lanceolata*, the principal host of *R. rhabdospora* belongs in *Plantago* subgen. *Psyllium*, and *P. major*, the principal host of *R. kriegeriana*, is a species of *Plantago* subgen. *Plantago* (Rønsted *et al.* 2002). Phylogenetically, these two strains cluster apart, with *R. rhabdospora* in clade 57 and *R. kriegeriana* in clade 65 (Fig. 2) and are morphologically easily distinguishable.

Ramularia rubella (Bonord.) Nannf., in Lundell & Nannf., Fungi Exs.. Suec., Fasc. 39–40: 33. 1950. Fig. 61.
Basionym: *Crocysporium rubellum* Bonord., Bot. Zeitung (Berlin) 19: 201. 1861.
≡ *Ovullaria rubella* (Bonord.) Sacc., Syll. Fung. 4: 145. 1886.
= *Oidium monosporium* Westend., Bull. Soc. Roy. Bot. Belgique 2: 252. 1863.
= *Ramularia obovata* Fuckel, Hedwigia. 5: 50. 1866.
= *Ramularia circumfusa* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 47: 437. 1895.
For additional synonyms see Braun (1998).

Mycelium consisting of hyaline, septate, branched, smooth to verruculose, 1.5–3 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth to verruculose, erect, multiseptate, cylindrical-oblong, straight, unbranched (31–)73–115(–282) × (2–)2.5–3(–5) µm. *Conidiogenous cells* terminal on conidiophores, cylindrical-oblong, 16–40 × 2–3 µm, with one conidiogenous locus, almost flat and in a terminal or lateral position thickened, darkened, refractive. *Conidia* formed singly, hyaline, thin-walled, smooth to verruculose, mostly aseptate and rarely 1-septate, ellipsoid to obovoid, (15–)26–35(–54) × (5–)6–7(–9) µm; *hila* thickened, darkened, refractive.

Culture characteristics: On MEA, 7 mm diam, surface raised, irregular, with flat mycelium, white, with undulate margins and colony reverse olivaceous; on OA, 8 mm diam, surface raised in the centre and flattening towards the edge, smooth rosy-buff mycelium, radially striated, producing tiny droplets of exudate in the centre, with undulate edge and colony reverse ochraceous; on PDA, 9 mm diam, surface raised, irregular, smooth mycelium, white to rosy-buff, producing tiny droplets of exudate, with crenate margins, colony reverse iron-grey.

Description in vivo: See Braun (1998: 210).

Specimens examined: **Germany**, Guestphalia, On *Rumex aquaticus*, Bonorden, holotype not preserved]. **Luxembourg**, Kantenbach, on leaf spot on *Rumex obtusifolius*, unknown collector and date, isol. L. Marvanová, 25 Sep. 1967, dep. L. Marvanová, Oct. 1967, culture CBS 433.67. **Mexico**, Montecillo, on *Rumex* sp., 22 Sep. 2008, M. de Jesús Yáñez-Morales, cultures CPC 15748–15750; Montecillo, on *Rumex* sp., 1 Oct. 2008, M. de Jesús Yáñez-Morales, culture CPC 15821. **Netherlands**, Utrecht, on *Rumex* sp., May 2013, U. Damm, (neotype designated here, herbarium CBS H-22528, MBT204835, culture ex-neotype CBS 141117 = CPC 25911); Gelderland Prov., Wageningen, on *Prunus* sp., 23 May 2011, W. Quaedvlieg, cultures CPC 19471, CPC 19472. **New Zealand**, Auckland, Mt. Albert, on *Rumex obtusifolius*, unknown collector and date, isol. C.F. Hill, Jul. 2005, dep. C.F. Hill, culture CBS 120161. **Sweden**,

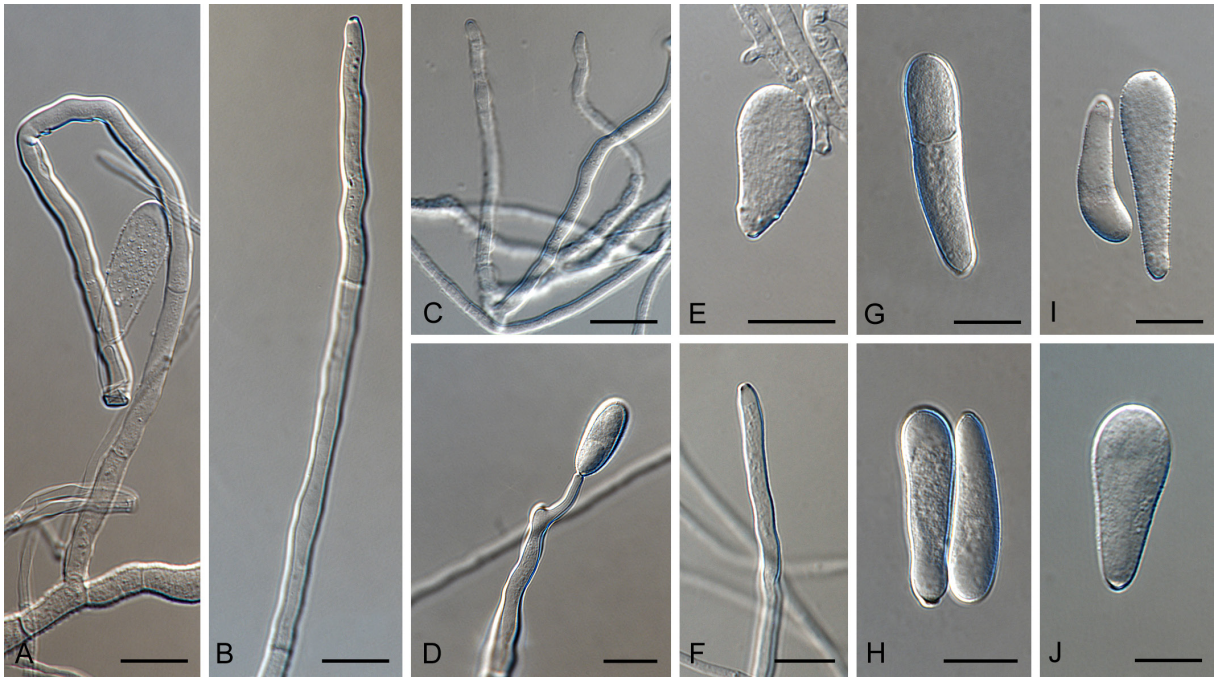


Fig. 61. *Ramularia rubella* (CBS 120161). A–J. Structures formed in culture. A, D. Conidiophore and conidia. B, C, F. Conidiophores. E, G–J. Conidia. Scale bars = 10 µm.

Uppland, Haga, Årtopet, on *Rumex longifolius*, 16 Sep. 1988, E. Gunnerbeck, culture CBS 114440.

Substrate and distribution: On *Polygonum s. lat.* and *Rumex* (*Polygonaceae*); almost circumglobal.

Notes: *Ramularia rubella* was originally described on *Rumex aquaticus* from Germany, but it has a wide geographical distribution in association with the host *Rumex*, while it is very rarely observed infecting *Polygonum s. lat.* (Braun 1998). As a necrotroph, *Ramularia rubella* shows promise as a biological control agent against *Rumex obtusifolius* by causing severe defoliation, shoot and root weight loss (Huber-Meinicke *et al.* 1989). The available strains form a highly supported clade based on the employed phylogenetic methods (Fig. 2, clade 79, 1/100/100). The morphological description of the isolates (Fig. 61) in this clade is in agreement with the one presented in literature (Braun 1998), except the conidiophores were reduced to conidiogenous cells in culture. Because of the long, solitary conidia and sometimes broad conidiogenous loci and hila, some of the strains were initially confused with *Cercosporella*.

Ramularia rufibasis (Berk. & Broome) Gunnerb. & Constant., Thunbergia 15: 77. 1991.
Basionym: *Peronospora rufibasis* Berk. & Broome, Ann. Mag. Nat. Hist. 15: 34. 1875.
≡ *Ovularia rufibasis* (Berk. & Broome) Massee, Brit. fung.-fl. 3: 322. 1893.
≡ *Phacellium rufibasis* (Berk. & Broome) U. Braun, Nova Hedwigia 54: 471. 1992.
= *Ramularia destructiva* W. Phillips & Plowr., Grevillea 6(37): 22. 1877.
= *Ovularia monilioides* Ellis & G. Martin, Amer. Naturalist 19: 76. 1885.

Description in vivo: See Braun (1998: 328).

Specimens examined: **Sweden**, Uppland, Järlåsa, on leaves of *Myrica gale*, 17 Sep. 1990, E. Gunnerbeck, culture CBS 114567. **UK**, Glamis, on *Myrica gale*, herb. Berkeley (holotype of *Peronospora rufibasis* in K); King's Lynn, on *Myrica gale*, May 1876, Plowright [Rabenh., Fungi. Eur. Exs. 2267; lectotype of *Ramularia destructiva*, designated in Braun (1998), in HAL]. **USA**, Massachusetts, Magnolia, *Myrica gale*, Jun. 1884, C.H. Clarke [lectotype of *Ovularia monilioides*, designated in Braun (1998), in NY 938246].

Substrate and distribution: On *Comptonia* and *Myrica* (*Myricaceae*); Asia, Canary Islands, Europe, N. America)

Notes: *Ramularia destructiva*, described on *Myrica gale* from England (holotype in K), was reassigned to the genus *Phacellium* as *Phacellium rufibasis* (Braun 1992) due to the production of synnematous conidiophores. The genus *Phacellium* is now considered a synonym of *Ramularia* as the production of synnemata was deemed as an unreliable character to separate these two genera. The strain used in this study clusters within the genus *Ramularia* (Fig. 1, clade XIV), and formed a single lineage (Fig. 2, clade 82) basal to *R. nyssicola* (clade 81), but positioned on a very long branch, which supports this species as unique. Unfortunately, the strain was sterile in culture and morphological data could not be evaluated. This lineage is for now maintained as a representative of *R. rufibasis*, until fresh material is collected and more information becomes available. This species causes the Ramularia dieback disease of *Myrica faya* in its natural habitat, affecting young shoots and causing leaf spots (Gardner & Hodges 1990). *Myrica faya* is considered an invasive plant in Hawaii and this pathogen represents a potentially good biocontrol agent, but no studies for field applications have been conducted thus far.

Ramularia rumicicola Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816852. Fig. 62.

Etymology: Named after the host genus from which it was collected, *Rumex*.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, straight, cylindrical-oblong, unbranched, (11.5–)33.5–50(–74) × (1.5–)2(–3) µm or reduced to conidiogenous cells. *Conidiogenous cells* integrated in mycelium or terminal in conidiophores, cylindrical-oblong to geniculate-sinuous, (8–)10.5–13(–18) × (1.5–)2(–3) µm, with 1–2 apical conidiogenous loci, thickened, darkened, refractive. *Conidia* hyaline, thin-walled, smooth, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical, (8.5–)13.5–16(–20) × 2–2.5(–3) µm, 0–1-septate, with 2–3 apical hila. *Intercalary conidia* subcylindrical to fusoid, 0–1-septate, (7.5–)11–13(–19) × 2–2.5(–3) µm, in branched chains of up to seven conidia. *Terminal conidia* subcylindrical to obovoid, aseptate, (5–)7.5–9(–13) × 2–2.5(–3) µm.

Culture characteristics: On MEA, 30 mm diam, surface concave, radially striated, smooth mycelium, white with greyish tinge, with margins undulate and feathery, colony reverse iron grey; on OA, 35 mm diam, surface flat and buff with a purplish grey centre except for a slice of white and grey olivaceous fluffy mycelium, margins entire, colony reverse buff with iron grey centre; on PDA, 40 mm diam, surface flat with short hairy mycelium, dark grey olivaceous, with margins entire, sparse in mycelium and feathery, colony reverse iron grey at the centre and grey olivaceous margin.

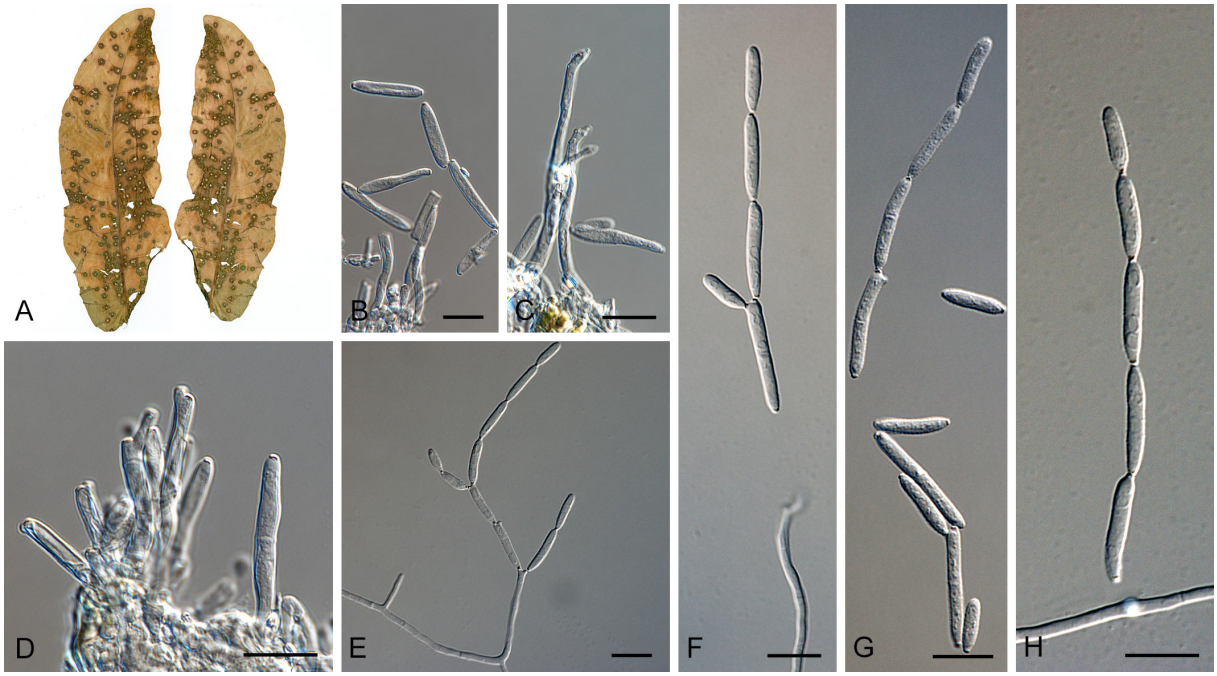


Fig. 62. *Ramularia rumicicola* (CBS 141118). A–D. Observations from herbarium material. E–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, C, E, F. Conidiophores and conidia. D. Conidiophores and conidiogenous cells. G. Conidia. H. Conidiogenous cell and conidia. Scale bars = 10 µm.

Specimen examined: **South Korea**, Jinju, on *Rumex crispus*, 14 May 2004, H.D. Shin (holotype KUS-F20194, isotype CBS H-22529, culture ex-type CBS 141118 = CPC 11294); *idem*. CPC 11295, CPC 11296.

Notes: *Ramularia rumicicola* formed a highly supported clade (Fig. 2, clade 24, 1/100/100). It differs from *R. pratensis* by having larger ramo-, intercalary and terminal conidia, and by culture characteristics (Fig. 62).

Ramularia rumicis Kalchbr. & Cooke, Grevillea 8: 23. 1880.
= *Ramularia decipiens* Ellis & Everh., J. Mycol. 1: 70. 1885.

Description in vivo: See Braun (1998: 216).

Specimens examined: **South Africa**, Cape, Somerset-East, on *Rumex obtusifolius*, MacOwan 1180 [lectotype, designated in Braun (1998), in B]. **Sweden**, Uppland, Dalby, Jerusalem, on *Rumex aquaticus*, 7 Sep. 1988, E. Gunnerbeck, culture CBS 114300.

Substrate and distribution: On *Rumex* (*Polygonaceae*); Asia, Caucasus, Europe, Africa, N. America.

Notes: *Ramularia rumicis* was originally described on *Rumex obtusifolius* from South Africa (lectotype in B) and has a very wide geographical distribution (Braun 1998). This species forms a single lineage (Fig. 2, clade 26). In literature (Braun 1998), a total of seven *Ramularia*

species, including four varieties, have been described from *Rumex*. *Ramularia rubella* (Fig. 2, clade 79) and *R. pratensis* var. *pratensis* (Fig. 2, clade 23) have a circumglobal distribution. *Ramularia bulgarica* (on *Rumex alpinus*, Bulgaria, holotype in BPI) is only known from Europe. *Ramularia occidentalis* var. *occidentalis* (on *Rumex britannica*, lectotype in NY), *Ramularia pseudodecipiens* (on *Rumex venosus*, holotype in NY) and *R. pratensis* var. *angustifolia* (on *Rumex acetosella*, holotype in NY) are only known from the USA. Braun (1998) stated that *R. bulgarica* is closely related to *R. pratensis* but no culture was available for this study.

***Ramularia* sp. D** Fig. 63

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, septate, cylindrical-oblong, straight, unbranched (44–)71–92(–129) × 2 µm, or reduced to conidiogenous cells. *Conidiogenous cells* integrated in the mycelium or terminal in the conidiophore, cylindrical-oblong, (24–)26.5–30(–35) × 2(–2.5) µm, with one *conidiogenous locus* almost flat, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, catenate, aseptate, with *hila* thickened, darkened and refractive. *Ramoconidia* cylindrical-oblong, sometimes curved, (16–)21–24(–34) × (1.5–)2(–3) µm, with two protruding apical hila. *Intercalary conidia* cylindrical-oblong, apical apex sometimes curved, (14–)20–22(–30) × (1.5–)2(–3) µm, in branched chains of up to five conidia. *Terminal conidia* cylindrical-obovoid, (7.5–)14–16(–22) × (1.4–)2–2.5 µm (on SNA, CBS 135.23).

Culture characteristics: On MEA, 10 mm diam, surface raised, fluffy aerial mycelium, white-buff, with margins lobate, colony reverse ochreous; on OA, 12 mm diam, surface flat, ochreous, with sparse white aerial mycelium, margins lobate, colony reverse cinnamon; on PDA, 11 mm diam, surface flat, fluffy white aerial mycelium, with margins lobate, colony reverse buff.

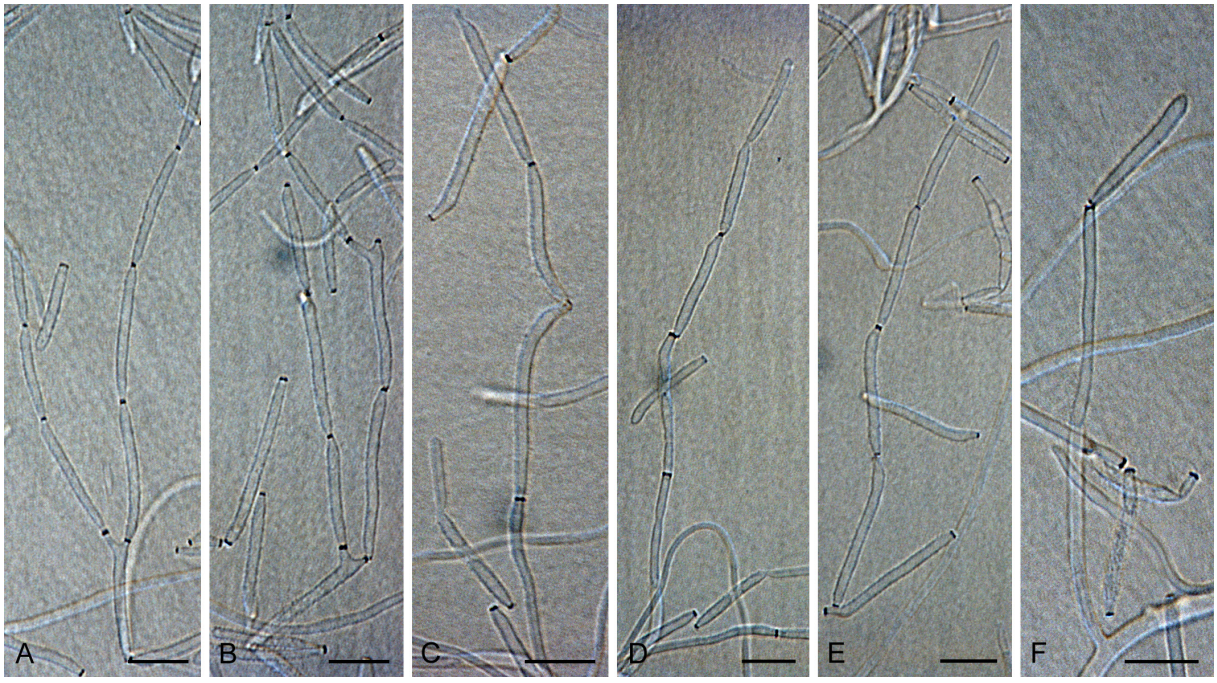


Fig. 63. *Ramularia* sp. D (CBS 135.23). A–F. Structures formed in culture. A, B, E. Conidia. C, D, F. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

Specimen examined: **Unknown country**, on *Viola odorata*, unknown collector and date, isol. and dep. L. Solberg, May 1923, culture CBS 135.23.

Notes: Although this isolate was originally identified as *R. lactea*, the morphological characteristics of this strain (Fig. 63) do not match with that of the original description of *R. lactea* (Braun 1998). *Ramularia lactea* has shorter conidiophores (5–50 × 1.5–4 µm), and smooth to verruculose conidia (5–)8–18(–25) × (1.5–)2–5(–6) µm. Three other *Ramularia* species have been described from *Viola*, namely *R. coleosporii* (Fig. 2, clade 66), *R. agrestis* and *R. biflorae*. *Ramularia agrestis* var. *agrestis*, *R. agrestis* var. *deflectans* and *R. biflorae* all produce septate conidia that are longer and wider than *Ramularia* sp. D. *Ramularia* sp. D (Fig. 2, clade 44) formed a single lineage closely related to *R. abscondita*. Although we suspect this culture to represent a new species, more material of other taxa occurring on *Viola* is required to make a suitable comparison.

Ramularia sphaeroidea Sacc., Michelia 1: 130. 1878. emend. U. Braun (1998: 151).
≡ *Ovularia sphaeroidea* (Sacc.) Sacc., Fungi ital. Del., Tab. 979. 1881.
= *Ramularia viciae* A.B. Frank, Krankh. Pfl., 1. Aufl.: 600. 1880.
= *Peronospora exigua* W.G. Smith, Diseases of Field and Garden Crops: 13. 1884.
= *Ovularia lotophaga* Ellis & Everh., Proc. Acad. Nat. Sci. Phil. 47: 432. 1895.
= *Pseudovularia trifolii* Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 20: 418. 1910.
For additional synonyms see Braun (1998) or MycoBank.

Description in vivo: See Braun (1998: 151).

Specimens examined: **Germany**, Berlin, Spandau, on *Lotus uliginosus*, Jul. 1875, Magnus (holotype PAD). **USA**, California, on *Vicia villosa* subsp. *varia*, Apr. 2002, S.T. Koike, culture CBS 112891.

Substrate and distribution: On *Chesneya*, *Glycyrrhiza*, *Lotus*, *Trifolium*, and *Vicia* (*Fabaceae*); Central Asia, Caucasus, Europe, N. and S. America, Australia, New Zealand.

Notes: *Ramularia sphaeroidea* was originally described on *Lotus uliginosus* from Germany (holotype in PAD), but it is able to infect other hosts from *Fabaceae* worldwide. Vetches (*Vicia* spp.) are planted alone or in combination with other plants as cover crops in vegetable production areas in California. From 2001 to 2003, purple vetches (*V. benhalensis*) and lana woollypod vetches (*V. villosa* subsp. *varia*) in the Salinas Valley (Monterey county, California) developed a foliar disease. Based on morphological and molecular (ITS) data (CBS 112891, GenBank AY352584), the fungus was identified as *Ramularia sphaeroidea*. Pathogenicity was confirmed by spraying healthy plants with a conidial suspension in water (Koike *et al.* 2004). This strain formed a single lineage (Fig. 2, clade 12), but positioned on a long branch, which supports this species as unique. This clade is tentatively maintained as representative of the species until material from the type host and location are recollected and examined.

Ramularia stellariicola (M.J. Park *et al.*) Videira, H.D. Shin & Crous, **comb. nov.** MycoBank MB817160
Basionym: *Pseudocercosporella stellariicola* M.J. Park *et al.*, Mycotaxon 119: 270. 2012.

Specimen examined: **South Korea**, Namyangju, Korea University, on *Stellaria aquatica*, 3 May 2006, H.D. Shin & M.J. Park (holotype KUS-F21740, culture ex-type KACC 42363 = CBS 130592 = CPC 11297, CPC 11298).

Substrate and distribution: On *Stellaria aquatica* (*Caryophyllaceae*); Asia (South Korea).

Notes: At the time *Pseudocercosporella stellariicola* was described the ITS sequence placed it within the genus *Ramularia*, but morphologically it was better accommodated in *Pseudocercosporella*. However, this species is not congeneric with the type of *Pseudocercosporella*, *P. bakeri* (Fig. 1, clade XIX). Therefore, we propose a new combination in *Ramularia*. This species clusters in a highly supported clade (Fig. 2, clade 13, 1/ 100/100). No sexual morph of this species is known. Although it formed a sister clade to "*Mycosphaerella cerastiicola*", the latter species displays a cryptic septoria-like to pseudocercosporella-like asexual morph and differs in several nucleotides in the seven genes amplified: 2 (LSU), 9 (*rpb2*), 10 (ITS), 5 (*actA*), 9 (*gapdh*), 5 (*tef1*-α), 11 (*his3*). These taxa are maintained as separate species until further studies are conducted.

Ramularia stellenboschensis Crous, Persoonia 27: 37. 2011.

Specimen examined: **South Africa**, Western Cape Province, Stellenbosch, J.S. Marais Botanical Garden, on leaves of *Protea* sp., associated with leaf spots of *Vizella interrupta*, 6 May 2010, P.W. Crous (holotype CBS H-20678, cultures ex-type CBS 130600 = CPC 18294).

Substrate and distribution: On *Protea* sp. (*Proteaceae*); Africa (South Africa).

Notes: *Protea* species are very popular due to their brightly coloured and textured flowers and fungal pathogens that damage the blooms are highly undesirable. *Ramularia stellenboschensis* was the first species of *Ramularia* described from *Proteaceae* in South Africa. This species formed a single lineage (Fig. 2, clade 22), but positioned in a long branch, basal to *R. hydrangeae-macrophyllae* (clade 21). It is closely related to *R. proteae* (Fig. 1, clade XIV) but differs from it by forming larger sudcylindrical conidia and by several nucleotides among the seven genes amplified: 16 (*rpb2*), 4 (ITS), 9 (*actA*), 12 (*gapdh*), 14 (*tub2)*, 2 (*his3*), 20 (*cmdA*).

Ramularia tovarae (Sawada) U. Braun, Internat. J. Mycol. Lichenol. 3: 283. 1988.
Basionym: *Ovularia tovarae* Sawada, Bull. Gov. Forest. Exp. Stat. Tokyo 105: 83. 1958.

Description in vivo: See Braun (1998: 212).

Specimens examined: **Japan**, on *Polygonum filiforme* [*Antenoron filiforme*, *Tovara filiforme*] (*Polygonaceae*), syntypes, 26 May 1948, 16 Jun 1948 and 7 Nov. 1947, Sawada (not seen!). **South Korea**, Hongcheon, on *Antenoron filiforme* (≡ *Polygonum filiforme*), 16 May 2003, H.D. Shin, KUS-F19471 (epitype designated here, MBT204827, HAL 1849 F, culture ex-epitype CBS 113305).

Substrate and distribution: Thus far only known from East Asia (Japan and South Korea), on *Polygonum filiforme* (*Polygonaceae*).

Notes: *Ramularia tovarae* was originally described on *Polygonum filiforme* from Japan and its distribution was limited to the type location. The only strain available representative of this species formed a single lineage (Fig. 2, clade 37), but positioned on a long branch that supports this species as unique. Although the strain did not sporulate in culture, the morphology observed in vivo corresponded to that described in literature (Braun 1998). Therefore, this specimen is considered as a good representative of the species and, despite being originary from South Korea, it is hereby designated as epitype.

Ramularia tricherae Lindr., Acta Soc. Fauna Fl. Fenn. 23: 38. 1902.
= *Ramularia succisae* var. *knautiae* C. Massal., Nuovo Giorn. Bot. Ital. 21: 169. 1889.
≡ *Ramularia knautiae* (C. Massal.) Bubák, Österr. Bot. Z. 53: 50. 1903.
= *Ovularia tricherae* Vestergr., Bot. Not. 1899: 169. 1899.
= *Ramularia knautiae* var. *arvensis* C. Massal., Malpighia 20: 169. 1906.

Description in vivo: See Braun (1998: 144).

Specimens examined: **Austria**, Ötztal, Ötz near Habichen, on leaf spot on *Knautia dipsacifolia*, 24 Jul. 2000, G. Verkley, culture CBS 108989, CBS 108990. **Former Czechoslovakia**, on *Knautia drymeia*, unknown collector and date, isol. L. Marvanová, Nov. 1972, dep. L. Marvanová, Jan. 1973, culture CBS 236.73. **Netherlands**, Limburg Prov., Gerendal, on leaf spot on *Knautia arvensis*, 28 Jun. 2000, G. Verkley, cultures CBS 108973, CBS 108974, CBS 108994, CBS 108995.

Substrate and distribution: On *Knautia* (*Dipsacaceae*); Caucasus, Europe.

Notes: *Ramularia tricherae* was originally described on *Knautia arvensis* from Finland [syntypes not seen by Braun (1998)] and has been reported from many European countries. In literature, this species is associated with the sexual morph *Sphaerella sylvatica* Sacc. & Speg. (Saccardo 1878) [syn. *Mycosphaerella scabiosae* Tomilin (Tomilin 1971)] but this connection has not been experimentally proven (Laibach 1921, Braun 1998, Aptroot 2006, Videira *et al.* 2015b). Phylogenetic analyses provided high support for this species clade (Fig. 2, clade 59, 1/ 100/100).

Ramularia trigonotidis Videira, H.D. Shin & Crous, **sp. nov.** MycoBank MB816853. Fig. 64.

Etymology: Named after the host genus from which it was collected, *Trigonotis*.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, septate, straight, cylindrical-oblong, geniculate-sinuous, unbranched, (16–)36–48(–94) × (1.5–)2(–3) µm, or reduced to conidiogenous cells. *Conidiogenous cells* terminal in conidiophores or intermediate in the mycelium, cylindrical-oblong, (7–)13–16.5(–31) × (1.5–)2(–3) µm, with one conidiogenous locus, almost flat to protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth, aseptate, catenate, with hila thickened, darkened and refractive. *Ramoconidia* subcylindrical, (12–)15–17(–25) × (2–)2.5–3(–4) µm, 0–1-septate, with two flat to protruding apical hila. *Intercalary conidia* subcylindrical, sometimes curved, (11–)14.5–16(–18) × (2–)2.5–3(–3.5) µm, in branched chains of up to five conidia. *Terminal conidia* cylindrical-oblong to ovoid, (4.5–)10.5–12.5(–16) × (2–)2.5–3(–4) µm (on SNA).

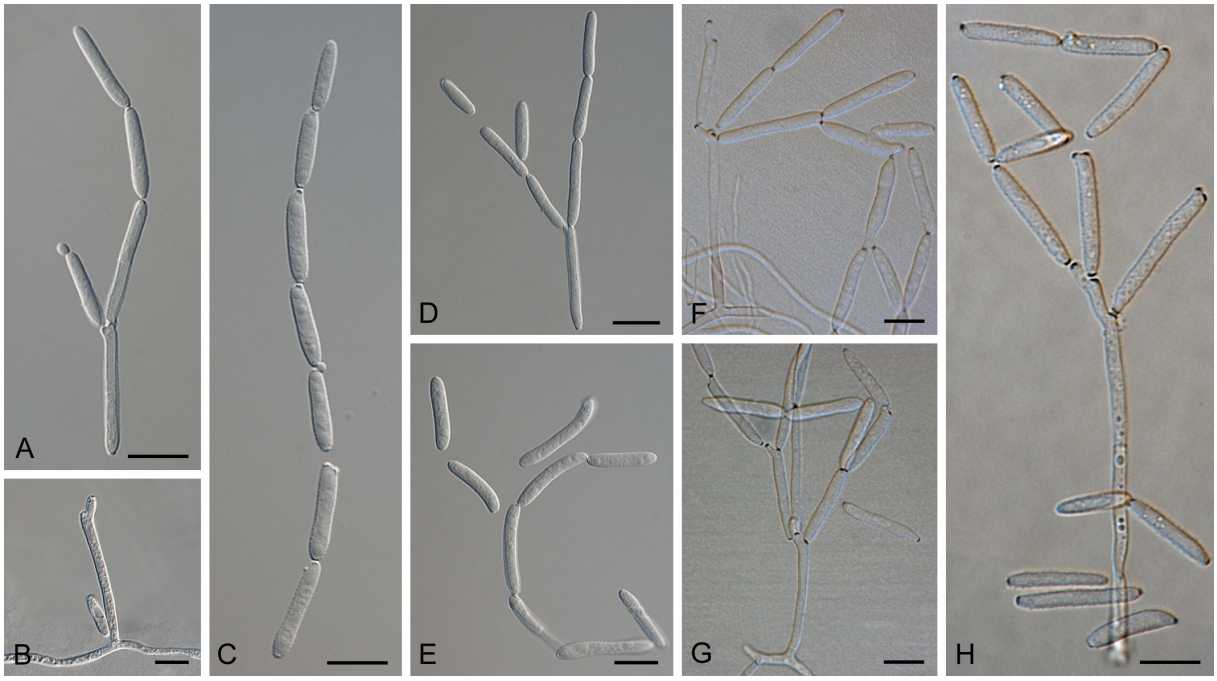


Fig. 64. *Ramularia trigonotidis* (CPC 14765). A–H. Structures formed in culture. A, C–E. Conidia. B. Conidiophore. F–H. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

Culture characteristics: On MEA, 13 mm diam, surface convex, smooth, smoke grey with a rosy tinge, with margins undulate, white, convex, feathery, colony reverse iron grey; on OA, 9 mm diam, surface convex, fluffy aerial mycelium, white in centre pale vinaceous towards the edges, margins olivaceous grey, feathery, colony reverse olivaceous grey; on PDA, 12 mm diam, surface
convex, pale vinaceous grey, smooth and uniform, with margins undulate, feathery, hazel, colony reverse brown vinaceous and buff at margin.

Specimens examined: **South Korea**, Hoengseong, on *Trigonotis radicans* subsp. *sericea* (= *T. nakaii*), 15 Oct. 2007, H.D. Shin (holotype KUS-F23007, isotype CBS H-22530, culture ex-type CBS 141119 = CPC 14764); *idem*. CPC 14765, CPC 14766.

Substrate and distribution: On *Trigonotis radicans* subsp. *sericea* (*Boraginaceae*); Asia (South Korea).

Notes: *Ramularia trigonotidis* (Fig. 64) is the first species of *Ramularia* described on *Trigonotis*, and the available strains form a highly supported clade (Fig. 2, clade 76, 1/100/100). In the phylogeny it is closely related to *R. actinidiae* (Fig. 2, clade 77), but the latter species produces conidiophores that are reduced to conidiogenous cells, and subcylindrical to fusoid conidia that are slightly narrower.

Ramularia trollii Iwanoff, Trudy Imp. S.-Peterburgsk. Obshch. Estestvoisp., Vyp. 3, Otd. Bot. 30(3): 12. 1900. Fig. 65.
= *Didymaria trollii* Jacz., Bull. Soc. Imp. Naturalistes Moscou, n.s., 3: 435. 1898.

Fig. 65. *Ramularia trollii* (CBS 109118). A–E. Observations from herbarium material. F–G. Structures formed in culture. A. Leaf spot symptoms on the host. B, C, E. Conidiophores and conidia. D, F, G. Conidia. Scale bars = 10 µm.

Description in vivo: See Braun (1998: 233).

Specimens examined: **Austria**, Tirol, Ober Inntal, Serfaus, Komperdell Alm near Kölnerhaus, on leaf spot on *Trollius europaeus*, 10 Aug. 2000, G. Verkley, cultures CBS 109118, CBS 109119. **Russia**, Prov. Vjatka, Distr. Kotelnitsh, on *Trollius europaeus*, 19 Jul 1921, Chochjakov, ex herb. Vjatskogo Obl. Mus. 78 [neotype, designated in Braun (1998), in LEP].

Substrate and distribution: On *Trollius* (*Ranunculaceae*); Europe, Asia.

Notes: The type material of *R. trollii* was not preserved and a neotype was proposed by Braun (1998) on the host *Trollius europaeus* from Russia (neotype in LEP). Thus far it has only been reported infecting *Trollius* hosts and is known from Asia and several European countries (Braun 1998). The representative isolates of this species clustered within the *Ramularia* clade (Fig. 1, clade XIV) and formed a highly supported clade based on the multigene phylogeny (Fig. 2, clade 17, 1/100/100). These strains were originally identified as *Pseudocercosporella trollii* but they produce catenate conidia with conspicuous hila that are consistent with the *R. trollii* description from literature (Braun 1998) (Fig. 65).

Ramularia unterseheri Videira & Crous, Fungal Biology 119: 836. 2015.

Specimens examined: **Germany**, Greifswald, Elisenhain, on leaf litter of *Fagus sylvatica*, 4 Jan. 2008, M. Unterseher (holotype CBS H-22285, culture ex-type CBS 124884); Greifswald, Elisenhain, on living leaves from the understorey of *Fagus sylvatica*, 8 Jan. 2008, M. Unterseher, cultures CBS 124826, CBS 124838; Munich, in room inside a castle, May 2011, unknown collector, dep. A.

Klein-Vehne, culture CBS 130721. **Netherlands**, Utrecht Prov., Baarn, on decaying leaves of *Acer pseudoplatanus*, 26 Apr. 2004, G. Verkley, culture CBS 117879 = CPC 11207.

Substrate and distribution: On *Fagus* (*Fagaceae*) and *Acer* (*Sapindaceae*); Europe (Germany, Netherlands).

Notes: See Videira *et al.* (2015b). The phylogenetic analyses places all the representatives of this species in one clade (Fig. 2, clade 86) closely related to *R. vizellae*.

Ramularia uredinicola Khodap. & U. Braun, Mycotaxon 91: 358. 2005.

Specimens examined: **Iran**, Guilan Prov., on *Melampsora* sp. on *Salix babylonica*, 3 Jul 2004, S.A. Khodaparast (holotype IRAN 12316 F, isotype CBS H-22531, culture ex-type CBS 141120 = CPC 11852). **Italy**, Roma, on leaf *Melampsora* sp. on *Populus* sp., unknown collector and date, isol. and dep. G. Magnani, Mar. 1968, culture CBS 179.68. South Korea, Hoengseong, on *Melampsora* sp. on *Salix* sp., 21 Aug. 2004, H.D. Shin, culture CPC 11481, CPC 11482; Hoengseong, on *Melampsora* sp. on *Salix gracilistyla*, 22 Jun. 2006, H.D. Shin & M.J. Park, culture CBS 131769 = KACC 42535; Hongcheon, on *Melampsora* sp. on *Populus alba* × *glandulosa*, 18 Oct. 2009, H.D. Shin & M.J. Park, culture CBS 131770 = KACC 44864; Hongcheon, on *Melampsora* sp. on *Salix pierotii* (= *S. koreensis*), 26 Oct. 2008, H.D. Shin & M.J. Park, culture CBS 131771 = KACC 44215; Suwon, on *Melampsora* sp. on *Salix matsudana* cv. *Tortuosa*, 30 Oct. 2008, H.D. Shin, M.J. Park, culture CBS 131772 = KACC 44218.

Substrate and distribution: Hyperparasite of *Melampsora* sp.; Asia (Iran, South Korea), Europe (Italy).

Notes: *Ramularia uredinicola* and *R. rosea* are closely related species (Khodaparast & Braun 2005) that form reddish or pink caespituli with age, probably due to the production of rubellins (Arnone *et al.* 1986, Miethbauer *et al.* 2003). However, they can be distinguished based on morphology and have different lifestyles. *Ramularia uredinicola* is mycophilic and has longer and branched conidiophores, while *R. rosea* causes leaf spots on leaves. *Ramularia uredinis* is also mycophilic but the caespitulli do not turn reddish with age and the conidiophores are shorter and unbranched. *Ramularia coleosporii* and *R. uredinearum* are also mycophilic, but the caespitulli are always hyaline (Braun 1998, Khodaparast & Braun 2005). The strains used in this study from South Korea clustered in a highly supported clade (Fig. 2, clade 68, 1/100/100).

Ramularia urticae Ces., in Rabenh., Herb. Viv. Mycol., Cent. XVII, no. 1680. 1852.
≡ *Cylindrospora urticae* (Ces.) J. Schröt., in Cohn, Krypt.-Fl. Schlesien 3.2(4): 492: 1897.
≡ *Septocylindrium urticae* (Ces.) Subram., Hyphomycetes: 310: 1971.
= *Sphaerella superflua* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 102. 1870 (1869–1870).
≡ *Mycosphaerella superflua* (Fuckel) Petr., Ann. Mycol. 38: 235. 1940.

Description in vivo: See Braun (1998: 273).

Specimens examined: **Germany**, Weimar, Belvedere, leaf spot on *Urtica dioica*,8 Oct. 1990, G. Arnold, culture CBS 162.91. **Italy**, Vercellis, on *Urtica dioica*, 1851, Cesati [Rabenh., Herb.

Viv. Mycol. 1680; lectotype, designated in Braun (1998), in HAL]. **South Korea**, Hoengseong, on *Aconitum pseudo-laeve* var. *erectum*, 15 Oct. 2007, H.D. Shin, culture CPC 14807. **Sweden**, Uppland, Haga par., Årtopet, on *Urtica dioica*, 29 Sep. 1987, E. Gunnerbeck, culture CBS 113974. **Unknown country**, on unknown host, unknown collector and date, dep. P. Redaelli, Mar. 1926, culture CBS 105.26.

Substrate and distribution: On *Urtica* (*Urticaceae*); Asia Caucasus, Europe, N. America.

Notes: *Ramularia urticae* was originally described on *Urtica dioica* from Italy (lectotype in HAL). It has a broad geographical distribution but it is thus far only known from the host *Urtica*. Since the morphological characters of the strains CBS 105.26 and CPC 14807 were not observed, and they clustered close to strains of *R. urticae* in a well-supported clade (Fig. 2, clade 53, 1/94/91), they are tentatively considered as the same species. However, we refrain to expand the host range and geographical distribution of the species until further evidence is available.

Ramularia valerianae (Speg.) Sacc. **var. *valerianae***, Fungi ital. Del., Tab. 1007. 1881.
Basionym: *Cylindrosporium valerianae* Speg., Michelia 1: 475. 1879.
= *Ramularia valerianae* var. *valerianae-montanae* Săvul. & Sandu, Hedwigia 73: 120. 1933.
= *Ramularia eamesii* Dearn & House, Bull. New York State Mus. Nat. Hist. 233–234: 39. 1920.
= *Ramularia basarabica* Săvul. & Sandu, Hedwigia 73: 120. 1933.

Description in vivo: See Braun (1998: 276).

Specimens examined: **Austria**, Tirol, Ötztal, Horlachtal near Umhausen, forest near Stuibenfalle, on leaf spot on *Valeriana* sp., 3 Aug. 2000, G. Verkley, cultures CBS 109123, CBS 109122. **Italy**, Conegliano, on *Valeriana officinalis*, herb. Saccardo (holotype PAD).

Substrate and distribution: On *Valeriana* (*Valerianaceae*), Asia, Caucasus, Europe, N. America.

Notes: Two varieties of *R. valerianae* have been described thus far, *R. valerianae* var. *centranthi* (type on *Centranthus ruber*, France) and *R. valerianae* var. *valerianae* (on *Valeriana officinalis*, Italy, holotypus in PAD). They differ in the type of lesions they form on plant hosts that are angular-irregular, sometimes vein delimited, pale greenish to reddish brown in *R. valerianae* var. *valerianae* and subcircular to irregular, pale brown with greyish white centre and purple brown margins in *R. valerianae* var. *centranthi*. *Ramularia valerianae* var. *valerianae* also produces longer and wider conidia [(8–)10–50(–55) × (–1.5)2–5.5(–7) µm] than *R. valerianae* var. *centranthi* [(6–)12–35 × 2–4 µm]. Strains of this species cluster in a highly supported clade (Fig. 2, clade 54, 1/100/100). Unfortunately these strains proved to be sterile in culture.

Ramularia vallisumbrosae Cavara, Rev. Mycol. (Toulouse) 21: 101. 1899.
= *Ramularia narcissi* Chittenden, Gard. Chron. 39: 277. 1906.
= *Ramularia ucrainica* Petr., Ann. Mycol. 19 (1–2): 78. 1921.

Description in vivo: See Braun (1998: 48).

Specimens examined: **Italy**, Vallombrosa, Orto botanico, on *Narcissus* sp., 1899, Cavara

[lectotype, designated in Braun (1998), PAD]. **UK**, Southwestern England, Cornwall, on *Narcissus* var. Victoria, unknown collector and date, isol. P.H. Gregory, dep. A. Beaumont, May 1938, culture CBS 271.38; Scilly Island, on *Narcissus* var. Golden Spur, unknown collector and date, isol. P.H. Gregory, Apr. 1938, dep. P.H. Gregory, Dec. 1938 (epitype designated here CBS H-22532, MBT204833, culture ex-epitype CBS 272.38).

Substrate and distribution: On *Leucojum*, *Narcissus*, and *Pancratium* (*Amaryllidaceae*); Europe, N. America.

Notes: *Ramularia vallisumbrosae* is the causal agent of white mould disease on leaves of daffodils (*Narcissus* cultivars) in commercial plantations in England and Scotland. The disease is not believed to be bulb-borne (Moore 1979), but poses a serious threat in these regions causing early defoliage die-down and associated reductions in bulb yield (O'Neill *et al.* 2002). This species formed a highly supported clade (Fig. 1, clade XIV; Fig. 2, clade 16, 1/100/100).

Ramularia variabilis Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 361. 1870. Fig. 66.
≡ *Ovularia variabile* (Fuckel) E. Bommer & M. Rousseau, Bull. Soc. Roy. Bot. Belgique 23(1): 274. 1884.
≡ *Cylindrosporium variabilis* (Fuckel) J. Schröt., Krypt.-Fl. Schlesien 3.2(4): 490. 1897.
≡ *Entylomella variabilis* (Fuckel) Cif., Ann. Mycol. 26 (1–2): 17. 1928.
= *Sphaerella mariae* Sacc. & E. Bommer, Bull. Soc. Roy. Bot. Belgique 25(1): 173. 1886
≡ *Mycosphaerella mariae* (Sacc. & E. Bommer) Lindau, Hilfsb. Sammeln Ascomyc.: 37. 1903.

Mycelium consisting of hyaline, septate, branched, smooth, 1–2 µm diam hyphae. *Conidiophores* hyaline, thin-walled, smooth, erect, 1–2-septate, cylindrical-oblong, straight to sinuous, unbranched,

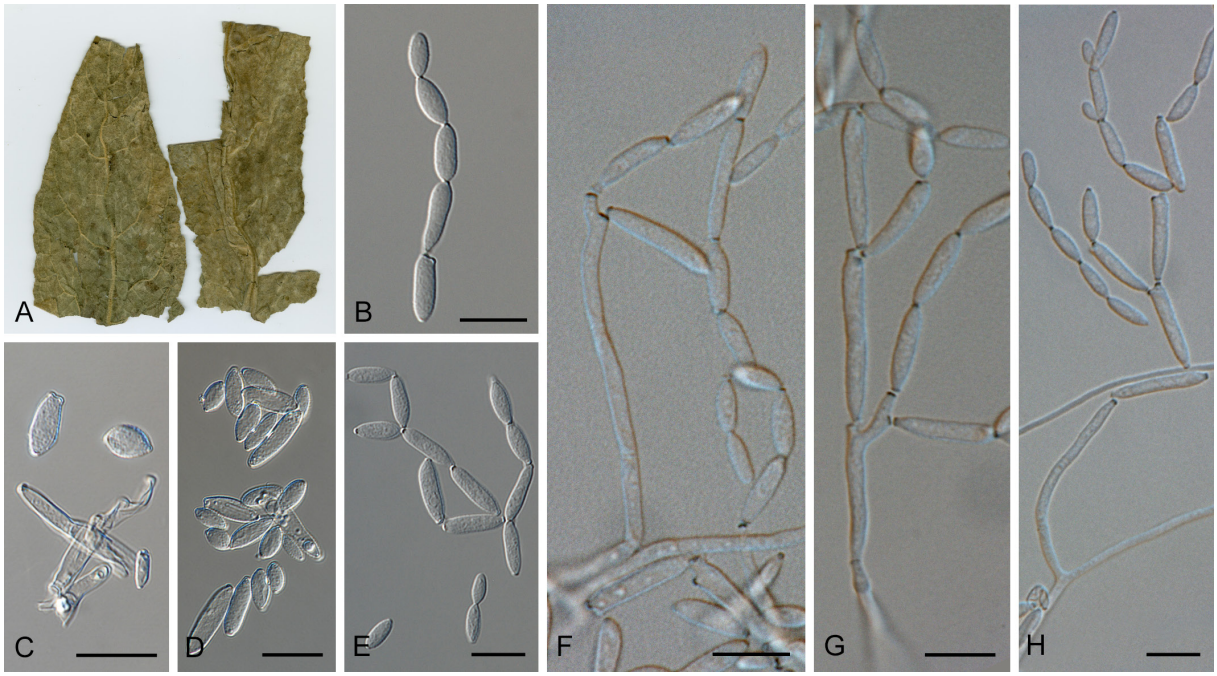


Fig. 66. *Ramularia variabilis* (CBS 141121). A, C, D. Observations from herbarium material. B, E–H. Structures formed in culture. A. Leaf spot symptoms on the host. B, D, E. Conidia. C, G. Conidiogenous cells and conidia. F, H. Conidiophores and conidia. Scale bars = 10 µm.

(10–)26.5–35(–54) × (1–)1.5–2(–3) µm, or reduced to conidiogenous cells. *Conidiogenous cells* terminal in conidiophores or intermediate in the mycelium, cylindrical-oblong, (5.5–)14.5–19(–29) × 1.5–2(–3) µm, with 1–3 conidiogenous loci almost flat to cylindrical-protuberant, thickened, darkened and refractive. *Conidia* hyaline, thin-walled, smooth to slightly verruculose, catenate, with hila thickened, darkened and refractive. *Ramoconidia* fusiform, (9.5–)14–17(–26.5) × (1.5–)2–2.5(–3) µm, 0–1-septate, with 2–3 apical hila. *Intercalary conidia* fusiform to oval, aseptate, (8–)11–13(–19.5) × (1.5–)2(–3) µm, in branched chains of up to five conidia. *Terminal conidia* obovoid, aseptate, (5–)7–8(–11) × (1.5–)2(–2.5) µm (on SNA).

Culture characteristics: On MEA, 11 mm diam, surface raised, folded, with sparse aerial mycelium, smooth, rosy-buff, with margins crenate and convex, colony reverse cinnamon with olivaceous grey patches; on OA, 9 mm diam, surface smooth, low convex, white with pale olivaceous grey tinge, with margins undulate, colony reverse fawn; on PDA, 10 mm diam, surface low convex, pale olivaceous grey, smooth, producing tiny transparent exudate droplets, with margins lobate, colony reverse olivaceous grey with a buff margin.

Description in vivo: See Braun (1998: 263).

Specimens examined: **Austria**, Graz, on *Verbascum* sp., Oct. 2012, C. Scheuer (epitype designated here CBS H-22533, MBT204834, culture ex-epitype CBS 141121 = CPC 25967). **Canada**, Stittsville, Ontario, on *Verbascum* sp., K.A. Seifert, 12 Jul. 2009, cultures CPC 16865, CPC 16866. **Germany**, on *Verbascum thapsus* [Fuckel, Fungi Rhen. Exs. 135; lectotype, designated in Braun (1998), in HAL].

Substrate and distribution: On *Digitalis*, *Verbascum* (*Scrophulariaceae*); Asia, Caucasus, Europe, N. America.

Notes: *Ramularia variabilis* has a broad geographical distribution and has been reported to infect plants from the genera *Digitalis* and *Verbascum*. In this study, the strains isolated from *Digitalis* and *Verbascum* were separated into distinct clades (Fig. 2), namely clades 50 and 58, respectively, clearly suggesting that two different species are involved (see *Ramularia digitalis-ambiguae*). Strain CPC 25967 was isolated from the same host and from a neighbouring country as the type, and is morphologically a good representative of this species (Fig. 66). All three phylogenetic methods applied to this dataset gave high support to this clade (Fig. 2, clade 50, 1/100/100). This species has been experimentally linked to the sexual morph *Mycosphaerella mariae* (Sacc. & Bommer) Lindau (Arx 1949; Videira *et al.* 2015b).

Ramularia veronicicola Videira & Crous, **nom. nov.** MycoBank MB817161.
Basionym: *Stysanus veronicae* Pass., Hedwigia 16(6): 123. 1877 (1876), non *Ramularia veronicae* Fuckel, 1870.
≡ *Isariopsis veronicae* (Pass.) Savile, Canad. J. Bot. 46: 465. 1968.
≡ *Phacellium veronicae* (Pass.) U. Braun, Nova Hedwigia 50: 511. 1990.

Description in vivo: See Braun (1998: 337).

Specimens examined: **Italy**, Parma, botanical garden, on *Veronica longifolia*, 1875/76, Passerini [Rabenh., Fungi Eur. Exs. 2268; lectotype, designated in Braun (1998), HAL]. **Sweden**,

Uppland, Danmark par., Bergsbrunna, on *Veronica spicata*, 25 Sep. 1987, E. Gunnerbeck, culture CBS 113981.

Substrate and distribution: On *Veronica* (*Scrophulariaceae*); Europe, N. America.

Notes: Previously named *Phacellium veronicae*, this species was originally isolated on *Veronica longifolia* from Italy (lectotype in HAL). Based on phylogenetic analyses in this study, strain CBS 113981 clustered within the *Ramularia* clade (Fig. 1, clade XIV) and formed a single lineage (Fig. 2, clade 64) in the multigene phylogeny. Since *Phacellium* is now considered a synonym of *Ramularia*, a new combination is proposed. Because the epithet "*veronicae*" is already occupied in *Ramularia* for a different species (Fig. 2, clade 64) the new epithet "*veroniciola*" is introduced. *Ramularia veroniciola* is the causative agent of leaf spot disease on *Veronica* species that are perennial plants used as ornamentals. The pathogen causes brown roundish spots and develops conidiophores aggregated in synnemata. This species has been observed in several European countries and also in North America (Canada) (Braun 1998). It has recently been reported from China infecting *V. sibirica* and, although the disease incidence was low, it may become significant with the increase of the cultivated area (Bai *et al.* 2013; ITS sequence GenBank HE995799). During recent field surveys in Hungary, the disease incidence affecting *V. spicata* and *V. spuria* varied between 90–100 %, and reached a severity between 30–60 % (Horvát *et al.* 2015; ITS sequences GenBank HQ690097 and JQ920427). The ITS sequence of the isolate CBS 113981 is identical to GenBank JQ920427, and differs from GenBank HQ690097 in 1 nucleotide and from GenBank HE995799 in 10 nucleotides. Unfortunately this strain did not sporulate in culture, and the corresponding herbarium specimen was not preserved.

Ramularia vizellae Crous, Persoonia 27: 37. 2011.

Specimens examined: **Netherlands**, Gelderland, Randwijk, on dead leaf litter from *Malus* sp., unknown collector and date, isol. G. Verkley, 26 Jun 2004, cultures CBS 115981, CBS 115982; Utrecht, Rhijnawen forest, on fruit scales of *Carpinus betulus*, 25 Apr. 2005, G. Verkley, culture CBS 117798; Utrecht Prov., Baarn, Park Groeneveld, on decaying leaves of *Quercus rubra*, collection date unknown, G. Verkley, culture CBS 117871; Utrecht Prov., Baarn, Park Kasteel Groeneveld, on *Amelanchier lamarckii*, 26 Apr. 2004, G. Verkley, culture CBS 117872. **South Africa**, Western Cape Prov., Hermanus Fernkloof Nature Reserve, on leaves of *Protea* sp., in association with *Vizella interupta*, 2 May 2010, P.W. Crous (holotype CBS H-20679, culture ex-type CBS 130601 = CPC 18283).

Substrate and distribution: On *Lotus*, *Phaseolus* (*Fabaceae*), *Acer*, *Aesculus* (*Sapindaceae*), *Protea* (*Proteaceae*), *Carpinus*, *Corylus* (*Betulaceae*), *Fagus*, *Quercus* (*Fagaceae*), *Amelanchier*, *Malus* (*Rosaceae*), *Brassica* (*Brassicaceae*), and *Tilia* spp. (*Malvaceae*); Europe (France, Germany, Netherlands, Switzerland, Germany), South Africa.

Notes: See Videira *et al.* (2015b). The phylogenetic analyses provide high support to this species clade (Fig. 2, clade 85, 1/ 100/99).

Ramularia weberiana Videira & Crous, **sp. nov.** MycoBank MB817162.

Etymology: Named after the depositor of the strain, A. Weber.

Culture sterile. *Ramularia weberiana* (Fig. 2, clade 25), differs from its closest phylogenetic neighbour, *R. rumicicola* (Fig. 2, clade 24), by unique allelles in five loci based on alignments of the separate loci deposited in TreeBASE as Study S19315: *rpb2* positions 15(C), 57(G), 63(C), 102(A), 117(G), 196(C), 228(C), 249(T), 267(A), 327(C), 330(G), 348(T), 357(T), 358(C), 378(T), 402(T), 414(T), 435(C), 445(T), 459(T), 493(A), 519(A), 531(T), 588(T), 591(C), 594(T), 606(T), 615(T), 627(G), 633(C), 636(C), 654(G), 657(G); ITS positions 33(G), 47(A), 167(T); *actA* positions 83(T), 96(C), 98(T), 121(A), 164(A), 166(A), 185(T), 186(C), 211(C), 212(C); *gapdh* positions 14(A), 29 deletion (C), 38(G), 39(T), 43(A), 45(C), 120(T), 131(A), 132(T), 158(T), 167(T), 185(C), 208(C), 257(A), 258(T), 259(A), 260(C), 262(A), 281(T), 286(G), 287(T), 289(T), 291(A), 293–295 insertion (CCA), 315(A), 347(T), 380(T), 431(C), 438(T), 440(T), 446(T), 479(C), 524(C), 572(C), 593(T); *tef1*-α positions 8(T), 15(T), 17(C), 18(T), 48(C), 56(T), 59(T), 145(C), 196(C), 233(G), 248(C), 284(C), 286(T), 289(T), 290(T), 294(A), 295(C), 296(T), 401(C), 409(A), 425(T), 430(A), 578(T).

Specimen examined: **Unknown country**, on unknown host, unknown collector and date, isol. and dep. by A. Weber, Aug. 1923 (holotype CBS H-22534, culture ex-type CBS 136.23).

Notes: The strain in this clade represents a new species that is clearly distinct from other species based on the phylogenetic analyses (Fig. 2, clade 25). Unfortunately this strain did not sporulate in culture and a comparison with the descriptions available in literature was not possible.

Ramularia weigelae Speg. (as *weigeliae*), Michelia 1(5): 475. 1879. Fig. 67.
≡ *Phaeoramularia weigelicola* H.D. Shin & U. Braun, Mycotaxon 58: 163. 1996.
≡ *Passalora weigelicola* (H.D. Shin & U. Braun) U. Braun & Crous, Mycosphaerella and its anamorphs: 1. Names published in Cercospora and Passalora: 475. 2003.

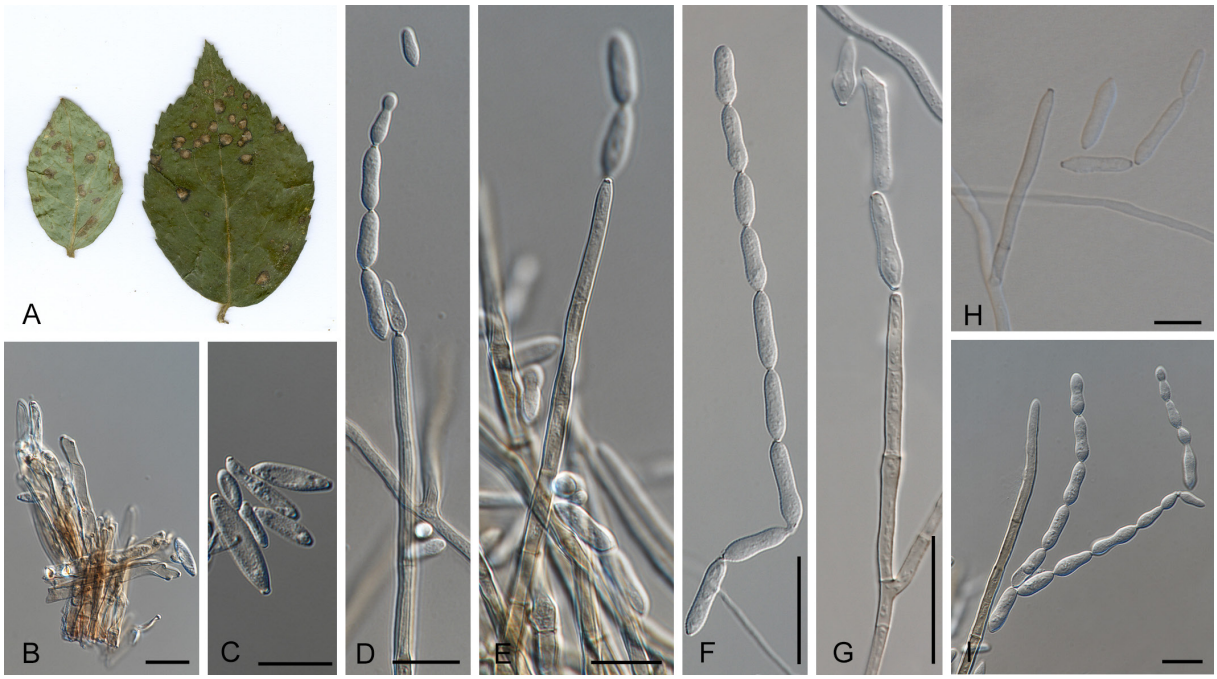


Fig. 67. *Ramularia weigelae* (CBS 113309). A–C. Observations from herbarium material. D–I. Structures formed in culture. A. Leaf spot symptoms on the host. B, D, E, G–I. Conidiophores and conidia. C, F. Conidia. Scale bars = 10 µm.

Description in vivo: See Braun (1998: 389).

Specimen examined: **South Korea**, on *Weigela subsessilis*, 4 Jun. 2003, H.D. Shin, KUS-F19549, culture CBS 113309.

Substrate and distribution: On *Weigela* (*Diervillaceae*); Asia, Europe.

Notes: *Ramularia weigelae* was originally described on *Weigela florida* from Italy (holotype). Braun (1998) stated that the type material of *R. weigelae* is probably not preserved but a specimen collected from South Korea corresponded to the description of the species. Since the conidiophores were pigmented, the species was transferred to *Phaeoramularia* as *P. weigelicola*. However, isolate CBS 113309 (Fig. 67), previously identified as *Phaeoramularia weigelicola*, clustered within the genus *Ramularia* (Fig. 1, clade XIV). The strain was not used in the multigene analysis since it lacked the *rpb2* partial gene sequence at the time the tree was run.

Important phytopathogenic *Ramularia* species lacking cultures in this study

Ramularia cercosporelloides U. Braun & Crous, Monogr. *Cercosporella*, *Ramularia* Allied Genera (Phytopath. Hyphom.) 2: 419. 1998.
≡ *Cercosporella carthami* Murashk., Izv. Zapadno-Sibirsk. Otd. Russk. Geogr. Obshch 5: 4. 1926.
Description in vivo: See Braun (1998: 419).

Substrate and distribution: On *Carthamus* (*Asteraceae*), Asia, Caucasus, Europe.

Notes: The type material of this species, on *Carthamus tinctorius* from Russia (near Omsk), could not be traced by Braun (1998) and the placement of the species in the genus *Ramularia* was based on the observation of a fresh specimen from the Netherlands on *Carthamus tinctorius* that is currently deposited in HAL. Some studies point to this pathogen as the causative agent of leaf spot disease on safflower in Sonora, Mexico, leading to severe yield losses on this crop. Morphological identification followed by pathogenicity tests of the isolates was performed by Huerta-Espino *et al.* (2006). However, in a more recent study (Quintana-Obregón *et al.*, 2013), isolates of the false mildew of safflower collected from the field were morphologically identified as *R. cercosporelloides* but, based on DNA sequences of the LSU and ITS regions, they were similar to *Cercosporella acroptili* (= *Ramularia acroptili*). Other studies point to *R. carthami* (now *R. cynarae*) as the causative agent (Montoya-Coronado *et al.* 2008, Borbon-Garcia *et al.* 2011). More work needs to be done to understand which fungus is causing the disease.

Ramularia oryzae Deighton & D.E. Shaw, Trans. Brit. Mycol. Soc. 43: 516. 1960.
≡ *Mycovellosiella oryzae* (Deighton & D.E. Shaw) Deighton, Mycol. Pap. 144: 25. 1979.

Description in vivo: See Braun (1998: 201).

Substrate and distribution: On *Oryza* (*Poaceae*); Asia and Africa.

Notes: *Ramularia oryzae* was described on *Oryza sativa* from Papua New Guinea [holotype in K(IMI)] and has been reported from Asia and Africa (Braun 1998). White leaf streak, caused

by *Mycovellosiella oryzae* (= *Ramularia oryzae*) was observed in Louisiana, USA, in 1996, developing on leaves of the rice cultivar Lemont. Pathogenicity tests were performed on the rice cultivars Lemont and Cypress by spraying a conidial suspension onto leaves at boot stage. Many elongated lesions were produced 3–4 wk after inoculation. With the same method, 45 other cultivars were tested. Most of the cultivars grown in southern US were moderately susceptible to susceptible. Foreign cultivars tested (BR-7, BR-11, Cica-4, Cica-7 to Cica-9, Oryzica Ilanos, Rax clear, Tequing, and Tetep) were resistant. As symptoms of both white leaf streak and narrow brown leaf spot were observed on the same leaf it is possible that the disease was present but not identified separately because of the similarity of the symptoms of the two diseases. At present it appears to be a minor problem for rice cultivation in Louisiana. White leaf streak has previously been reported from Papua New Guinea on cultivated *Oryza sativa*, and from the Solomon Islands, Sabah, Nigeria, and Sierra Leone on cultivated *O. glabberima*, and on wild perennial rice *O. berthii* (Webster & Gunnell 1992, Shahjahan *et al.* 1998, Zhou *et al.* 2010).

Ramularia phaseoli (O.A. Drumm.) Deighton, Trans. Brit. Mycol. Soc. 50: 125. 1967.
Basionym: *Ovularia phaseoli* O.A. Drumm., Revista Ceres 6(33): 169. 1945.
≡ *Mycovellosiella phaseoli* (O.A. Drumm.) Deighton, Mycol. Pap. 137: 70. 1974.
= *Ramularia phaseolina* Petr., Sydowia 4(1–6): 584. 1950.

Description in vivo: See Braun (1998: 128).

Substrate and distribution: Asia, Africa, S. America on *Glycine* and *Phaseolus* (*Fabaceae*).

Notes: *Ramularia phaseoli* is a pathogen that was first observed on *Phaseolus vulgaris* from Brazil (lectotype in CUP). This species is the causative agent of floury leaf spot disease on leaves of dry beans. Leaf spots usually appear first on older leaves, progresses to new foliage, and a severe infection may cause plant defoliation. Conidiophores and conidia develop mostly on the lower surface of the leaf in white, floury mats. It is among the more serious diseases of common bean at relatively high altitudes in the tropics and has been reported from Eastern and Central Africa, Europe, Malaysia, Papua New Guinea, South and Central America. It is usually controlled with chemical sprays with benomyl and thiophanate methyl and by rotation with non-host crops such as cereals and corn (Schwartz *et al.* 2005).

Ramularia primulae Thüm., Oesterr. Bot. Z. 28(5): 147. 1878.
≡ *Cylindrosporium primulae* (Thüm.) J. Schröt., Krypt.-Fl. Schlesien 3.2(4): 492. 1897.

Description in vivo: See Braun (1998: 228).

Substrate and distribution: On *Primula* (*Primulaceae*); Asia, Caucasus, Europe, N. and S. America, Australia, New Zealand.

Notes: *Ramularia primulae* was originally described on *Primula elatior* from Germany (neotype in PAD), but it has a worldwide distribution and has been reported infecting other species of the genus *Primula* (Braun 1998). This species is responsible for the Ramularia leaf spot disease on *Primula* spp. It is able to infect both *Primula* × *pruhonicensis* (polyanthus) and *P. malacoides* (fairy primrose) leaves creating tan or brown leaf spots that may be accompanied by chlorosis.

Conidiophores and conidia develop preferentially on the lower surface of lesions forming white spore masses under humid conditions. It is a disease mainly prevalent in the USA, but easily controlled by removing infected plants from the general population and keeping the seedlings away from older plants to avoid inoculum transfer (Daughtrey *et al.* 1995).

DISCUSSION

The genera covered in the present study include species with very diverse lifestyles that sometimes have a negative impact on the crops we depend on for food, feed and bioenergy. Although some species may cause significant yield losses, none of them are included in plant protection quarantine lists. The identification of species of *Ramularia* and allied genera has thus far mainly relied on host taxonomy and morphological characters such as the shape, size and septation of conidia and the type of conidiogenous loci and conidial hila. Reliable identification of these species based on morphological characters alone is difficult since their morphology is rather reduced. In order to improve the identification of cryptic species, the use of DNA phylogenetic markers, also known as DNA barcoding, is becoming an increasingly popular tool (Crous *et al.* 2009c, 2013a, Groenewald *et al.* 2013, Verkley *et al.* 2013).

The present study provides a broad phylogenetic overview of *Ramularia* and allied genera, thereby establishing a foundation of reference sequences in public databases that can be used for species identification, and at the same time promote further research. The phylogenetic analysis of *Ramularia* allied genera generally provided good resolution with maximum to high bootstrap and posterior probability values for almost all terminal nodes and several of the deeper nodes. Phylogenetic support based on three different methods facilitated the resolution of several genera based on their type species, such as *Ramularia* and *Ramulariopsis*. The genus *Ramularia* proved to be polyphyletic, and not monophyletic as previously thought, and the species non-congeneric with the type *R. pusilla* were assigned to the new genera *Xenoramularia*, *Epicoleosporium* and *Teratoramularia*. This was also the first time species with a ramularia-like morphology were observed in the *Teratosphaeriaceae*, which renders morphology-based identifications more difficult, and underlines the necessity of molecular data for accurate identification. The genus *Cercosporella*, although not epitypified, was analysed in two different studies (Kirschner 2009; present study), and based on its phylogenetic position and morphology, is considered to be reliably represented by the species used in this study. The phylogenetic position of *Pseudocercosporella* was reiterated as confined to its type species, *P. bakeri*, and the pseudocercosporella-like species not congeneric with the type were reassigned to new or existing genera such as *Apseudocercosporella*, *Filiella*, *Microcyclosporella*, *Neopseudocercosporella*, *Pseudocercospora*, *Ramularia* and *Sphaerulina*. An isolate previously identified as representative of *Pseudocercosporella fraxinea* was found to belong to the genus *Acrodontium*, typified by *A. crateriforme*, which prompted a short review of this genus, with the eventual description of three new species.

Although many more genera allied to *Ramularia* are treated in literature, most have not yet been preserved in culture, such as *Hawksworthiana*, *Neoovularia*, *Neoramularia*, *Monodidymaria*, *Pseudodidymaria* and *Tretovularia*. These genera need to be recollected, cultured and compared by means of DNA sequence analysis. In order to facilitate their identification, photoplates of their type specimens or representative species were produced in this study. The relationship between these genera and *Ramularia* is based on morphological characters but their phylogenetic position is still unknown and they may even not belong to the *Mycosphaerellaceae*. One example of this relates to the genus *Thedgonia* that was morphologically related to *Pseudocercosporella*,

and later found to belong to *Helotiales* (Crous *et al.* 2013a). *Ramularia* and allied genera are much undersampled and are frequently described without culture or DNA sequence data. In the last 15 years, among the 41 novel *Ramularia* names released on MycoBank, only 13 included cultures and DNA sequence data while the rest relied only on morphological descriptions based on herbarium specimens.

The present study includes the largest number of *Ramularia* isolates and species ever subjected to DNA sequence analysis. Combined with a recent classic monograph of the genus (Braun 1998), it provides powerful tools to better understand and promote further research on these species. The phylogenetic overview of the species belonging to *Ramularia* generally provided good resolution with maximum to high bootstrap and posterior probability values for almost all terminal nodes, while several of the deeper nodes were only supported by the Bayesian analysis. Several species were morphologically and molecularly characterised, two new combinations and two new names were proposed, nine new species were described, and 12 species epitypified. The type species of *Ramularia*, *R. pusilla*, was epitypified providing a reliable phylogenetic anchor for this genus. The *Ramularia* species analysed in this study generally agree with the concept presented in literature (Braun 1998), which regards them as being host-specific. Of the 88 taxa subjected to analysis 39 were found to occur in only one host genus, a number that rises to 60 when the single lineages are also considered. With the phylogeny we observed that some species previously thought to have a broad host range and geographical distribution were in fact different species (e.g. *R. lamii* var. *lamii*, *R. agastaches*, *R. leonuri*). While some species are reported to have a broad host range in literature (Braun 1998), this was not observed in the phylogeny, which could be due to undersampling (e.g. *R. asteris*, *R. belunensis*, *R. collo-cygni*, *R. grevilleana*, *R. heraclei*, *R. inaequalis*, *R. macrospora*, *R. pusilla* and *R. sphaeroidea*). Only six of the 88 taxa analysed proved to have a broad host range (e.g. *R. cynarae*, *R. hydrangeae-macrophyllae*, *R. vizellae*, *R. unterseheri*, *R. glennii* and *R. eucalypti*). The clades representing *R. hydrangeae-macrophyllae*, *R. vizellae*, *R. endophylla*, *R. unterseheri* and *R. cynarae* show some intraspecific variation in the genes investigated. Among these, only *R. cynarae* has not been observed to develop a sexual morph. Although in literature 20 connections between asexual and sexual morphs are reported for *Ramularia* species alone, only seven have been proven thus far, including the newly observed *R. hydrangeae-macrophyllae*. Sexual reproduction is known to introduce variability in the genes and this may explain the variation observed. The gene regions used in this study were selected based on their extensive use in fungal phylogenetic studies. They have proved suitable to explore phylogenetic relationships within and between genera of the *Mycosphaerellaceae* (Crous *et al.* 2013a, Groenewald *et al.* 2013, Verkley *et al.* 2013). Based on the individual genes, ITS was able to discriminate 58 % of the species while *tef1*-α recognised 62 %, *actA* 72%, *gapdh* 76 % and *rpb2* 84 %. The K2P results show that the ITS barcode has a lower ability to discriminate species than protein-coding genes, since it displayed the smallest barcode gap and highest overlap percentage of inter-intra specific distances among all genes. The *gapdh*, with its big barcode gap and low overlap would be a good candidate for a secondary barcode gene, but its amplification proved to be challenging. The *rpb2* gene displayed the widest barcode gap of all genes, but it had a relatively higher overlap percentage when compared to the other genes. Nevertheless, it was able to discriminate 84 % of the *Ramularia* species studied here, and the amplification of *rpb2* with the primers developed in this study was successful for all the isolates. The best statistical support for each genus was obtained using *rpb2*, therefore this locus should in future be more extensively used to determine relations within *Mycosphaerellaceae*. A recent publication on fungal barcoding genes recommends *tef1*-α as a secondary universal DNA

barcode for the fungal kingdom (Stielow *et al.* 2015). However, the fragment amplified by the primers used in that study is different from the fragment amplified in this study, and therefore cannot be compared directly.

Genomic studies of *Ramularia* species are presently unavailable but the amplification of the complete genome of two *Ramularia* species, *R. endophylla* (Grigoriev *et al.* 2013) and *R. collo-cygni* (Havis *et al.* 2015), are underway. They are likely to provide valuable insights into the genetic diversity of these species, their biological cycles and their hability to produce secondary metabolites that influence pathogenesis. *Ramularia collo-cygni*, *R. rubella* and *R. uredinicola* are able to produce a non-host specific phytotoxin, rubellin. They appear quite separate in the phylogenetic analysis suggesting this is a trait that evolved multiple times and is not confined to a single lineage. In this study, the species *R. archangelicae* and *R. calcea* have been observed to produce pigments of pink and brick colours, respectively, that diffused into the culture media, suggesting these species may also be able to produce rubellins. Besides the rubellins, no other secondary metabolites have been attributed to *Ramularia* and allied genera species, which indicates this is a fairly unexplored research line in this group of agricultural important species.

The present study includes several taxa that are of major concern for agriculture such as *Neopseudocercosporella capsellae* and *N. brassicicola* (*Brassica* spp.), *Ramulariopsis gossypii* (cotton), *Ramularia collo-cygni* (barley) and *Ramularia beticola* (sugar beet), since they affect important crops planted worldwide. We believe that this study serves as a backbone for future studies on the taxonomy of *Ramularia* and allied genera. Although many important species have been reliably identified and epitypified, many puzzles remain unsolved (e.g. the identity of *R. cercosporelloides*). More than 1000 names are known in *Ramularia* alone and this study covered only 88 taxa, which means many species still need to be recollected and characterised based on their DNA sequence data. With the reference cultures that this study has now made available to the community, further genomic research on the more important agricultural pathogens may shed some light on the mechanisms driving their evolution, and allow the development of more appropriate control measures.

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CHAPTER 5

Mycosphaerellaceae - chaos or clarity?

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Key words: Multi-gene phylogeny, *Mycosphaerella*, Plant pathogen, Taxonomy.

Abstract: The *Mycosphaerellaceae* represent thousands of fungal species that are associated with diseases on a wide range of plant hosts. Understanding and stabilising the taxonomy of genera and species of *Mycosphaerellaceae* is therefore of the utmost importance given their impact on agriculture, horticulture and forestry. Based on previous molecular studies, several phylogenetic and morphologically distinct genera within the *Mycosphaerellaceae* have been delimited. In this study a multigene phylogenetic analysis (LSU, ITS and *rpb2*) was performed based on 415 isolates representing 297 taxa and incorporating ex-type strains where available. The main aim of this study was to resolve the phylogenetic relationships among the genera currently recognised within the family, and to clarify the position of the cercosporoid fungi among them. Based on these results many well-known genera are shown to be paraphyletic, with several synapomorphic characters that have evolved more than once within the family. As a consequence, several old generic names including *Cercosporidium*, *Fulvia*, *Mycovellosiella*, *Phaeoramularia* and *Raghnildiana* are resurrected, and 32 additional genera are described as new. Based on phylogenetic data 120 genera are now accepted within the family, but many currently accepted cercosporoid genera still remain unresolved pending fresh collections and DNA data. The present study provides a phylogenetic framework for future taxonomic work within the *Mycosphaerellaceae*.

Taxonomic novelties: **New genera**: *Australosphaerella* Videira & Crous, *Brunswickiella* Videira & Crous, *Catenulocercospora* C. Nakash., Videira & Crous, *Cercoramularia* Videira, H.D. Shin, C. Nakash. & Crous, *Chuppomyces* Videira & Crous, *Clarohilum* Videira & Crous, *Collarispora* Videira & Crous, *Coremiopassalora* U. Braun, C. Nakash., Videira & Crous, *Deightonomyces* Videira & Crous, *Devonomyces* Videira & Crous, *Distocercosporaster* Videira, H.D. Shin, C. Nakash. & Crous, *Distomycovellosiella* U. Braun, C. Nakash., Videira & Crous, *Exopassalora* Videira & Crous, *Exutisphaerella* Videira & Crous, *Graminopassalora* U. Braun, C. Nakash., Videira & Crous, *Hyalocercosporidium* Videira & Crous, *Hyalozasmidium* U. Braun, C. Nakash., Videira & Crous, *Madagascaromyces* U. Braun, C. Nakash., Videira & Crous, *Micronematomyces* U. Braun, C. Nakash., Videira & Crous, *Neocercosporidium* Videira & Crous, *Neophloeospora* Videira & Crous, *Nothopassalora* U. Braun, C. Nakash., Videira & Crous, *Nothopericoniella* Videira & Crous, *Nothophaeocryptopus* Videira, C. Nakash., U. Braun, Crous, *Pachyramichloridium* Videira & Crous, *Paracercosporidium* Videira & Crous, *Paramycovellosiella* Videira, H.D. Shin & Crous, *Parapallidocercospora* Videira, Crous, U. Braun, C. Nakash., *Pleopassalora* Videira & Crous, *Pleuropassalora* U. Braun, C. Nakash., Videira & Crous, *Pluripassalora* Videira & Crous, *Pseudopericoniella* Videira & Crous, *Pseudophaeophleospora* U. Braun, C. Nakash., Videira & Crous, *Pseudozasmidium* Videira & Crous, *Rhachisphaerella* Videira & Crous, *Rosisphaerella* Videira & Crous, *Sultanimyces* Videira & Crous, *Virosphaerella* Videira & Crous, *Xenosonderhenioides* Videira & Crous. **New species**: *Cercoramularia koreana* Videira, H.D. Shin, C. Nakash. & Crous, *Hyalocercosporidium desmodii* Videira & Crous, *Hyalozasmidium sideroxyli* U. Braun, C. Nakash., Videira & Crous, *Neoceratosperma legnephoricola* U. Braun, C. Nakash., Videira & Crous, *Neoceratosperma haldinae* U. Braun, C. Nakash., Videira & Crous, *Ramulispora sorghiphila* U. Braun, C. Nakash., Videira & Crous, *Zasmidium elaeocarpi* U. Braun, C. Nakash., Videira & Crous, *Zasmidium grevilleae* U. Braun, C. Nakash., Videira & Crous, *Zasmidium hakeae* U. Braun, C. Nakash., Videira & Crous, *Zasmidium eucalypticola* U. Braun, C. Nakash., Videira & Crous, *Zasmidium schini* U. Braun, C. Nakash., Videira & Crous, *Xenosonderhenioides indonesiana* C. Nakash., Videira & Crous. **New combinations**: *Amycosphaerella keniensis* (Crous & T.A. Cout.) Videira & Crous, *Australosphaerella nootherensis* (Carnegie) Videira & Crous,

Brunswickiella parsonsiae (Crous & Summerell) Videira & Crous, *Chuppomyces handelii* (Bubák) U. Braun, C. Nakash., Videira & Crous, *Catenulocercospora fusimaculans* (G.F. Atk.) C. Nakash., Videira & Crous, *Cercosporidium californicum* (S.T. Koike & Crous) Videira & Crous, *Clarohilum henningsii* (Allesch.) Videira & Crous, *Clypeosphaerella calotropidis* (Ellis & Everh.) Videira & Crous, *Coremiopassalora eucalypti* (Crous & Alfenas) U. Braun, C. Nakash., Videira & Crous, *Coremiopassalora leptophlebae* (Crous *et al.*) U. Braun, C. Nakash., Videira & Crous, *Collarispora valgourgensis* (Crous) Videira & Crous, *Deightonomyces daleae* (Ellis & Kellerm.) Videira & Crous, *Devonomyces endophyticus* (Crous & H. Sm. Ter) Videira & Crous, *Distocercosporaster dioscoreae* (Ellis & G. Martin) Videira, H.D. Shin, C. Nakash. & Crous, *Distomycovellosiella brachycarpa* (Syd.) U. Braun, C. Nakash., Videira & Crous, *Exopassalora zambiae* (Crous & T.A. Cout.) Videira & Crous, *Exutisphaerella laricina* (R. Hartig) Videira & Crous, *Fusoidiella anethi* (Pers.) Videira & Crous, *Graminopassalora graminis* (Fuckel) U. Braun, C. Nakash., Videira & Crous, *Hyalozasmidium aerohyalinosporum* (Crous & Summerell) Videira & Crous, *Madagascaromyces intermedius* (Crous & M.J. Wingf.) Videira & Crous, *Micronematomyces caribensis* (Crous & Den Breeÿen) U. Braun, C. Nakash., Videira & Crous, *Micronematomyces chromolaenae* (Crous & Den Breeÿen) U. Braun, C. Nakash., Videira & Crous, *Neocercosporidium smilacis* (Thüm.) U. Braun, C. Nakash., Videira & Crous, *Neophloeospora maculans* (Bérenger) Videira & Crous, *Nothopassalora personata* (Berk. & M.A. Curtis) U. Braun, C. Nakash., Videira & Crous, *Nothopericoniella perseae-macranthae* (Hosag. & U. Braun) Videira & Crous, *Nothophaeocryptopus gaeumannii* (T. Rohde) Videira, C. Nakash., U. Braun, Crous, *Pachyramichloridium pini* (de Hoog & Rahman) U. Braun, C. Nakash., Videira & Crous, *Paracercosporidium microsorum* (Sacc.) U. Braun, C. Nakash., Videira & Crous, *Paracercosporidium tiliae* (Peck) U. Braun, C. Nakash., Videira & Crous, *Paramycosphaerella wachendorfiae* (Crous) Videira & Crous, *Paramycovellosiella passaloroides* (G. Winter) Videira, H.D. Shin & Crous, *Parapallidocercospora colombiensis* (Crous *et al.*) Videira & Crous, *Parapallidocercospora thailandica* (Crous *et al.*) Videira & Crous, *Phaeocercospora juniperina* (Georgescu & Badea) U. Braun, C. Nakash., Videira & Crous, *Pleopassalora perplexa* (Beilharz *et al.*) Videira & Crous, *Pleuropassalora armatae* (Crous & A.R. Wood) U. Braun, C. Nakash., Videira & Crous, *Pluripassalora bougainvilleae* (Munt.-Cvetk.) U. Braun, C. Nakash., Videira & Crous, *Pseudocercospora convoluta* (Crous & Den Breeÿen) U. Braun, C. Nakash., Videira & Crous, *Pseudocercospora nodosa* (Constant.) U. Braun, C. Nakash., Videira & Crous, *Pseudocercospora zambiensis* (Deighton) Crous & U. Braun, *Pseudopericoniella levispora* (Arzanlou, W. Gams & Crous) Videira & Crous, *Pseudophaeophleospora atkinsonii* (Syd.) U. Braun, C. Nakash., Videira & Crous, *Pseudophaeophleospora stonei* (Crous) U. Braun, C. Nakash., Videira & Crous, *Pseudozasmidium eucalypti* (Crous & Summerell) Videira & Crous, *Pseudozasmidium nabiacense* (Crous & Carnegie) Videira & Crous, *Pseudozasmidium parkii* (Crous & Alfenas) Videira & Crous, *Pseudozasmidium vietnamense* (Barber & T.I. Burgess) Videira & Crous, *Ragnhildiana ampelopsidis* (Peck) U. Braun, C. Nakash., Videira & Crous, *Ragnhildiana diffusa* (Heald & F.A. Wolf) Videira & Crous, *Ragnhildiana ferruginea* (Fuckel) U. Braun, C. Nakash., Videira & Crous, *Ragnhildiana gnaphaliaceae* (Cooke) Videira, H.D. Shin, C. Nakash. & Crous, *Ragnhildiana perfoliati* (Ellis & Everh.) U. Braun, C. Nakash., Videira & Crous, *Ragnhildiana pseudotithoniae* (Crous & Cheew.) U. Braun, C. Nakash., Videira & Crous, *Rhachisphaerella mozambica* (Arzanlou & Crous) Videira & Crous, *Rosisphaerella rosicola* (Pass.) U. Braun, C. Nakash., Videira & Crous, *Sultanimyces vitiphyllus* (Speschnew) Videira & Crous, *Utrechtiana roumeguerei* (Cavara) Videira & Crous, *Virosphaerella irregularis* (Cheew. *et al.*) Videira & Crous, *Virosphaerella pseudomarksii* (Cheew. *et al.*) Videira & Crous, *Zasmidium arcuatum*

(Arzanlou *et al.*) Videira & Crous, *Zasmidium biverticillatum* (Arzanlou & Crous) Videira & Crous, *Zasmidium cerophilum* (Tubaki) U. Braun, C. Nakash., Videira & Crous, *Zasmidium daviesiae* (Cooke & Massee) U. Braun, C. Nakash., Videira & Crous, *Zasmidium gupoyu* (R. Kirschner) U. Braun, C. Nakash., Videira & Crous, *Zasmidium iteae* (R. Kirschner) U. Braun, C. Nakash., Videira & Crous, *Zasmidium proteacearum* (D.E. Shaw & Alcorn) U. Braun, C. Nakash. & Crous, *Zasmidium pseudotsugae* (V.A.M. Mill. & Bonar) Videira & Crous, *Zasmidium pseudovespa* (Carnegie) U. Braun, C. Nakash., Videira & Crous, *Zasmidium strelitziae* (Arzanlou *et al.*) Videira & Crous, *Zasmidium tsugae* (Dearn.) Videira & Crous, *Zasmidium velutinum* (G. Winter) Videira & Crous. **New names and their replaced synonyms**: *Exosporium livistonicola* U. Braun, Videira & Crous for *Distocercospora livistonae* U. Braun & C.F. Hill, *Pseudocercospora platanigena* Videira & Crous for *Stigmella platani* Fuckel, non *Pseudocercospora platani* (J.M. Yen) J.M. Yen 1979, *Zasmidium musae-banksii* Videira & Crous for *Ramichloridium australiense* Arzanlou & Crous, non *Zasmidium australiense* (J.L. Mulder) U. Braun & Crous 2013, *Zasmidium musigenum* Videira & Crous for *Veronaea musae* Stahel ex M.B. Ellis, non *Zasmidium musae* (Arzanlou & Crous) Crous & U. Braun 2010. **Epitypes**: *Cercospora brachycarpa* Syd., *Cercospora smilacis* Thüm., *Cercospora gomphrenicola* Speg., *Cercospora microsora* Sacc., *Cercospora tiliae* Peck, *Cladosporium bacilligerum* Mont. & Fr., *Cladosporium chaetomium* Cooke, *Cladosporium fulvum* Cooke, *Cladosporium lonicericola* Yong H. He & Z.Y. Zhang, *Cladosporium personatum* Berk. & M.A. Curtis, *Clasterosporium degenerans* Syd. & P. Syd., *Cryptosporium acicola* Thüm., *Helicoma fasciculatum* Berk. & M.A. Curtis., *Isariopsis griseola* Sacc., *Septoria martiniana* Sacc. **Neotypes**: *Cercospora cajani* Henn., *Cercospora mangiferae* Koord., *Sphaerella laricina* R. Hartig. **Lectotypes** (basionyms): *Adelopus gaeumannii* T. Rohde, *Biharia vangueriae* Thirum. & Mishra, *Cercospora desmodii* Ellis & Kellerm., *Cercospora ferruginea* Fuckel, *Cercospora gnaphaliacea* Cooke, *Cercospora rosicola* Pass., *Cercosporidium helleri* Earle, *Cercospora henningsii* Allesch., *Cladosporium fulvum* Cooke, *Cladosporium bacilligerum* Mont. & Fr., *Cercospora microsora* Sacc., *Cercospora henningsii* Allesch., *Coryneum vitiphyllum* Speschnew, *Cryptosporium acicola* Thüm., *Isariopsis griseola* Sacc., *Scolicotrichum roumeguerei* Briosi & Cavara, *Sphaerella araneosa* Rehm, *Stictosepta cupularis* Petr., *Stigmella platani* Fuckel, *Tapeinosporium viride* Bonord.

INTRODUCTION

Fungi within the *Dothideomycetes* have a global distribution and occur in diverse habitats, ranging from marine to freshwater or terrestrial. They are mainly characterised by having bitunicate asci, often with fissitunicate dehiscence. The *Dothideomycetes* currently includes more than 25 orders, 100 families and over 1 500 genera (Schoch *et al.* 2009, Hyde *et al.* 2013, Trakunyingcharoen *et al.* 2014, Crous *et al.* 2015a, c, van Nieuwenhuijzen *et al.* 2016, Bezerra *et al.* 2017). Among them, the order *Capnodiales* includes nine families, one of which is *Mycosphaerellaceae*.

Members of *Mycosphaerellaceae* are able to colonise diverse niches and vary in lifestyle from pathogens to endophytes, saprobes, epiphytes and fungicolous species. Some important plant pathogens in this family include the species associated with Sigatoka disease on banana (Arzanlou *et al.* 2007, Churchill 2010, Chang *et al.* 2016), angular leaf spot of bean (Crous *et al.* 2006a), tomato leaf mould (de Wit 2016) and Cercospora leaf spot of olive (A,vila *et al.* 2005).

In addition, several members of *Mycosphaerellaceae* are quarantine regulated (Quaedvlieg *et al.* 2012) such as *Pseudocercospora angolensis* causing fruit and leaf spot disease on citrus (Kirk 1986, Pretorius *et al.* 2003), *Pseudocercospora pini-densiflorae* causing brown needle blight of pine (Deighton 1987, Crous *et al.* 1990), *Sphaerulina musiva* causing canker of poplar (Peace 1962, Waterman 1954, Quaedvlieg *et al.* 2013), *Mycosphaerella laricis-leptolepidis* causing needle cast of Japanese larch (Peace 1962), *Septoria malagutii* causing angular leaf spot of potato (Cline & Rossman 2006), *Lecanosticta acicula* causing brown spot needle blight on *Pinus* spp. (Quaedvlieg *et al.* 2012) and *Dothistroma* spp. causing red band disease of pine (Evans 1984, Barnes *et al.* 2004, 2016). In order to facilitate plant host invasion some species are known to produce fungal toxins such as dothistromin (Bradshaw 2004, Bradshaw & Zhang 2006) and cercosporin (Chen *et al.* 2007) or secrete proteinaceous effectors suppressing host defence responses and facilitating biotrophic growth (Wit 2016). The potential ability of endophytic species as sources of natural products important in medicine and agriculture is known among taxa of several families (Strobel & Daisy 2003, Aly *et al.* 2012, Gond *et al.* 2014), but is thus far unknown among species within the *Mycosphaerellaceae*. No species of *Mycosphaerellaceae* has hitherto been reported as a human pathogen although, in a rare occurrence, a species of *Ramularia* (*R. plurivora*) reportedly obtained from bone marrow has shown the ability to grow above 37 °C by changing its filamentous morphology into an arthroconidial yeast (Videira *et al.* 2015a).

As initially circumscribed *Mycosphaerellaceae* was polyphyletic (Crous *et al.* 2007, 2009a, e) and was later, therefore, split into several families, namely *Schizothyriaceae* (Batzer *et al.* 2008), *Cladosporiaceae* (Schubert *et al.* 2007, Dugan *et al.* 2008, Bensch *et al.* 2012, 2015), *Dissoconiaceae* and *Teratosphaeriaceae* (Crous *et al.* 2009b, Li *et al.* 2012, Quaedvlieg *et al.* 2014). From these results, it became evident that the mycosphaerella-like morphology has evolved multiple times and a new circumscription of *Mycosphaerella* was urgently required. Approximately 56 genera have until now been recognised in *Mycosphaerellaceae* (Wijayawardene *et al.* 2014), although the mycosphaerella-like sexual morphs are usually morphologically conserved, and hence these genera are chiefly distinguished based on the morphology of their asexual morphs (Crous *et al.* 2009e). In addition, if one includes all genera that are currently synonymised based on the similarity of morphological characters, a total of 118 generic names can be accounted for in the *Mycosphaerellaceae* (Braun 1995, 1998, Crous & Braun 2003, Seifert *et al.* 2011). *Mycosphaerella s. str*. has *Ramularia* asexual morphs, which is also the name now applied to members of this genus, while *Mycosphaerella s. lat.*

represents numerous genera distributed over different families. The name *Ramularia* (1833) is older than *Mycosphaerella* (1884) and choosing *Ramularia* over *Mycosphaerella* required less name changes since most established connections already had species names in *Ramularia*. Based on the one fungus = one name initiative (Wingfield *et al.* 2012, Crous *et al.* 2015b) the name *Ramularia* was selected over *Mycosphaerella* and included in a list of protected names (Wijayawardene *et al.* 2014, Rossman *et al.* 2015, Videira *et al.* 2015a, b).

Many asexual morphs linked to mycosphaerella-like sexual morphs are cercosporoid in morphology. Cercosporoid fungi are mostly defined as dematiaceous hyphomycetes with conidiophores formed singly, in groups (fascicles), synnemata or even sporodochia, having integrated, terminal or intercalary conidiogenous cells. Conidiogenesis is holoblastic and generates amerosporous to scolecosporous conidia, which are solitary or in chains (Braun *et al.* 2013). In a broader sense, it also includes ramularioid fungi that are the hyaline counterparts of cercosporoid fungi, forming conidia singly or in chains. Species in this group are mostly asexual with a relation to mycosphaerella-like sexual morphs, which are characterised by pseudothecial ascomata, with ostiolar periphyses but without interascal tissue, hyaline or slightly pigmented ascospores that are predominantly 1-septate (Barr 1987, Crous *et al.* 2009c).

Four genera were initially recognised as true cercosporoid genera, namely *Cercospora*, *Passalora*, *Pseudocercospora*, and *Stenella* (Crous & Braun 2003). The genus *Stenella* was allocated to the *Teratosphaeriaceae* based on the phylogenetic placement of the type species, *Stenella araguata*, while the stenella-like species remaining in *Mycosphaerellaceae* were included in the genus *Zasmidium* (Arzanlou *et al.* 2007, Braun *et al.* 2010a, 2013). Currently, the recognised cercosporoid and ramularioid fungi include the latter four and a large assortment of genera that are cercospora-, passalora-, pseudocercospora-, pseudocercosporella-, ramularia- and zasmidium-like in morphology.

These fungi represent a very large heterogeneous group for which the existing monographs (Chupp 1954, Braun 1995, 1998, Crous & Braun 2003) are in urgent need of revision (e.g. Braun *et al.* 2013, 2014, 2015a). With the introduction of phylogenetic analyses based on DNA sequences, the *Mycosphaerellaceae* has been more narrowly defined with names of asexual genera now being used to identify morphologically distinct monophyletic clades, e.g. *Cercospora* (Groenewald *et al.* 2013), *Pseudocercospora* (Crous *et al.* 2013a, Nakashima *et al.* 2016), *Ramularia* (Videira *et al.* 2016), and *Zymoseptoria* (Quaedvlieg *et al.* 2011). However, several genera appear to be paraphyletic, showing that some morphological characters have evolved more than once within the family (e.g. *Passalora* and *Zasmidium*). Several accepted cercosporoid genera also have an uncertain status since no suitable type, or ex-type culture, is available (e.g. *Distocercospora*, *Phaeoramularia* and *Mycovellosiella*). Understanding and stabilising the taxonomy of cercosporoid fungi, most of which are plant pathogens, is urgent, given their impact on agriculture, horticulture and forestry. In the present study, we compiled a multigene phylogenetic analysis based on LSU, ITS and *rpb2* DNA sequence data, including 415 isolates representing 297 taxa that we have managed to cultivate since this project started in the year 2000. We include ex-type strains when available. Several old generic names are resurrected based on the type species having been recollected, and new genera are described for monophyletic clades where necessary.

MATERIALS AND METHODS

Isolates

The isolates included in this study were obtained from the culture collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands, which houses the CBS culture collection, and from the working collection of Pedro Crous (CPC), housed at the Westerdijk Institute, or were freshly isolated from a range of different plant hosts (Table 1). Single-conidial and ascospore cultures were obtained using the techniques described for species of *Mycosphaerella* and associated asexual morphs (Crous *et al.* 1991, Crous 1998). Representative cultures of the new species described in this study were deposited in the CBS culture collection.

DNA extraction, amplification and sequencing

Fungal mycelium of strains (Table 1) was harvested with a sterile scalpel and the genomic DNA was isolated using the UltraClean Microbial DNA Isolation Kit (MoBio Laboratories, Inc., Solana Beach, CA, USA) following the manufacturers' protocols. Three partial nuclear genes were targeted for PCR amplification and sequencing: 28S nrRNA gene (LSU), internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS) of the nrDNA operon, RNA polymerase II second largest subunit (*rpb2*). The primers employed are listed in Table 2, with the respective annealing temperatures used. The PCR amplifications were performed on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA). The PCR mixtures consisted of 1 µL genomic DNA, 1× NH_4 reaction buffer (Bioline, Luckenwalde, Germany), 2 mM $MgCl_2$, 40 µM of each dNTP, 0.2 µM of each primer and 0.5 U *Taq* DNA polymerase (Bioline) in a total volume of 12.5 µL. The PCR mixture for *rpb2* contained 2 µL genomic DNA. The general PCR conditions were: initial denaturation (94 °C, 3 min); 35 cycles amplification [denaturation 94 °C, 30 s; locus-specific annealing temperature (Table 2), 30 s; extension 72 °C, 45 s], and final extension (72 °C, 5 min). To obtain the partial *rpb2*, a touchdown PCR protocol was used: initial denaturation (94 °C, 3 min), 5 amplification cycles (denaturation 94 °C, 45 s; annealing 60 °C, 45 s; extension 72 °C, 1 min), 5 amplification cycles (denaturation 94 °C, 45 s; annealing 58 °C, 45 s; extension 72 °C, 1 min), 30 amplification cycles (denaturation 94 °C, 45 s; annealing 54 °C, 45 s; extension 72 °C, 1 min) and a final extension (72 °C, 8 min). The resulting fragments were sequenced in both directions using the PCR primers and the BigDye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems Life Technologies, Carlsbad, CA, USA). DNA sequencing amplicons were purified through Sephadex G-50 Superfine columns (Sigma-Aldrich, St. Louis, MO, USA) in MultiScreen HV plates (Millipore, Billerica, MA, USA). Purified sequence reactions were analysed on an Applied Biosystems 3730xl DNA Analyzer (Life Technologies, Carlsbad, CA, USA). The DNA sequences generated were analysed and consensus sequences were computed using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium).

Phylogenetic analysis

The generated sequences for each gene were aligned with the online version of MAFFT v. 7 (Katoh & Standley 2013). The alignments were manually checked and improved where necessary using MEGA v. 5 (Tamura *et al.* 2011) and were concatenated with Mesquite v. 2.75 (Maddison & Maddison 2011). From the strains listed in Table 1, only those with the complete dataset of

Table 1. Collection details and GenBank accession numbers of isolates included in this study. Cultures with a type status are indicated in **bold** text.

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Cladosporiaceae								
Cladosporium allicinum	–	CBS 188.53 = IFO 5267	–	Japan	–	MF951115	KT600367	MF951411
Cladosporium cf. *subtilissimum*	*Fusicladium effusum*	CBS 172.52 = ATCC 11320	*Carya illinoensis*	USA	–	EF679390	EF679390	MF951412
C. cladosporioides	–	**CBS 112388^{NT}**	Air	Germany	Ch. Trautmann	KX286982	HM148003	KX288432
C. ramotenellum	*Fusicladium subsessile*	CBS 133.29 = ATCC 36970	*Populus tremuloides*	–		MF951116	MF951281	MF951413
Cladosporium sp. A	*Fusicladium carpophillum*	CBS 145.33 = ATCC 12117	*Prunus persica*	USA: Wisconsin	–	MF951117	MF951282	MF951414
Cladosporium sp. B	*Fusicladium pomi*	CBS 179.47	–	Portugal	–	MF951118	MF951283	MF951415
Dissoconiaceae								
Ramichloridium apiculatum	*Chloridium apiculatum*	**CBS 156.59^{T}** = ATCC 13211 = IMI 100716 = JCM 6972 = MUCL 15753 = MUCL 7991 = QM 7716	Forest soil	USA: Georgia	–	EU041848	EU041791	MF951416
	Rhinocladiella indica	CBS 400.76 = IMI 088021	Soil	Pakistan	–	EU041851	EU041794	KX348077
R. luteum	–	**CBS 132088^{T}** = CPC 18961 = ZXR-SD-2	*Malus domestica*	China	G.Y. Sun, Oct. 2006	JQ622099	EU329730	MF951417
Uwebraunia australiensis	*Dissoconium australiensis*	CBS 120729 = CPC 13282	*Eucalyptus platyphylla*	Australia: Queensland	P.W. Crous, 26 Aug. 2006	KF442553	KF442513	KX348105
U. dekkeri	*Mycosphaerella lateralis*	CBS 110748 = CMW 14906 = CPC 825	*Eucalyptus grandis*	South Africa: Northern Province	G. Kemp, Oct. 1994	KF442534	KF442495	MF951418
U. musae	*Dissoconium musae*	CBS 122453 = X1021	*Musa acuminata* cv. Nendran (Plantain) AAB	India	I. Buddenhagen, 28 Feb. 2005	JQ739816	EU514225	KX348107
Dothioraceae								
Cylindroseptoria ceratoniae	*Septoria ceratoniae*	**CBS 477.69^{T}** = H.A 1731	*Ceratonia siliqua*	Spain: Mallorca	H.A. van der Aa, 24 May 1969	KF251655	KF251151	MF951419
Mycosphaerellaceae								

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Acervuloseptoria ziziphicola	*Acervuloseptoria ziziphicola*	**CBS 138009**^{T} = CPC 23707	*Ziziphus mucronata*	South Africa: Northern Cape	J. Roux, Sep. 2013	KJ869221	KJ869164	MF951425
Amycosphaerella africana	*Mycosphaerella africana*	**CBS 680.95**^{T} = CPC 796	*Eucalyptus viminalis*	South Africa: Western Cape	P.W. Crous, Oct. 1994	KF902048	KF901701	MF951426
	Mycosphaerella aurantia	**CBS 110500**^{T} of *Mycosphaerella aurantia* = CMW 14460	*Eucalyptus globulus*	Australia: Western Australia	A. Maxwell, 1 May 2000	KF901837	AY725531	MF951427
	Mycosphaerella ellipsoidea	**CBS 110843**^{T} of *Mycosphaerella ellipsoidea* = CPC 850	*Eucalyptus cladocalyx*	South Africa: Western Cape	P.W. Crous, 7 Nov. 1994	GQ852602	AY725545	MF951431
	Mycosphaerella buckinghamiae	**CBS 111996**^{T} of *Mycosphaerella buckinghamiae* = CPC 3006	*Buckinghamia* sp.	Australia: New South Wales	P.W. Crous & B. Summerell, Aug. 1999	MF951124	EU707855	MF951430
	Mycosphaerella africana	**CBS 116154**^{T} = CMW 4945 = CPC 794	*Eucalyptus viminalis*	South Africa	P.W. Crous, Oct. 1994	GQ852601	KF901700	MF951429
	Mycosphaerella gregaria	**CBS 134927**^{T} of *Mycosphaerella gregaria* = DAR 72368	*Eucalyptus grandis*	Australia: Victoria	A.J. Carnegie, 11 Nov. 1990	MF951125	MF951289	MF951432
	Mycosphaerella aurantia	CPC 12678	*Dracaena draco*	New Zealand	M. Braithwaite, 1 Mar. 2004	MF951123	MF951288	MF951428
A. keniensis	*Mycosphaerella keniensis*	**CBS 111001**^{T} = CPC 1084 = CMW 5147	*Eucalyptus grandis* litter	Kenya	M.J. Wingfield, May 1995	GQ852610	MF951290	MF951433
	Mycosphaerella mozambica	CBS 121391 = UQ 438 = X884	*Musa* sp.	Australia	–	MF951126	EU514258	MF951434
Amycosphaerella sp.	*Crinipellis perniciosa*	CBS 441.80	*Theobroma cacao*	Brazil	H.C. Evans	MF951127	MF951291	MF951435
Annellosympodiella juniperi	–	**CBS 137992**^{T} = CPC 23276	*Juniperus procera*	Ethiopia	P.W. Crous & A. Assefa, 25 Jun. 2013	KJ869204	KJ869204	MF951436
Apseudocercosporella trigonotidis	*Pseudocercosporella* sp.	**CBS 131890**^{T} = CPC 10864	*Trigonotis peduncularis*	Republic of Korea	H.D.. Shin, 12 Nov. 2003	JQ324972	GU269858	KX288414
Asperisporium caricae	–	**CBS 130298**^{ET}	*Carica papaya*	Brazil	C. Weight, 16 Apr. 2010	MF951128	JN190955	MF951437

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	Asperisporium sp.	CPC 22691	*Carica papaya*	Brazil	A.C. Alfenas, Mar. 2013	MF951129	MF951292	MF951438
Asperisporium caricicola	–	**CBS 139998^{T}** = CPC 24348 = TSU:MUMH 11477	*Carica papaya*	Republic of Fiji	C. Nakashima, 10 Sep. 2013	KR611891	KR611869	MF951439
Australosphaerella nootherensis	*Mycosphaerella nootherensis*	**CBS 130522^{T}**	*Corymbia intermedia*	Australia: Queensland	A.J. Carnegie, 11 Aug. 2008	KF901835	MF951293	MF951440
Brunneosphaerella jonkershoekensis	–	**CPC 13902^{ET}**	*Protea repens*	South Africa: Western Cape	P.W. Crous, Apr. 2007	JN712503	JN712439	MF951441
B. nitidae	–	**CBS 130595^{T}** = CPC 15231	*Protea nitida* leaf litter	South Africa: Western Cape	L. Mostert, 12 Apr. 2008	GU214396	GU214625	MF951442
B. protearum	–	**CBS 130597^{ET}** = CPC 16338	*Protea* sp.	South Africa: Western Cape	P.W. Crous, 13 Jan. 2009	GU214397	GU214626	MF951443
Brunswickiella parsonsiae	–	**CBS 137979^{T}** = CPC 22537	*Parsonsia straminea*	Australia	B.A. Summerell, 9 Mar. 2013	KJ869188	KJ869131	MF951593
Caryophylloseptoria lychnidis	–	CBS 109099	*Silene pratensis*	Austria	G. Verkley, 4 Aug. 2000	KF251791	KF251287	MF951444
	–	CBS 109102	*Silene pratensis*	Austria	G. Verkley, 4 Aug. 2000	KF251793	KF251289	MF951445
C. pseudolychnidis	–	CBS 128614 = KACC 42904 = SMKC 22691	*Lychnis cognata*	Republic of Korea	–	KF251794	KF251290	KX348049
	–	**CBS 128630^{T}** = KACC 43866 = SMKC 23519	*Lychnis cognata*	Republic of Korea	–	KF251795	KF251291	MF951446
C. silenes	*Septoria silenes*	CBS 109103	*Silene nutans*	Austria	G. Verkley, 3 Aug. 2000	KF251797	KF251293	MF951447
C. spergulae	–	**CBS 109010^{ET}**	*Spergula morisonii*	Netherlands	A. Aptroot, 13 Jun. 2000	KF251798	KF251294	MF951448
"Septoria" gladioli	–	CBS 353.29	–	Netherlands	–	KF251932	KF251428	MF951449
Catenulocercospora fusimaculans	*Passalora fusimaculans*	CPC 17277	*Agrostis* sp.	Thailand	P. Pheng, 15 Sep. 2009	KF251817	KF251313	MF951450
Cercoramularia koreana	*Phaeoramularia* sp.	**CBS 142175^{T}** = CPC 10709	*Styrax japonicus*	Republic of Korea	H.D.. Shin, 17 Sep. 2003	MF951132	MF951296	MF951453

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	Phaeoramularia sp.	CPC 10639	*Styrax japonicus*	Republic of Korea	H.D.. Shin, 2003	MF951130	MF951294	MF951451
	Phaeoramularia sp.	CPC 10641	*Styrax japonicus*	Republic of Korea	H.D.. Shin, 2003	MF951131	MF951295	MF951452
Cercospora apii	–	**CBS 116455**[ET] = CPC 11556	*Apium graveolens*	Germany	K. Schrameyer, 10 Aug. 2004	MF951133	AY840519	–
C. armoraciae	–	CBS 538.71 = IMI 161109 = CPC 5090	*Berteroa incana*	Romania	O. Constantinescu, 4 Sep. 1969	MF951134	JX143547	MF951454
C. beticola	–	CPC 18813	*Beta vulgaris*	USA: California	S.T. Koike, 1 Nov. 2010	MF951135	JX143556	MF951455
C. campi-silii	–	CBS 132625 = CPC 14585	*Impatiens noli-tangere*	Republic of Korea	H.D.. Shin, 29 Sep. 2007	KX286965	JX143561	KX288415
C. capsici	–	CBS 132622 = CPC 14520	*Capsicum annuum*	Republic of Korea	H.D.. Shin, 29 Aug. 2005	MF951136	JX143568	MF951456
Cercospora cf. *chenopodii*	*Passalora dubia*	CBS 126.29	–	–	–	MF951139	MF951299	MF951459
	Passalora dubia	CBS 256.67	*Atriplex hortensis*	Romania	–	MF951140	MF951300	MF951460
	Passalora dubia	CBS 543.71 = BUCM 2006	*Atriplex oblongifolia*	Romania	O. Constantinescu & G. Negrean, 13 Jul. 1970	MF951141	MF951301	MF951461
	Passalora dubia	CBS 123192 = CPC 15387	*Chenopodium album*	New Zealand	C.F. Hill, 2 Mar. 2008	MF951138	MF951298	MF951458
	–	CPC 10303	*Chenopodium ficifolium*	Republic of Korea	H.D.. Shin, 3 Oct. 2002	MF951137	MF951297	MF951457
	–	CPC 12450	*Chenopodium ficifolium*	Republic of Korea	H.D.. Shin, 27 Oct. 2005	KX286967	JX143574	KX288417
C. euphorbiae-sieboldianae	–	**CBS 113306**[T]	*Euphorbia sieboldiana*	Republic of Korea	H.D.. Shin, 8 May 2003	MF951142	JX143593	MF951462
C. fagopyri	–	**CBS 132623**[NT] = CPC 14541	*Fagopyrum esculentum*	Republic of Korea	H.D.. Shin	MF951143	JX143594	MF951463

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
C. janseana	*Passalora janseana*	CBS 145.37 = IMI 303642	–	USA	–	KF251818	KF251314	MF951464
C. lactucae-sativae	–	CPC 10082	*Ixeris chinensis* subsp. *strigosa* (≡ *Ixeris strigosa)*	Republic of Korea	H.D.. Shin, 11 Oct. 2002	MF951144	JX143622	MF951465
C. senecionis-walkeri	–	CBS 132636 = CPC 19196	*Senecio walkeri*	Laos	P. Phengsintham, 20 Feb. 2010	MF951145	JX143649	MF951466
C. sojina	*Passalora personata*	CBS 220.31	–	Italy	–	KX286971	KX287279	KX288421
	–	CBS 132018 = CPC 12322	*Glycine soja*	Republic of Korea	H.D.. Shin, 20 Jul. 2004	GU214655	GU214655	MF951467
	–	**CBS 132615^{NT}** = CPC 11353	*Glycine soja*	Republic of Korea	H.D.. Shin, 20 Jul. 2004	KX286969	JX143659	KX288419
	–	CPC 11422	*Glycine soja*	Republic of Korea	H.D.. Shin	KX286972	KX287280	KX288422
Cercospora sp.	*Passalora dulcamarae*	CBS 544.71 = BUCM 2008	*Solanum dulcamara*	Romania	O. Constantinescu & G. Negrean, 14 Oct. 1970	MF951146	MF951302	MF951468
C. zeina	–	**CBS 118820^{T}** = CPC 11995	*Zea mays*	South Africa: KwaZulu-Natal	P. Caldwell, 2005	MF951147	DQ185081	MF951469
Cercosporella catenulata	*Ramularia deusta* var. *alba*	**CBS 355.73^{T}**	*Phaseolus vulgaris*	Rwanda	D. Froment, 10 Jan. 1973	KX286973	KX287281	KX288424
C. dolichandrae	–	**CBS 138101^{T}** = CPC 22948	*Dolichandra unguiscati*	South Africa: KwaZulu-Natal	A. King,15 Nov. 2011	KJ869197	KJ869140	KX288423
C. virgaureae	*Cercosporella vergaweae*	CBS 113304	*Erigeron annuus*	Republic of Korea	H.D.. Shin, 21 May 2003	KF251805	GU214658	KX348051
	–	CPC 10286	*Erigeron annuus*	Republic of Korea	H.D.. Shin, 9 Oct. 2002	KX286978	KX287285	KX288428
	–	CPC 11456	*Erigeron annuus*	Republic of Korea	H.D.. Shin, 1 Jul. 2004	KX286974	MF951303	KX348050
	–	CPC 11457	*Erigeron annuus*	Republic of Korea	H.D.. Shin, 1 Jul. 2004	KX286975	KX287282	KX288425

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	–	CPC 11460	*Erigeron annuus*	Republic of Korea	H.D.. Shin, 1 Jul. 2004	KX286976	KX287283	KX288426
Cercosporidium californicum	*Passalora californica*	**CBS 128857^{T}** = CPC 18389	*Asclepias fascicularis*	USA: California	S.T Koike, 19 Jul. 2010	MF951148	HQ728115	MF951470
	Passalora californica	CPC 18390	*Asclepias fascicularis*	USA: California	S.T Koike, 19 Jul. 2010	MF951149	MF951304	MF951471
C. chaetomium	*Passalora* sp.	**CBS 142177^{ET}** = CPC 18624	*Euphorbia* sp.	Canada	P.W. Crous & K. Seifert, 28 Sep. 2010	MF951151	MF951306	MF951474
C. miurae	*Passalora miurae*	CBS 142235 = CPC 14628	*Metaplexis japonica*	Republic of Korea	H.D.. Shin, 1 Oct. 2007	MF951150	MF951305	MF951472
	Passalora miurae	CPC 14643	*Metaplexis japonica*	Republic of Korea	H.D.. Shin, 22 Sep. 2007	KJ633268	KJ633264	MF951473
Chuppomyces handelii	*Mycosphaerella handelii*	CBS 113302	*Rhododendron* sp.	Netherlands	P.W. Crous & U. Braun, 2002	GU214437	EU167581	MF951475
Clarohilum henningsii	*Passalora henningsii*	CPC 17314	*Manihot esculenta*	Laos	P. Pheng, 5 May 2006	MF951152	MF951307	MF951476
Clypeosphaerella calotropidis	*Passalora calotropidis*	CBS 129.30	*Calotropis procera*	Egypt	–	MF951153	MF951308	MF951477
C. quasiparkii	*Mycosphaerella quasiparki*	**CBS 123243^{T}** = CPC 15409	*Eucalyptus* sp.	Thailand	P. Suwannawong, Jul. 2007	KF902128	KF901771	MF951478
Collarispora valgourgensis	*Passalora* sp.	CBS 125311 = CS2 OH3 gH1c	*Malus* sp.	USA: Ohio	M. Ellis, 29 Sep. 2005	MF951154	MF951309	MF951480
	Mycosphaerella valgourgensis	**CBS 129531^{T}** = CPC 18385	*Yucca* sp.	France	P.W. Crous, 15 Jul. 2010	JF951175	JF951152	MF951479
Coremiopassalora eucalypti	*Passalora eucalypti*	**CBS 111306^{T}** of *Mycovellosiella eucalypti* = CPC 1455 = CMW 14907	*Eucalyptus saligna*	Brazil	P.W. Crous & A.C. Alfenas, Jun. 1995	GU253860	GU269845	MF951481
	Passalora eucalypti	CBS 111318 = CPC 1457	*Eucalyptus saligna*	Brazil	P.W. Crous & A.C. Alfenas, Jun. 1995	GU253860	GU269845	MF951482

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
C. leptophlebae	*Passalora leptophlebiae*	**CBS 129524^{T}** = CPC 18480	*Eucalyptus leptophleba*	Brazil	P.W. Crous, A.C. Alfenas, R. Alfenas & O.L. Pereira, 23 Aug. 2010	KF901939	MF951310	MF951483
Cytostagonospora martiniana	*Septoria* sp.	**CBS 135102^{ET}** = CPC 17727	*Acacia pycnantha*	Australia: Victoria	P.W. Crous, 21 Oct. 2009	KF251657	KF251153	MF951484
Deightonomyces daleae	*Passalora daleae*	CBS 113031	*Dalea spinosa*	Mexico	L.B. Sparrius, Apr. 2003	MF951155	EU040236	MF951485
Devonomyces endophyticus	*Phaeophleospora gregaria*	CBS 110501 = CMW 14462	*Eucalyptus globulus*	Australia: Western Australia	A. Maxwell, 15 Dec. 2000	EU167580	EU167580	MF951589
	Phaeophleospora gregaria	CBS 111167 = CPC 1225	*Eucalyptus cladocalyx*	South Africa: Western Cape	A.R. Wood, 22 Sep. 1995	KF902058	KF901711	MF951588
	Mycosphaerella endophytica	**CBS 114662^{T}** of *Mycosphaerella endophytica* = CPC 1193	*Eucalyptus* sp.	South Africa: Western Cape	P.W. Crous, Jun. 1995	KF902060	KF901713	MF951590
	Mycosphaerella pseudoellipsoidea	CBS 114709 = CMW 9099	*Eucalyptus nitens*	South Africa	–	EU167585	EU167585	MF951591
	Stenella sp.	CPC 15580	*Hakea undulata*	Australia	A.R. Wood, 2 Aug. 2008	MF951212	MF951357	MF951592
Distocercospora pachyderma	–	**CBS 138247^{ET}** = CPC 24144	*Dioscorea* sp.	Japan	C. Nakashima & K. Motohashi, 13 Sep. 2010	MF951156	MF951311	MF951486
Distocercosporaster dioscoriae	*Passalora dioscoreae*	CBS 135460 = CPC 10855	*Dioscorea tokoro*	Republic of Korea	H.D.. Shin, 16 Oct. 2003	GU214665	GU214665	MF951488
	Passalora dioscoreae	CBS 135463 = CPC 11513	*Dioscorea tenuipes*	Republic of Korea	H.D.. Shin, 2003	KF251815	KF251311	MF951489
	Passalora dioscoreae	KACC 44723	*Dioscorea* sp.	Republic of Korea	H.D.. Shin	MF951157	MF951312	MF951487
Distomycovellosiella brachycarpa	*Passalora brachycarpa*	CBS 114855	–	New Zealand	–	MF951159	MF951314	MF951491
	Passalora brachycarpa	CBS 115124	*Solanum mauritianum*	New Zealand	–	GU214664	GU214664	MF951492

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	Mycovellosiella brachycarpa	**CBS 142178[ET]** = CPC 18381	*Solanum mauritianum*	South Africa: KwaZulu-Natal	A.R. Wood, 6 Jul. 2010	MF951158	MF951313	MF951490
Dothistroma pini	–	CBS 116486	*Pinus nigra*	USA: Michigan	G. Adams, 2001	JX901823	JX901735	KX348053
	–	CBS 121005 = CMW 24852	*Pinus pallasiana*	Russia	T.S. Bulgakov, 8 Oct. 2006	KF251659	KF251155	KX348052
D. septosporum	–	CBS 128782 = CPC 16798	*Pinus mugo* 'Rostrata'	Netherlands	W. Quaedvlieg, 1 Jun. 2009	JX901829	JX901741	KX348054
	–	CBS 128783 = CPC 16799	*Pinus mugo* 'Rostrata'	Netherlands	W. Quaedvlieg, 1 Jun. 2009	JF700938	JX901742	MF951493
Epicoleosporium ramularioides	–	**CBS 141103[T]** = CPC 10672	*Coleosporium phellodendri* on leaves of *Phellodendron amurense*	Republic of Korea	H.D.. Shin, 4 Sep. 2003	GU214688	GU214688	KX288433
	–	CPC 10673	*Coleosporium phellodendri* on leaves of *Phellodendron amurense*	Republic of Korea	H.D.. Shin, 4 Sep. 2003	MF951160	KX287289	KX288434
Exosporium livistonae	*Passalora* sp.	**CBS 131313[T]** = CPC 19357	*Livistona benthamii*	Australia: Northern Territory	P.W. Crous & B.A. Summerell, 25 Apr. 2011	JQ044446	JQ044427	MF951494
E. livistonicola	–	MUCC 190	*Livistona chinensis*	Japan	T. Kobayashi & Y. Ono, 27 Feb. 2003	MF951161	MF951315	MF951495
Exutisphaerella laricina	*Mycosphaerella laricina*	**CBS 326.52[NT]**	*Larix decidua*	Switzerland	–	GU253693	GU269643	MF951496
Filiella pastinacae	*Pseudocercosporella pastinacae*	CBS 114116 = UPSC 2633	*Laserpitium latifolium*	Sweden	K. & L. Holm, 2 Jun. 1988	KF251832	KF251328	KX348056
Fulvia fulva	*Passalora fulva*	CBS 120.46 = VKM F-3053	*Solanum lycopersicum*	Switzerland	–	MF951162	MF951316	MF951497

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	Passalora fulva	**CBS 142314**^{ET} = CPC 13652	*Solanum lycopersicum*	Cuba	B. Summerell, 2006	MF951163	MF951317	MF951498
Fusoidiella anethi	*Passalora puncta*	CBS 296.32	–	Italy	–	MF951164	MF951318	MF951499
	Passalora puncta	CBS 117584	*Foeniculum vulgare*	New Zealand	–	MF951165	MF951319	MF951500
F. depressa	*Passalora depressa*	CBS 141335 = CPC 14915	*Angelica gigas*	Republic of Korea	H.D.. Shin, 18 Oct. 2007	KF251813	KF251309	KX348055
Genus A: "*Passalora*" *vaginae*	*Passalora vaginae*	CBS 140.34 = DSM 1148 = IMI 303641	*Saccharum officinarum*	Taiwan	–	MF951166	MF951320	–
Graminopassalora graminis	*Passalora graminis*	CBS 113303	*Alopecurus aequalis* var. *amurensis*	Republic of Korea	H.D.. Shin, 24 May 2003	GU214666	GU214666	MF951502
	Cercosporidium graminis	MAFF 510604 = MUCC 1429	*Dactylis glomerata*	Japan	N. Nishihara, –	MF951167	MF951321	MF951501
Hyalinozasmidium aerohyalinosporum	*Zasmidium aerohyalinosporum*	**CBS 125011**^{T} of *Zasmidium aerohyalinosporum* = CPC 14636	*Eucalyptus tectifica*	Australia: New South Wales	B.A. Summerell, 23 Sep. 2007	KF901930	GQ852839	MF951504
H. sideroxyli	*Zasmidium* sp.	**CBS 142191**^{T} = CPC 23462	*Sideroxylon inerme*	South Africa: Eastern Cape	A.R. Wood, 8 May 2013	MF951169	MF951323	MF951505
Hyalocercosporidium desmodii	*Passalora* sp.	**CBS 142179**^{T} = CPC 19483	*Desmodium tortuosum*	Brazil: Minas Gerais	R.W. Barreto, 2 Aug. 2009	MF951168	MF951322	MF951503
Lecanosticta acicola	–	CBS 871.95 = MPFN 314	*Pinus radiata*	France	M. Morelet, Apr. 1995	GU214663	GU214663	MF951506
	–	**CBS 133791**^{ET} = WPF13.12	*Pinus strobus*	USA: New Hampshire	B. Ostrofsky, 15 Jun. 2011	KC013017	KC012999	MF951507
L. brevispora	–	**CBS 133601**^{T} = CPC 18092	*Pinus* sp.	Mexico	M. de Jesús Yáñez-Morales, 24 Oct. 2009	KF902021	JX901763	MF951508
L. longispora	–	**CBS 133602**^{ET} = CPC 17940	*Pinus* sp.	Mexico	M. de Jesús Yáñez-Morales & C. Méndez-Inocencio, 24 Oct. 2009	JX901858	JX901766	MF951510

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	–	CPC 17941	*Pinus* sp.	Mexico	M. de Jesús Yáñez-Morales & C. Méndez-Inocencio, 24 Oct. 2009	KF902022	JX901766	MF951509
Madagascaromyces intermedius	*Passalora intermedia*	**CBS 124154**^{T} = CPC 15745	*Eucalyptus camaldulensis*	Madagascar	M.J. Wingfield, Aug. 2007	FJ790297	FJ790267	MF951511
	Stenella sp.	CPC 15719	*Eucalyptus camaldulensis*	Madagascar	M.J. Wingfield, Oct. 2007	MF951170	FJ790251	MF951512
Microcyclosporella mali	–	CBS 125651 = RH1 = OH1 34D2a	*Malus* sp.	USA: Ohio	M. Ellis, 5 Sep. 2005	FJ031989	FJ425196	KX288442
	–	CBS 125653 = RH6 = MI3 20F1a	*Malus* sp.	USA: Michigan	G. Sundin, 1 Sep. 2005	FJ031994	FJ425201	KX288440
	–	CBS 126132 = CPC 16180	*Malus domestica*	Slovenia	J. Frank, 17 Oct. 2007	MF951171	MF951324	MF951513
	–	**CBS 126136**^{T} = CPC 16184	*Malus domestica*	Slovenia	J. Frank, 7 Aug. 2007	GU570547	GU570535	KX288436
Micronematomyces caribensis	*Passalora caribensis*	CBS 113374 = MJM 1545 = C481	*Chromolaena odorata*	Jamaica	M.J. Morris	MF951172	DQ676512	MF951514
	Passalora caribensis	CBS 113375 = MJM 1543 = C482	*Chromolaena odorata*	Jamaica	M.J. Morris	MF951173	DQ676513	MF951515
	Passalora caribensis	CBS 113376 = MJM 1539 = C487	*Chromolaena odorata*	Cuba	S. Neser, 28 Oct. 1997	MF951174	DQ676514	MF951516
	Passalora perfoliati	CBS 113378 = MJM 1552 = C494	*Chromolaena odorata*	Jamaica	M.J. Morris, 1 Nov. 1997	MF951178	DQ676520	MF951520
	Passalora perfoliati	CBS 113379 = MJM 1544 = C495	*Chromolaena odorata*	Jamaica	M.J. Morris, 30 Oct. 1997	MF951177	DQ676521	MF951519
	Passalora caribensis	**CBS 113380**^{T} = MJM 1550 = C498	*Chromolaena odorata*	Jamaica	M.J. Morris, 31 Oct. 1997	MF951175	DQ676515	MF951517
	Passalora caribensis	CBS 113381 = MJM 1549 = C500	*Chromolaena odorata*	Jamaica	M.J. Morris, 30 Oct. 1997	MF951176	DQ676516	MF951518

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
M. chromolaenae	*Septoria chromolaenae*	CBS 113371 = MJM 1490 = C450	*Chromolaena odorata*	Mexico	M.J. Morris, 12 Oct. 1997	MF951179	DQ676517	MF951521
	Septoria chromolaenae	**CBS 113611^{T}** = MJM 1498 = C452	*Chromolaena odorata*	Mexico	M.J. Morris, 12 Oct. 1997	MF951180	DQ676518	MF951522
Miuraea degenerans	*Miuraea degenerans*	**MAFF 239265^{ET}** = MUCC 1514	*Prunus mume*	Japan	T. Kobayashi, Sep. 2003	MF951181	MF951325	MF951523
M. persica	*Miuraea persica*	CBS 131935 = CPC 10828	*Prunus armeniaca*	Republic of Korea	H.D.. Shin, 7 Oct. 2003	JQ324939	GU269844	MF951524
Mycodiella sumatrensis	*Mycosphaerella sumatrensis*	CBS 118501 = CPC 11175	*Eucalyptus* sp.	Indonesia	M.J. Wingfield, Feb. 2004	JX901872	DQ303049	MF951525
Mycosphaerelloides madeirae	*Mycosphaerella madeirae*	**CBS 112895^{T}** = CPC 3745 = CMW 14458	*Eucalyptus globulus*	Portugal	S. Denman, Apr. 2000	KF902017	AY725553	KX348057
	Mycosphaerella madeirae	CBS 116066	*Quercus robur*	Netherlands	–	KX286989	AY853188	KX288444
	Mycosphaerella madeirae	CBS 116068	*Quercus robur*	Netherlands	–	KX286990	AY853189	KX288445
Mycovellosiella cajani	*Passalora* sp.	CBS 113998 = CPC 5335	*Cajanus cajan*	South Africa: Mpumalanga	L. van Jaarsveld, 17 May 2002	KF251819	KF251315	MF951527
	Passalora sp.	CBS 113999 = CPC 5339	*Cajanus cajan*	South Africa: Mpumalanga	L. van Jaarsveld, 17 May 2002	KF251820	KF251316	MF951528
	Passalora sp.	CBS 114275 = CPC 5334	*Cajanus cajan*	South Africa: Mpumalanga	L. van Jaarsveld, 17 May 2002	KF251821	KF251317	MF951529
	–	**CBS 142174^{NT}** = CPC 30580 = RWB 2071	*Cajanus cajan*	Brazil	R.W. Barreto, 2016	MF951182	MF951326	MF951526
Neoceratosperma cyatheae	*Passalora* sp.	CPC 18580	*Cyathea delgadii*	Brazil: Rio de Janeiro	R.W. Barreto, 11 Jul. 2009	KT037580	KT037539	MF951530
N. eucalypti	–	**CBS 137998^{T}** = CPC 23465	*Eucalyptus* sp.	Thailand	R. Cheewangkoon, Sep. 2013	KJ869210	KJ869153	MF951531
N. haldinae	*Passalora haldinae*	**CBS 142190^{T}** = CPC 19202	*Haldina cordifolia*	Laos	P. Pheng	MF951184	MF951328	MF951533
N. legnophoricola	*Stenella* sp.	**CBS 142189^{T}** = CPC 16411	*Legnephora moorei*	Australia: New South Wales	B. Summerell, Mar. 2009	MF951183	MF951327	MF951532

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
N. yunnanensis	*Xenomycosphaerella yunnanensis*	**CBS 119975^{T}** = CMW 23443 = MUCC 410 = PAB 05.05 B2	*Eucalyptus urophylla*	China	B. Dell, May 2005	KF901962	KF901628	MF951534
Neocercospora ammicola	–	**CBS 136450^{T}** = CCTU 1186	*Ammi majus*	Iran	M. Arzanlou, Sep. 2012	KR232405	KR232407	KX288446
Neocercosporidium smilacis	*Passalora smilacis*	CBS 556.71	*Smilax aspera*	Italy	W. Gams, 18 May 1971	KJ633269	KJ633265	MF951535
	Passalora sp.	**CBS 122888^{ET}**	*Smilax aspera*	Portugal	G. Verkley, 23 Jan. 2008	MF951185	MF951329	MF951536
	Passalora sp.	CBS 122889	*Smilax aspera*	Portugal	G. Verkley, 23 Jan. 2008	MF951186	MF951330	MF951537
	Passalora sp.	CBS 122890	*Smilax aspera*	Portugal	G. Verkley, 23 Jan. 2008	MF951187	MF951331	MF951538
	Passalora sp.	CBS 123352	*Smilax aspera*	Portugal	G. Verkley, 23 Jan. 2008	MF951188	MF951332	MF951539
	Passalora sp.	CBS 123353	*Smilax aspera*	Portugal	G. Verkley, 23 Jan. 2008	MF951189	MF951333	MF951540
	Passalora sp.	CPC 19342	*Smilax* sp.	Italy	W. Gams, 30 Apr. 2011	MF951190	MF951334	MF951541
Neodeightoniella phragmiticola	–	**CBS 136418^{T}** = CPC 22059	*Phragmites australis*	South Africa: Free State	W.J. Swart, 31 Jan. 2013	KF777224	KF777171	MF951543
	–	CPC 22057	*Phragmites australis*	South Africa: Free State	W.J. Swart, 31 Jan. 2013	KF777223	KF777170	MF951542
	–	CPC 22061	*Phragmites australis*	South Africa: Free State	W.J. Swart, 31 Jan. 2013	KF777225	KF777172	MF951544
Neomycosphaerella pseudopentameridis	–	**CBS 136407^{T}** = CPC 21126	*Pseudopentameris macrantha*	South Africa: Western Cape	P.W. Crous, 22 Jul. 2012	KF777226	KF777173	MF951545
Neopenidiella nectandrae	*Cladosporium ferrugineum*	**CBS 734.87^{T}** of *Cladosporium ferrugineum* = ATCC 200932 = INIFAT 87/45	*Nectandra coriacea*	Cuba	R.F. Castañeda & G. Arnold, 24 Jan. 1987	KF901982	MF951335	MF951546

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Neophloeospora maculans	*Phloeospora maculans*	CBS 115123	*Morus alba*	New Zealand	–	GU214670	GU214670	MF951547
Neopseudocercosporella brassicicola	*Mycosphaerella brassicicola*	CBS 163.26	–	–	–	MF951192	MF951337	MF951548
	Mycosphaerella brassicicola	CBS 228.32	*Brassica oleracea*	Denmark	–	KF251808	KF251304	KX348058
	Mycosphaerella brassicicola	CBS 267.53	*Brassica oleracea* var. *acephala* subvar. *sabelica*	Netherlands	–	KF251809	KF251305	KX348059
N. capsellae	*Pseudocercosporella capsellae*	CBS 112032 = HJS 601	*Brassica* sp.	–	–	KF251824	KF251320	KX348060
	Pseudocercosporella capsellae	CBS 112033 = HJS 600	*Brassica* sp.	–	–	KF251810	KF251306	KX348061
	Pseudocercosporella capsellae	CBS 118412	*Brassica* sp.	New Zealand	–	MF951193	MF951338	MF951549
	Pseudocercosporella capsellae	MAFF 237605 = MUCC 1254	*Brassica rapa* var. *oleifera*	Japan	K. Kishi,–	MF951194	MF951339	MF951550
Neoseptoria caricis	–	**CBS 135097^{T}** = S653	*Carex acutiformis*	Netherlands	W. Quaedvlieg, Aug. 2012	KF251663	KF251159	MF951551
Nothopassalora personata	*Mycosphaerella berkeleyii*	**CBS 222.38^{IT}** of *Mycosphaerella berkeleyii*	*Arachis hypogaea*	USA: Georgia	W.A. Jenkins, 23 Jun. 1937	MF951234	MF951373	MF951631
	Passalora sp.	**CBS 142236^{ET}** = CPC 19466	*Arachis hypogaea*	Australia: Northern Territory	P.W. Crous, 30 Apr. 2011	MF951235	MF951374	MF951632
Nothopericoniella persea-macranthae	*Periconiella persea-macranthae*	CBS 122097 = RoKi 2995	*Machilus zihoensis*	Taiwan	R. Kirschner & C.-J. Chen, 18 Mar. 2007	GU452682	MF951354	MF951583
	Periconiella persea-macranthae	CBS 122282 = RoKi 3030	Unidentified *Lauraceae*	Taiwan	R. Kirschner & C.-J. Chen, 1 Apr. 2007	GU452681	MF951355	MF951584
Nothophaeocryptopus gaeumannii	*Adelopus balsamicola* f. *douglasii*	CBS 244.38	–	Austria	–	MF951191	MF951336	GU357766

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	Adelopus gaeumannii	CBS 267.37	*Pseudotsuga menziesii*	Germany	–	EF114698	EU700365	GU357770
Pachyramichloridium pini	*Ramichloridium pini*	**CBS 461.82^{T}** = MUCL 28942	*Pinus contorta*	UK: Scotland	–	EU041859	EU041802	MF951552
Pallidocercospora acaciigena	*Mycosphaerella acaciigena*	**CBS 112515^{T}** = CPC 3837	*Acacia mangium*	Venezuela	M.J. Wingfield, May 2000	KF902166	KF901805	KX348062
P.crystallina	–	CBS 111045 = CPC 1179	*Eucalyptus grandis* litter	South Africa: KwaZulu-Natal	M.J. Wingfield, 22 Jun. 1995	KF442659	KF901704	KX348063
	Passalora sp.	CPC 14140	*Eucalyptus* sp.	China	X. Zhao, 1 Mar. 2007	MF951195	MF951340	MF951553
P. heimii	–	**CBS 110682^{T}** = CPC 760	*Eucalyptus* sp.	Madagascar	P.W. Crous, 16 Apr. 1994	GQ852604	KF901671	MF951554
	–	CPC 11716	–	Brazil	A.C. Alfenas, Jan. 2004	KF901937	KF901612	KX348064
P. heimioides	*Mycosphaerella heimioides*	**CBS 111190^{T}** of *Mycosphaerella heimioides* = CMW 3046 = CPC 1312	*Eucalyptus* sp.	Indonesia	M.J. Wingfield, 12 Mar. 1996	GQ852607	KF901659	MF951555
P. irregulariramosa	*Mycosphaerella irregulariramosa*	**CBS 111211^{T}** = CPC 1362	*Eucalyptus saligna*	South Africa: Northern Province	M.J. Wingfield, Mar. 1996	KF902053	KX287297	KX348065
P. konae	*Mycosphaerella konae*	**CBS 111028^{T}** = CPC 2125	*Leucadendron* cv. 'Safari Sunset'	USA: Hawaii	P.W. Crous & M.E. Palm, 17 Nov. 1998	KF902158	KF901798	KX348066
Pantospora guazumae	–	**CBS 130299^{ET}**	*Guazuma ulmifolia*	Mexico	J. Moore, 12 Feb. 2009	MF951196	JN190956	MF951556
Paracercospora egenula	–	CBS 485.81	–	India	–	MF951197	GU269699	MF951558
	–	CBS 132030 = CPC 12537	*Solanum melongena*	Republic of Korea	H.D.. Shin, 26 Oct. 2005	GU253738	GU269698	MF951557
Paracercosporidium microsorum	*Mycosphaerella microsora*	CBS 254.67	*Tilia tomentosa*	Romania	O. Constantinescu, 16 Jun. 1965	MF951198	MF951341	MF951559

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	Mycosphaerella microsora	CBS 552.71 = BUCM 2014	*Tilia platyphyllos*	Romania	O. Constantinescu, 8 Oct. 1969	MF951199	MF951342	MF951560
	Mycosphaerella microsora	CBS 100352	*Tilia cordata*	Netherlands	H.A. van der Aa, 19 Oct. 1997	EU167599	EU167599	MF951561
	Mycosphaerella microsora	CBS 101017	*Tilia cordata*	Netherlands	H.A. van der Aa, 1 Apr. 1998	MF951200	MF951343	MF951562
	Passalora microsora	CBS 123735	*Tilia* sp.	Czech Republic	G. Verkley, 16 Sep. 2008	KJ633266	KJ633262	MF951563
	Passalora microsora	**CBS 142176^{ET}** = CPC 15550	*Tilia cordata*	Ukraine	A. Akulov, 18 Jul. 2008	MF951201	MF951344	MF951564
P. tiliae	*Passalora* sp.	**CBS 112734^{ET}** = CPC 3952	*Tilia americana*	Canada	K.A. Seifert	MF951202	MF951345	MF951565
	Passalora sp.	CBS 115526 = CPC 3953	*Tilia americana*	Canada	K.A. Seifert	MF951203	MF951346	MF951566
Paramycosphaerella brachystegiae	–	**CBS 136436^{T}** = CPC 21136	*Brachystegia* sp.	Zimbabwe	J. Roux, 2 Apr. 2012	KF777230	KF777178	MF951567
P. intermedia	–	**CBS 114356^{T}** = NZFS 301.10 = CMW 7163 = CPC 10902	*Eucalyptus saligna*	New Zealand	L. Renney, 30 Jun. 1998	KF902026	KF901681	MF951569
	–	CBS 114415 = NZFS 301.13 = CMW 7164 = CPC 10922	*Eucalyptus saligna*	New Zealand	K. Dobbie, 12 Aug. 1998	KF902027	KF901682	MF951568
P. marksii	*Pseudocercospora epispermogonia*	CBS 110750 = CPC 822	*Eucalyptus grandis*	South Africa	G. Kemp, Oct. 1994	DQ303075	DQ267596	MF951573
	–	CBS 110963 = CPC 4632 = KS cl 42	*Musa* sp.	South Africa: Northern Province	K. Surridge	KF902054	KF901707	MF951570
	–	CBS 110964 = CPC 4633 = KS 41	*Musa* sp.	South Africa	K. Surridge	KF902055	KF901708	MF951571
	Mycosphaerella marksii	CBS 110920 = CPC 935	*Eucalyptus botryoides*	Australia: Victoria	A. Carnegie, 14 Oct. 1994	GU253694	GU269644	MF951572

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Paramycosphaerella sp. A	*Mycosphaerella colombiensis*	CBS 118825 = CMW 10904	*Musa* cv. Grand Naine	South Africa	K. Surridge	MF951204	MF951347	MF951574
	Mycosphaerella colombiensis	CBS 118849 = CMW 10902	*Musa* cv. Williams	South Africa	K. Surridge	MF951205	MF951348	MF951575
Paramycosphaerella sp. B	*Colletogloeum* sp.	CBS 118968 = CUF2d	*Malus* sp.	USA: Illinois	J. Batzer, Sep. 2000	MF951206	MF951349	MF951576
	Colletogloeum sp.	CBS 125300 = NY1 3.2F1c	*Malus* sp.	USA: New York	D. Rosenberger , 30 Oct. 2005	MF951207	MF951350	MF951577
P. wachendorfiae	*Mycosphaerella wachendorfiae*	**CBS 129579**^{T} = CPC 18338	*Wachendorfia thyrsifolia*	South Africa	K.L. Crous & P.W. Crous, 2 May 2010	JF951163	JF951143	MF951578
Paramycovellosiella passaloroides	*Mycovellosiella passaloroides*	CPC 10770	*Amorpha fruticosa*	Republic of Korea	H.D.. Shin, 23 Oct. 2002	MF951209	MF951352	MF951580
	Mycovellosiella passaloroides	CPC 14694	*Amorpha fruticosa*	Republic of Korea	H.D.. Shin, 30 Oct. 2007	MF951208	MF951351	MF951579
Parapallidocercospora colombiensis	*Mycosphaerella colombiensis*	**CBS 110968**^{T} = CPC 1105	*Eucalyptus urophylla*	Colombia	M.J. Wingfield, May 1995	KF901969	AY752148	MF951581
P. thailandica	*Pallidocercospora thailandica*	CBS 120723 = CPC 13478	*Eucalyptus calmadulensis*	Thailand	W. Himaman, Oct. 2006	KF442667	MF951353	MF951582
Passalora bacilligera	–	**CBS 131547**^{ET} = CPC 19944	*Alnus glutinosa*	Poland	D. Karasinski, 20 Sep. 2011	MF951210	MF951356	MF951585
Phaeocercospora colophospermi	–	**CBS 132687**^{T} = CPC 19812	*Colophospermum mopane*	South Africa: Mpumalanga	P.W. Crous, 11 Jul. 2011	JX069854	JX069870	MF951586
P. juniperina	*Passalora juniperina*	CBS 142238 = CPC 11258	*Juniperus virginiana*	USA: North Carolina	C.S. Hodges, 1 Mar. 2004	MF951211	GU214667	MF951587
Phaeophloeospora eugeniae	–	CBS 142184 = CPC 15143	*Eugenia uniflora*	Brazil	A.C. Alfenas, 1 Mar. 2008	FJ493206	FJ493188	MF951594
	–	CPC 15159	*Eugenia uniflora*	Brazil	A.C. Alfenas, 1 Apr. 2008	FJ493207	FJ493189	MF951595
Phaeoramularia capsicicola	–	CBS 156.62	*Capsicum annuum*	Italy	–	KJ633267	KJ633263	–
	Passalora sp.	CBS 113382 = C460	*Chromolaena odorata*	USA	M.J. Morris	MF951213	DQ676522	MF951596

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	Passalora sp.	CBS 113384 = C499	*Chromolaena odorata*	Jamaica	M.J. Morris	MF951214	DQ676524	MF951597
P. gomphrenicola	*Phaeoramularia gomphrenicola*	**CBS 142182^{ET}** = CPC 23248 = COAD 570	*Pfaffia glomerata*	Brazil	R. Barreto, 29 Oct. 2012	MF951216	MF951359	MF951599
	Phaeoramularia gomphrenicola	CPC 23249 = COAD571	*Pfaffia glomerata*	Brazil	R. Barreto	MF951215	MF951358	MF951598
Phloeospora ulmi	–	CBS 613.81	*Ulmus* sp.	Austria	H.A. van der Aa, 21 Sep. 1981	GU253842	GU269825	MF951601
	–	CBS 101564	*Ulmus* sp.	Netherlands	H.A. van der Aa, 26 Aug. 1998	KF251703	KF251200	MF951602
	–	CBS 109835	*Ulmus* sp.	Netherlands	G. Verkley, 27 Aug. 2001	KF251704	KF251201	MF951600
Pleopassalora perplexa	*Passalora perplexa*	**CBS 116363^{T}** = CPC 11147	*Acacia crassicarpa*	Indonesia	M.J. Wingfield, Feb. 2004	MF951220	AY752162	MF951606
	Passalora perplexa	CBS 116364 = CPC 11150	*Acacia crassicarpa*	Indonesia	M.J. Wingfield, Feb. 2004	GU214459	AY752163	MF951607
	Passalora acaciae	CPC 11152	*Acacia crassicarpa*	Indonesia	M.J. Wingfield, 1 Mar. 2004	MF951217	MF951360	MF951603
	Passalora perplexa	CPC 12168	*Acacia* sp.	Indonesia	M.J. Wingfield, 1 May 2005	MF951218	MF951361	MF951604
	Passalora perplexa	CPC 12170	*Acacia* sp.	Indonesia	M.J. Wingfield, 1 May 2005	MF951219	MF951362	MF951605
"Passalora" sp. 1	*Passalora loranthicola*	CBS 122466 = X138	*Citrus* sp.	USA: Florida	R. C. Ploetz	MF951221	EU514280	MF951608
Pleuropassalora armatae	*Passalora armatae*	**CBS 125420^{T}** = CPC 15419	*Dalbergia armata*	South Africa: KwaZulu-Natal	A.R Wood, 28 May 2008	GU214456	GU214640	MF951609
	Passalora sp.	CPC 15420	*Dalbergia armata*	South Africa	A.R Wood, 28 May 2008	MF951222	MF951363	MF951610
	Passalora sp.	CPC 17084	*Dalbergia obovata*	South Africa	A.R. Wood, 15 Jun. 2009	MF951223	MF951364	MF951611
Pluripassalora bougainvilleae	*Passalora* sp.	CBS 142237 = CPC 19327	*Bougainvillea* sp.	Australia: Northern Territory	P.W. Crous, 30 Apr. 2011	MF951224	MF951365	MF951612

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Polyphialoseptoria tabebuiae-serratifolia	–	**CBS 112650^{T}** = CPC 3944	*Tabebuia serratifolia*	Brazil	A.C. Alfenas, 1999	KF251716	KF251213	MF951613
P. terminaliae	–	**CBS 135106^{T}** = CPC 19611	*Terminalia catappa*	Brazil	R.W. Barreto, 18 May 2010	KF251717	KF251214	MF951615
	–	CBS 135475 = CPC 19487	*Terminalia catappa*	Brazil	R.W. Barreto, 18 May 2010	KF251718	KF251215	MF951614
Pseudocercospora catappae	–	MAFF 238312 = MUCC 1109	*Terminalia catappa*	Japan	T. Kobayashi & C. Nakashima, 18 Nov. 1999	MF951225	MF951366	MF951616
P. dingleyae	*Pseudocercosporella dingleyae*	**CBS 114645^{T}**	*Haloragis erecta*	New Zealand	C.F. Hill, 21 Jan. 2001	KX286997	KX287299	KX288454
P. convoluta	*Passalora convoluta*	**CBS 113377^{T}** = MJM 1533 = C488	*Chromolaena odorata*	Costa Rica	M.J. Morris, 15 Oct. 1997	MF951226	DQ676519	MF951617
P. cratevicola	*Prathigada cratevicola*	MUCC 1088	*Crataeva falcata*	Japan	S. Uematsu & C. Nakashima, –	MF951233	MF951372	–
P. eucalyptorum	–	**CBS 114866^{T}** = CPC 11	*Eucalyptus nitens*	South Africa: Western Cape	P.W. Crous, Aug. 1988	JQ739817	KF901720	MF951618
P. flavomarginata	–	CBS 124990 = CPC 13492	*Eucalyptus camaldulensis*	Thailand	W. Himaman, Oct. 2006	GU253817	GU269799	MF951619
P. fori	–	CBS 113286 = CMW 9096 = BOT 1290	*Eucalyptus* sp.	South Africa	J. Roux	KF902068	KF901721	KX348072
P. macadamiae	–	**CBS 133432^{ET}**	*Macadamia integrifolia*	Australia: Queensland	O.A. Akinsanmi, 12 Nov. 2011	KX286998	KX287300	KX288455
P. metrosideri	*Pseudocercosporella metrosideri*	CBS 114294	*Metrosideros excelsa*	New Zealand	C.F. Hill, 17 Oct. 2003	KX286999	KX287301	KX288456
P. nodosa	*Passalora nodosa*	**CBS 554.71^{T}**	*Psoralea bituminosa*	Romania	O. Constantinescu, 23 Sep. 1966	MF951227	MF951367	MF951620
P. norchiensis	*Pseudocercospora schizolobii*	**CBS 120738^{T}** = CPC 13049	*Eucalyptus* sp.	Italy	W. Gams, Apr. 2005	GU253780	GU269753	KX348073
P. pistacina	*Pseudocercospora pistacina*	CPC 23118	*Pistacia vera*	Turkey	K. Sarpkaya, 2010	KF442674	KF442647	KX348074

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
P. prunicola	–	CBS 132107 = CPC 14511	*Prunus yedoensis*	Republic of Korea	H.D.. Shin, 2 Oct. 2007	GU253723	GU269676	MF951621
P. punctata	–	CBS 132116 = CPC 14734	*Syzygium* sp.	Madagascar	P.W. Crous, 1 Oct. 2007	GU253791	GU269765	MF951622
P. robusta	–	**CBS 111175^{T}** = CPC 1269 = CMW 5151	*Eucalyptus robusta*	Malaysia	M.J. Wingfield, May 1995	KF442539	DQ303081	MF951623
P. sambucigena	–	**CBS 126000^{ET}** = CPC 14397	*Sambucus nigra*	Netherlands	P.W. Crous, 29 Aug. 2007	GU253823	GU269805	MF951624
Pseudocercospora sp. A	*Passalora robiniae*	CBS 277.39	*Robinia pseudoacacia*	USA	–	MF951230	MF951369	MF951627
Pseudocercospora sp. B	*Tandonella cubensis*	CBS 500.92 = INIFAT C92/43-3	*Bauhinia cumanensis*	Cuba	R.F. Castañeda	MF951232	MF951371	MF951629
Pseudocercospora sp. C	*Passalora bolleana*	CBS 541.71 = IMI 161111	*Ficus carica*	Romania	O. Constantinescu	MF951229	MF951368	MF951626
	Passalora sp.	CPC 14819	*Ficus carica*	Republic of Korea	H.D.. Shin, 14 Nov. 2007	MF951231	MF951370	MF951628
Pseudocercospora sp. D	–	CBS 113386 = MJM 1511 = C469	*Chromolaena odorata*	Guatemala	M.J. Morris	MF951228	DQ676532	MF951625
Pseudocercospora sp. E	*Cercosporella* sp.	CPC 19537	*Eichhornia azurea*	Brazil	D.J. Soares, 30 Apr. 2005	KX287003	KX287304	KX288460
P. vitis	–	CBS 132012 = CPC 11595	*Vitis vinifera*	Republic of Korea	H.D.. Shin, 30 Sep. 2004	GU214483	GU269829	KX348076
P. zambiae	*Neopseudocercospora terminaliae*	**CBS 136423^{T}** = CPC 22686	*Terminalia* sp.	Zambia	M. van der Bank, 24 Feb. 2013	KF777228	KF777175	MF951630
Pseudocercosporella bakeri	–	CBS 119488	*Ipomoea indica*	New Zealand	C.F. Hill	KX287005	KX287306	KX288462
	–	**CBS 125685^{ET}** = CPC 17570	*Ipomoea aquatica*	Laos	P. Phengsintham, 8 Sep. 2009	KX287005	KX287306	KX288462
Pseudopericoniella levispora	*Periconiella levispora*	**CBS 873.73^{T}**	*Turpinia pomifera*	Sri Lanka	W. Gams, Jan. 1973	EU041837	EU041780	MF951633
Pseudopericoniella sp.	*Mycosphaerella rosigena*	CBS 330.51	*Rosa* sp.	Netherlands	–	GU214413	GU214632	MF951634
Pseudophaeophleospora atkinsonii	*Phaeophleospora atkinsonii*	CBS 124565 = ICMP 17860	*Hebe* sp.	New Zealand	–	MF951236	GU214643	MF951635

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
P. stonei	*Phaeophleospora stonei*	**CBS 120830^T** = CPC 13330	*Eucalyptus* sp.	Australia: Queensland	P.W. Crous & J. Stone, 19 Aug. 2006	FJ493210	EF394856	MF951636
Pseudozasmidium eucalypti	*Zasmidium eucalypti*	**CBS 121101^T** = CPC 13302	*Eucalyptus tereticornis*	Australia: Queensland	P.W. Crous, 26 Aug. 2006	KF901931	KF901606	MF951637
P. nabiacense	*Zasmidium nabiacense*	**CBS 125010^T** = CPC 12748	*Eucalyptus* sp.	Australia	A.J. Carnegie, 30 Nov. 2005	KF901933	GQ852841	MF951638
P. parkii	*Zasmidium parkii*	**CBS 387.92^T** = CPC 353	*Eucalyptus grandis*	Brazil	M.J. Wingfield, 24 Feb. 1990	GU214448	KF901785	–
P. vietnamense	*Paramycosphaerella vietnamensis*	**CBS 119974^T** = CMW 23441 = MUCC 66 = VTN1	*Eucalyptus grandis*	Vietnam	T.I. Burgess, 6 Jul. 2004	JF700944	DQ632675	MF951639
Ragnhildiana ampelopsidis	*Passalora ampelopsis*	CBS 249.67 = IMI 124968	*Parthenocissus tricuspidata*	Romania	–	MF951238	AY293063	MF951641
R. diffusa	*Sirosporium diffusum*	CBS 106.14	*Carya illinoinensis*	USA: Georgia	–, 29 Aug. 1911	MF951239	MF951375	MF951642
R. ferruginea	*Passalora ferruginea*	CBS 255.67 = IMI 124973	*Artemisia vulgaris*	Romania	–	MF951241	MF951377	MF951644
	Passalora ferruginea	CBS 546.71	*Artemisia vulgaris*	Romania	–	MF951242	MF951378	MF951645
	Mycovellosiella ferruginea	CPC 10075	*Artemisia sylvatica*	Republic of Korea	H.D.. Shin, 23 Oct. 2002	MF951240	MF951376	MF951643
R. gnaphaliaceae	*Passalora gnaphaliaceae*	CBS 142181 = CPC 12517	*Gnaphalium affine*	Republic of Korea	H.D.. Shin, May 2005	MF951243	MF951379	MF951646
R. perfoliati	*Passalora* sp.	CBS 113613 = MJM 1506 = C486	*Ageratina adenophora*	Guatemala	M.J. Morris	MF951246	DQ676525	MF951650
	Passalora assamensis	CBS 115119	–	New Zealand	–	MF951244	MF951380	MF951648
	Passalora ageratinae	**CBS 125419^T** = CPC 15365	*Ageratina adenophora*	South Africa: KwaZulu-Natal	A.R Wood, 28 May 2008	GU214453	GU214639	MF951647
	Passalora perfoliata	CBS 142180 = CPC 17321	*Chromolaena* sp.	Laos	P. Pheng, 17 Jun. 2006	MF951245	MF951381	MF951649
	Phaeoramularia sp.	CPC 15366	*Ageratina adenophora*	South Africa: KwaZulu-Natal	A.R Wood, 28 May 2008	MF951247	MF951382	MF951651

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
R. pseudotithoniae	*Passalora pseudotithoniae*	**CBS 136442**^{T} = CPC 21688	*Tithonia diversifolia*	Thailand	P.W. Crous, 5 Nov. 2012	KF777231	KF777179	MF951652
Ramularia carneola	–	CBS 108975	*Scrophularia nodosa*	Netherlands	G. Verkley, 22 Jun. 2000	KX287048	KX287348	KX288507
R. cynarae	–	**CBS 128912**^{T} = CPC 18426	*Cynara cardunculus*	USA: California	S.T Koike, 10 Aug. 2010	KX287096	HQ728117	KX288554
R. endophylla	*Mycosphaerella punctiformis*	**CBS 113265**^{ET}	*Quercus robur*	Netherlands	G. Verkley, Apr. 2003	AY490776	AY490763	KP894673
R. hydrangeae-macrophyllae	–	**CBS 122273**^{T}	*Hydrangea macrophylla*	New Zealand	C.F. Hill, 2 Jul. 2007	KX287135	KX287433	KX288592
R. nyssicola	–	**CBS 127665**^{ET} = AR 4656 = DM 2	*Nyssa ogeche* × *sylvatica*	USA: Maryland	R. Olsen, 18 Jun. 2009	KJ504724	KJ504765	KJ504636
R. plurivora	–	**CBS 118743**^{T} = CPC 12207	Human bone marrow	Netherlands	–	KJ504739	KJ504780	KJ504651
R. pusilla	–	**CBS 124973**^{ET} = RoKi 3143	*Poa annua*	Germany	R. Kirschner, 25 Feb. 2008	KP894141	KP894248	KP894687
R. stellariicola	*Pseudocercosporella stellariicola*	**CBS 130592**^{T} = CPC 11297 = KACC 42363	*Stellaria aquatica*	Republic of Korea	H.D.. Shin & M.J. Park, 3 May 2006	GU214693	GU214693	KX288675
R. stellenboschensis	–	**CBS 130600**^{T} = CPC 18294	*Protea* sp.	South Africa	P.W. Crous, 6 May 2010	JN712566	JN712499	KX288676
Ramulariopsis gossypii	–	**CBS 141099**^{ET} = CPC 25909 = X30	*Gossypium* sp.	Brazil	–	KX287243	KX287540	KX288702
R. pseudoglycines	–	**CBS 141100**^{T} = CPC 18242	*Gossypium* sp.	Brazil	–, 2000	KX287246	KX287543	KX288705
	–	CPC 18241	*Gossypium* sp.	Brazil	–	KX287245	KX287542	KX288704
	–	CPC 20036	*Gossypium barbadense*	Togo	M. Piatek	KX287244	KX287541	KX288703
Ramulispora sorghi	*Cercospora sorghi*	CBS 110578 = CPC 905	*Sorghum bicolor*	South Africa: KwaZulu-Natal	D. Nowell, Mar. 1995	GQ852653	MF951383	MF951653
	Cercospora sorghi	CBS 111032 = CPC 899 = IMI 153076	*Sorghum bicolor*	South Africa: KwaZulu-Natal	D. Nowell, Mar. 1995	MF951248	MF951384	MF951654

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	Cercospora sorghi	CBS 115522 = CPC 902	*Sorghum bicolor*	South Africa: KwaZulu-Natal	D. Nowell, Mar. 1995	MF951249	MF951385	MF951655
R. sorghiphila	*Ramulispora sorghi*	**CBS 255.82^{T}** = IMI 153077	–	India	–, Oct. 1969	MF951250	MF951386	MF951656
Rhachisphaerella mozambica	*Mycosphaerella mozambica*	**CBS 122464^{T}** = X34	*Musa acuminata*	Mozambique	A. Viljoen, 2003	MF951237	EU514257	MF951640
Rosisphaerella rosicola	*Passalora rosicola*	CBS 138.35 = ATCC 52313	–	USA	–	MF951252	MF951388	MF951658
	Passalora rosicola	CBS 142183 = CPC 12548	*Rosa hybrid*	USA: North Carolina	C.S. Hodges, 2005	MF951251	MF951387	MF951657
Ruptoseptoria unedonis	*Ruptoseptoria unedonis*	CBS 755.70	*Arbutus unedo*	Croatia	J.A. von Arx, Jul. 1970	KF251732	KF251229	MF951659
Scolecostigmina mangiferae	*Scolecostigmina mangiferae*	**CBS 125467^{NT}** = CPC 17351	*Mangifera indica*	Australia	P.W. Crous & R.G. Shivas, 10 Aug. 2009	GU253877	GU269870	MF951660
Septoria chrysanthemella	–	CBS 128617 = KACC 43086 = SMKC 22860	*Chrysanthemum morifolium*	Republic of Korea	–	KF251882	KF251378	MF951661
S. cucurbitacearum	–	CBS 178.77	*Cucurbita maxima*	New Zealand	–	KF251903	KF251399	MF951662
S. lycopersici	–	CBS 128654 = KACC 42519 = SMKC 22002	*Lycopersicon esculentum*	Republic of Korea	–	KF251966	KF251462	KX348091
S. protearum	–	CBS 135477 = CPC 19675	*Zantedeschia aethiopica*	South Africa: Mpumalanga	P.W. Crous, 15 Jul. 2011	KF252029	KF251524	MF951663
	–	CPC 19691	*Zantedeschia aethiopica*	South Africa	P.W. Crous, 15 Jul. 2011	KF252030	KF251525	MF951664
Septoria sp. A	–	CBS 135472 = CPC 19304	*Vigna unguiculata* subsp. *sesquipedalis*	Austria	P.W. Crous, Apr. 2011	KF252063	KF251558	MF951665
Septoria sp. B	–	CBS 135474 = CPC 19485	*Conyza canadensis*	Brazil	R.W. Barreto	KF252064	KF251559	MF951666
Septoria sp. C	–	CBS 135479 = CPC 19793	*Syzygium cordatum*	South Africa	P.W. Crous, 16 Jul. 2011	KF252066	KF251561	MF951667

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
S. urticae	–	**CBS 102375[ET]**	*Urtica dioica*	Netherlands	H.A. van der Aa & G. Verkley, 14 Oct. 1999	JN940675	KF251583	MF951668
"Sirosporium" celtidis	–	CBS 158.25	*Celtis australis*	Algeria	C. Killian, Nov. 1923	MF951253	MF951389	MF951669
	–	CBS 238.48	–	Portugal	–	MF951254	MF951390	MF951670
	–	CBS 289.50	*Celtis australis*	Italy	V. Mezzetti, Aug. 1949	MF951255	MF951391	MF951671
Sonderhenia eucalypticola	–	CBS 112502 = CPC 3749	*Eucalyptus* sp.	Portugal: Madeira	–	KF902019	KF901677	MF951672
S. eucalyptorum	*Mycosphaerella swartii*	CBS 120220	*Eucalyptus coccifera*	Australia: Tasmania	C. Mohammed, Jan. 2006	DQ923536	DQ923536	MF951673
Sphaerulina aceris	*Sphaerulina aceris*	CBS 652.85	*Acer pseudoplatanus*	Netherlands	H.A. van der Aa, 23 Jul. 1985	MF951258	MF951394	MF951676
S. berberidis	*Mycosphaerella berberidis*	CBS 324.52	*Berberis vulgaris*	Switzerland	E. Müller, 2 Jun. 1951	KF252106	KF251601	KX348093
S. betulae	–	CBS 128597 = KACC 43119 = SMKC 23059	*Betula schmidtii*	Republic of Korea	–	KF252109	KF251604	KX348094
S. chaenomelis	*Pseudocercosporella chaenomelis*	CBS 131897 = CPC 14795	*Chaenomeles speciosa*	Republic of Korea	H.D.. Shin, 14 Nov. 2007	GU253834	GU269817	KX288706
	Pseudocercosporella chaenomelis	**CBS 132131[ET]** of *Pseudocercosporella chaenomelis* = MUCC 1510	*Chaenomeles sinensis*	Japan	C. Nakashima, 29 Oct 2011	MF951259	JQ793663	MF951677
S. gei	–	CBS 128632 = KACC 44051 = SMKC 23686	*Geum japonicum*	Republic of Korea	–	KF252120	KF251615	KX348095
S. koreana	*Sphaerulina viciae*	**CBS 131898[T]** of *Sphaerulina viciae* = CPC 11415	*Vicia amurensis*	Republic of Korea	H.D.. Shin	KF252144	KF251639	KX348096
	Pseudocercosporella koreana	**CBS 135462[T]** of *Pseudocercosporella koreana* = CPC 11414	*Vicia amurensis*	Republic of Korea	H.D.. Shin	GU214683	GU269852	KX288707
S. populicola	–	CBS 100042	*Populus trichocarpa*	USA: Washington	–	KF252131	KF251626	MF951678
S. quercicola	–	CBS 115016	*Quercus robur*	Netherlands	–	KF252133	KF251628	MF951679

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
S. tirolensis	–	**CBS 109018^T**	*Rubus idaeus*	Austria	G. Verkley	KF252143	KF251638	MF951680
"Mycosphaerella" grossulariae	*Mycosphaerella grossulariae*	CBS 235.37	*Ribes nigrum*	Netherlands	M.S.J. Ledeboer	MF951256	MF951392	MF951674
"Mycosphaerella" harthensis	*Mycosphaerella harthensis*	CBS 325.52	*Betula* sp.	Switzerland	–	MF951257	MF951393	MF951675
Stromatoseptoria castaneicola	–	CBS 102322	*Castanea sativa*	Netherlands	G. Verkley, 29 Aug. 1999	KF251774	KF251271	MF951681
	–	CBS 102377	*Castanea sativa*	Netherlands	G. Verkley, 9 Sep. 1999	KF251775	KF251272	MF951682
Sultanimyces vitiphyllus	*Asperisporium vitiphyllum*	CBS 206.48	*Vitis* sp.	South Africa	S.J. du Plessis, 1948	MF951260	MF951395	MF951683
Trochophora fasciculata	*Trocophora simplex*	CBS 124744 = SMKC 21713	*Daphniphyllum macropodum*	Republic of Korea	H.D.. Shin, 29 Oct. 2005	GU253880	GU269872	MF951684
Uwemyces elaeidis	–	CPUwZC-01	*Elaeis oleifera*	Colombia	G.A. Sarria, May 2013	KX228356	KX22829	KX228371
Virosphaerella irregularis	*Mycosphaerella irregulari*	**CBS 123242^T** = CPC 15408	*Eucalyptus* sp.	Thailand	R. Cheewangkoon, Jul. 2007	KF901769	KF902126	MF951685
V. pseudomarksii	*Mycosphaerella pseudomarksii*	**CBS 123241^T** = CPC 15410	*Eucalyptus* sp.	Thailand	R. Cheewangkoon, Jun. 2007	KF902127	KF901770	MF951686
Xenomycosphaerella elongata	–	**CBS 120735^T** = CPC 13378	*Eucalyptus calmadulensis* × *urophylla*	Venezuela	M.J. Wingfield, Oct. 2006	JF700942	EF394833	MF951687
Xenoramularia arxii		**CBS 342.49^T**	*Acorus calamus*	Netherlands	J.A. von Arx, 5 Sep. 1949	KX287258	KX287552	KX288720
X. neerlandica	–	CBS 113615	*Sparganium ramosum*	Netherlands	–	KX287259	KX287553	KX288721
	–	**CBS 141101^T** = CPC 18377	*Iris pseudacorus*	Netherlands	P.W. Crous, 26 Jun. 2010	KX287260	KX287554	KX288722
X. polygonicola	–	**CBS 141102^T** = CPC 10852	*Polygonum* sp.	Republic of Korea	H.D.. Shin, 20 Sep. 2003	GU214695	GU214695	KX288723

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
	–	CPC 10853	*Polygonum* sp.	Republic of Korea	H.D.. Shin, 20 Sep. 2003	KX287262	KX287555	KX288724
Xenosonderhenia eucalypti	–	**CBS 138858^{T}** = CPC 24247	*Eucalyptus urophylla*	Mozambique	M.J. Wingfield, 2 Feb. 2014	KP004485	KP004457	MF951688
Xenosonderhenioides indonesiana	*Passalora* sp.	**CBS 142239^{T}** = CPC 15066	*Eucalyptus* sp.	Indonesia	M.J. Wingfield, 26 Mar. 2008	MF951261	MF951396	MF951689
Zasmidium angulare	–	**CBS 132094^{T}** = CPC 19042 = GA2 27B1a	*Malus domestica*	USA: Georgia	M. Wheeler, Aug. 2005	JQ622096	JQ622088	MF951690
Z. anthuriicola	–	**CBS 118742^{T}**	*Anthurium* sp.	Thailand	C.F. Hill, 3 Aug. 2005	FJ839662	FJ839626	MF951691
Z. arcuatum	*Periconiella arcuata*	**CBS 113477^{T}**	*Ischyrolepsis subverticillata*	South Africa: Western Cape	S. Lee, 1 May 2001	EU041836	EU041779	MF951692
Z. aucklandicum	*Stenella aucklandica*	CPC 13569	*Geniostoma rupestre*	New Zealand	C.F. Hill, 15 Oct. 2005	MF951280	MF951409	MF951733
Z. biverticillatum	*Ramichloridium biverticillatum*	CBS 335.36	*Musa sapientum*	–	–	EU041853	EU041796	–
Z. cellare	–	**CBS 146.36^{NT}** = ATCC 36951 = IFO 4862 = IMI 044943 = LCP 52.402 = LSHB BB274 = MUCL 10089	Wall in wine cellar	–	–	EU041878	EU041821	MF951693
	–	CBS 892.85	Wall in wine cellar	Germany	M. Schlag, Aug. 1985	MF951262	MF951397	KT356875
Z. cerophillum	*Ramichloridium cerophilum*	**CBS 103.59^{T}** of *Acrotheca cerophila* = MUCL 10034	*Sasa* sp.	Japan	–, May 1955	GU214485	EU041798	MF951694
Z. citri-griseum	–	CBS 122455 = CPC 15289 = X126	*Citrus* sp.	USA: Florida	R.C. Ploetz, 2003	KF902151	KF901792	MF951695
	–	CPC 13467	*Eucalyptus* sp.	Thailand	W. Himaman, 2006	KF251729	KF251226	MF951697
	–	CPC 15291	*Citrus* sp.	USA: Florida	R.C. Ploetz, 2003	KF902152	KF901793	MF951696
Z. daviesiae	*Verrucisporota daviesiae*	CBS 116002 = VPRI 31767	*Daviesia latifolia*	Australia: Victoria	V. & R. Beilharz, 30 Dec. 2003	FJ839669	FJ839633	MF951698

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Z. elaeocarpi	*Stenella* sp.	**CBS 142187**^{T} = CPC 16642	*Elaeocarpus kirtonii*	Australia: New South Wales	B. Summerell, 1 Mar. 2009	MF951263	MF951398	MF951699
	Stenella sp.	CPC 16640	*Elaeocarpus kirtonii*	Australia: New South Wales	B. Summerell, 1 Mar. 2009	MF951264	MF951399	MF951700
Z. eucalypticola	*Stenella* sp.	**CBS 142186**^{T} = CPC 15149	*Eucalyptus* sp.	Brazil	A.C. Alfenas, 1 Mar. 2008	MF951265	MF951400	MF951701
Z. eucalyptorum	–	**CBS 118500**^{T} = CPC 11174	*Eucalyptus urophylla*	Indonesia: Sumatra	M.J. Wingfield, Mar. 2004	MF951266	KF901652	MF951702
Z. fructicola	–	**CBS 139625**^{T} = CPC 24487 = ZJUM 80	*Citrus reticulata*	China	X.H. Wang, Jan. 2010	KP895922	KP896052	MF951703
Z. fructigenum	–	**CBS 139626**^{T} = CPC 24471 = ZJUM 36	*Citrus paradisi* × *Citrus* sp.	China	L. Zhu, Nov. 2009	KP895926	KP896056	MF951704
Z. grevilleae	*Verrucisporota grevilleae*	**CBS 124107**^{T} = CPC 14761	*Grevillea decurrens*	Australia: Northern Territory	B. Summerell, 22 Sep. 2007	FJ839670	FJ839634	MF951705
Z. gupoyu	*Parastenella gupoyu*	CBS 122099 = RoKi 3022	*Alocasia odora*	Taiwan	R. Kirschner & C.-J. Chen, 31 Mar. 2007	MF951267	MF951401	MF951706
Z. hakeae	*Stenella* sp.	**CBS 142185**^{T} = CPC 15577	*Hakea undulata*	Australia: Western Australia	A.R. Wood, 2 Aug. 2008	MF951268	MF951402	MF951707
	Stenella sp.	CPC 15583	*Hakea undulata*	Australia: Western Australia	A.R. Wood, 2 Aug. 2008	MF951269	MF951403	MF951708
	Stenella sp.	CPC 17213	Leaves in shop (Loma tea)	Australia: Queensland	P.W. Crous, 13 Jul. 2009	MF951270	MF951404	MF951709
Z. indonesianum	–	**CBS 139627**^{T} = CPC 15300	*Citrus* sp.	Indonesia	M. Arzanlou, 2004	KF902086	KF901739	MF951710
Z. iteae	*Stenella iteae*	**CBS 113094**^{T} = RoKi 1279	*Itea parvifolia*	Taiwan	R. Kirschner & C.-J. Chen, 2 Jun. 2002	MF951271	MF951405	MF951711

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Z. lonicericola	–	**CBS 125008**^{ET} of *Cladosporium lonicericola* = CPC 11671	*Lonicera japonica*	Republic of Korea	H.D.. Shin, 30 Oct. 2004	KF251787	KF251283	MF951712
Z. musae	*Stenella musae*	CBS 121384 = CIRAD 41 = X877	*Musa* sp.	France: Martinique	–	MF951272	EU514292	MF951713
	Stenella musae	CBS 122476 = X47	*Musa* sp.	Netherlands Antilles: Windward Islands	E. Reid, 2003	MF951273	EU514288	MF951714
	Stenella musae	CBS 122478 = X70	*Musa* sp.	Netherlands Antilles: Windward Islands	E. Reid, 2003	MF951274	EU514290	MF951715
Z. musae-banksii	*Ramichloridium australiensis*	**CBS 121710**^{T} = X1100	*Musa banksii*	Australia: Queensland	P.W. Crous & B. Summerell, Aug. 2006	EU041852	EU041795	MF951716
Z. musicola	*Stenella musicola*	**CBS 122479**^{T} = X1019	*Musa* cv. Grand Nain	India	I.W. Buddenhagen, 23 Feb. 2005	MF951275	EU514294	MF951717
Z. musigenum	*Ramichloridium musae*	CBS 190.63 = MUCL 9557	*Musa sapientum*	–	–	EU041857	EU041800	MF951718
Z. nocoxi	–	**CBS 125009**^{T} = CPC 14044	Twig debris of unknown host	USA: Virginia	P.W. Crous, 14 May 2007	KF251788	KF251284	MF951719
Z. pitospori	*Stenella pittospori*	CBS 122274 = ICMP 17098	*Pittosporum tenuifolium*	New Zealand	C.F. Hill, 15 Jul. 2007	MF951276	MF951406	MF951720
Z. proteacearum	*Verrucisporota proteacearum*	CBS 116003 = VPRI 31812	*Grevillea* sp.	Australia: Queensland	J.L. Alcorn, 3 Feb. 2004	FJ839671	FJ839635	MF951721
Z. pseudoparkii	–	CBS 110988 = CPC 1090	*Eucalyptus grandis*	Colombia	M.J. Wingfield, May 1995	KF901975	DQ303021	MF951722
	–	**CBS 110999**^{T} = CPC 1087	*Eucalyptus* sp.	Colombia	M.J. Wingfield, 1995	JF700965	DQ303023	MF951723
Z. pseudotsugae	*Rasutoria pseudotsugae*	rapssd	*Pseudotsuga menziesii*	USA: Oregon	–	EF114704	EF114687	–

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Z. pseudovespa	*Mycosphaerella pseudovespa*	**CBS 121159^{T}** = AC0466	*Eucalyptus biturbinata*	Australia: New South Wales	A.J. Carnegie, 14 Apr. 2005	KF901836	MF951407	MF951724
Z. queenslandicum	*Stenella queenslandica*	**CBS 122475^{T}** = X1084	*Musa banksii*	Australia: Queensland	P.W. Crous, 1 Aug. 2006	MF951277	EU514295	MF951725
Z. scaevolicola	–	**CBS 127009^{T}** = CPC 17344	*Scaevola taccada*	Australia: Queensland	R.G. Shivas & P.W. Crous, 8 Aug. 2009	KF251789	KF251285	MF951726
Z. schini	*Stenella* sp.	**CBS 142188^{T}** = CPC 19516	*Schinus terebinthifolius*	Brazil	A.B.V. Faria, 1 Sep. 2005	MF951278	MF951408	MF951727
Zasmidium sp.	*Mycosphaerella* sp.	CBS 118494 = CPC 11004	*Eucalyptus* sp.	Colombia	M.J. Wingfield, 2004	MF951279	DQ303039	MF951728
Z. strelitziae	*Ramichloridium strelitziae*	**CBS 121711^{T}** = X1029	*Strelitzia* sp.	South Africa: KwaZulu-Natal	W. Gams & H. Glen, 5 Feb. 2005	EU041860	EU041803	MF951729
Z. syzygii	–	**CBS 133580^{T}** = CPC 19792	*Syzigium cordatum*	South Africa: Mpumalanga	P.W. Crous, M.K. Crous, M. Crous & K.L. Crous, 16 Jul. 2011	KC005798	KC005777	MF951730
Z. tsugae	*Rasutoria tsugae*	ratstk	*Tsuga heterophylla*	USA: Oregon	–	EF114705	EF114688	–
Z. velutinum	*Periconiella velutina*	**CBS 101948^{ET}** = CPC 2262	*Brabejum stellatifolium*	South Africa	J.E. Taylor, 21 Jan. 1999	EU041838	EU041781	MF951731
Z. xenoparkii	*Stenella xenoparkii*	**CBS 111185^{T}** = CPC 1300	*Eucalyptus grandis*	Indonesia	M.J. Wingfield, Mar. 1996	JF700966	DQ303028	MF951732
Zymoseptoria brevis	–	**CBS 128853^{T}** = CPC 18106	*Phalaris minor*	Iran	M. Razavi	JQ739833	JF700867	KX348109
Z. halophila	–	**CBS 128854^{T}** = CPC 18105 = IRAN1483C	*Hordeum glaucum*	Iran	M. Razavi, 25 Apr. 2007	KF252150	KF251645	KX348110
Z. passerini	–	**CBS 120382^{ET}**	*Hordeum vulgare*	USA: North Dakota	S. Goodwin	JQ739843	JF700877	KP894763
Z. tritici	–	**CBS 115943^{ET}** = IPO 323	*Triticum aestivum*	Netherlands	R. Daamen, 6 May 1981	GU214436	AF181692	KX348112

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Phaeothecoidiellaceae								
Exopassalora sp.	*Passalora* sp.	CBS 118964 = GTF1a	*Malus* sp.	USA: Illinois	J. Batzer, Sep. 2000	MF951119	MF951284	MF951420
E. zambiae	*Passalora zambiae*	**CBS 112971^{T}** = CMW 14782 = CPC 1227	*Eucalyptus globulus*	Zambia	T. Coutinho, 21 Aug. 1995	EU019273	AY725523	MF951421
Houjia pomigena	–	**CBS 125224^{T}** = CPC 16109 = CMG UIF2b	*Malus* sp.	USA: Illinois	M. Gleason, Sep. 2000	MF951120	MF951285	MF951422
Phaeothecoidiella missouriensis	–	**CBS 125222^{T}** = CPC 16116 = CMG AHE7c	*Malus* sp.	USA: Missouri	M. Gleason, Sep. 2000	MF951121	MF951286	MF951423
Sporidesmajora pennsylvaniensis	–	**CBS 125229^{T}** = CPC 16112 = CMG PA1-9F1a	*Malus* sp.	USA: Pennsylvania	J.W. Travis, Sep. 2005	MF951122	MF951287	MF951424
Schizothyriaceae								
Schizothyrium pomi	*Schizothyrium pomi*	CBS 228.57	–	Italy	–	EF134947	EF134947	MF951734
	Schizothyrium pomi	CBS 486.50	*Polygonum sachalinense*	Netherlands	–	EF134948	EF134948	MF951735
Teratosphaeriaceae								
Acrodontium crateriforme	*Chloridium crateriforme*	**CBS 144.33^{T}** = ATCC 15679 = MUCL 15748 = MUCL 8978	Associated with *Tuberculina maxima*	Netherlands	–	KX286952	MF951410	KX288399
Batcheloromyces proteae	–	**CBS 110696^{ET}** =CPC 1518 = CPC 18701	*Protea cynaroides*	South Africa: Western Cape	L. Viljoen, 30 Aug. 1996	EU019247	JF746163	MF951736
B. sedgefieldii	–	**CBS 112119^{T}** = CPC 3026 = JT 851	*Protea repens*	South Africa: Western Cape	J.E. Taylor, 10 Aug. 1999	KF937222	EU707893	MF951737
Myrtapenidiella corymbia	*Penidiella corymbia*	**CBS 124769^{T}** = CPC 14640	*Corymbia foelscheana*	Australia: Northern Territory	B.A. Summerell, 22 Sep. 2007	KF901838	GQ303286	MF951738
Parapenidiella pseudotasmaniensis	–	**CBS 124991^{T}** = CPC 12400	*Eucalyptus globulus*	Australia: Victoria	I.W. Smith, Sep. 2005	KF901844	KF901522	KX348067
P. tasmaniensis	–	**CBS 111687^{T}** = CMW 14780 = CPC 1555	*Eucalyptus nitens*	Australia: Tasmania	M.J. Wingfield, 21 Nov. 1996	GU214452	KF901521	MF951739

Table 1. (Continued).

Family and Current name	Previous name (if different)	Culture accession number(s)[1,2]	Substrate	Country	Collector, Collection date	LSU[3]	ITS[4]	*rpb2*[5]
Pseudoteratosphaeria flexuosa	*Mycosphaerella flexuosa*	CBS 110743 = CPC 673	*Eucalyptus globulus*	Colombia	M.J. Wingfield, 6 Jul. 1993	KF902098	DQ302955	MF951740
Readeriella nontingens	*Readeriella nontingens*	CPC 14444	*Eucalyptus oblonga*	Australia: New South Wales	B. Summerell, 23 Sep. 2007	GQ852663	GQ852786	MF951741
Stenella araguata	–	**CBS 105.75**[T] of *Cladosporium castellanii*	Man, tinea nigra	Venezuela	–	EU019250	EU019250	MF951742
Teratosphaeria stellenboschiana	–	CBS 125215 = CPC 13764	*Eucalyptus punctata*	South Africa: Gauteng	P.W. Crous, 28 Feb. 2007	KF937247	KF901733	MF951743

[1] Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CCTU: Culture Collection of Tabriz University, Tabriz, East Azarbaijan, Iran; CMG: Personal collection of Mark Gleason, Department of Plant Pathology and Microbiology, Iowa State University, Ames, Iowa, USA; CMW: Culture Collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa; COAD: Coleção Octávio de Almeida Drumond (COAD), housed at the Universidade Federal de Viçosa, Viçosa, Brazil; CPC: Culture collection of Pedro Crous, housed at the Westerdijk Institute; DAOM: Plant Research Institute, Department of Agriculture (Mycology), Ottawa, Canada; DSM: Deutsche Sammlung von Mikrorrganismen und Zellkulturen GmbH, Braunschweig, Germany; HJS: Personal culture collection of Hans-Josef Schroers, Agricultural institute of Slovenia, Ljubljana, Slovenia; ICMP = PDDCC: International Collection of Micro-organisms from Plants, Landcare Research, Private Bag 92170, Auckland, New Zealand; IFO: Institute for Fermentation, Osaka, Japan; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, United Kingdom; INIFAT: Alexander Humboldt Institute for Basic Research in Tropical Agriculture, Ciudad de La Habana, Cuba; JCM: Japan Collection of Microorganism, RIKEN BioResource Center, Japan; KACC: Korean Agricultural Culture Collection, National Institute of Agricultural Biotechnology, Rural Development Administration, Suwon, Republic of Korea; LCP: Laboratory of Cryptogamy, National Museum of Natural History, Paris, France; LSHB: London School of Hygiene & Tropical Medicine, London, UK; MAFF: Ministry of Agriculture, Forestry and Fisheries, Tsukuba, Ibaraki, Japan; MPFN: Culture collection at the Laboratoire de Pathologie Forestière, INRA, Centre de Recherches de Nancy, 54280 Champenoux, France; MUCC (in TSU): Culture Collection, Laboratory of Plant Pathology, Mie University, Tsu, Mie Prefecture, Japan; MUCL: Université Catholique de Louvain, Louvain-la-Neuve, Belgium; MUMH: Mycological Herbarium in TSU, Mie University, Tsu, Mie, Japan; QM: Quartermaster Research and Development Center, U.S. Army, Massachusetts, USA; RoKI: Personal culture collection of Roland Kirschner, Department of Life Sciences, National Central University, Taoyuan City, Taiwan; RWB: Personal collection of Robert Barreto, Departmento de Fitopatologia, Universidade Federal de Viçosa, Viçosa, Brazil; SMKC: Culture collection of the Division of Environmental Science and Ecological Engineering, Korea University, Republic of Korea; VKM: All-Russian Collection of Microorganisms, Russian Academy of Sciences, Institute of Biochemistry and Physiology of Microorganisms, 142292 Pushchino, Moscow Region, Russia; X: Personal collection of Mahdi Arzanlou, Tabriz University, Tabriz, East Azarbaijan, Iran; ZJUM: Culture collection at Zhejiang University, China.

[2] Status of the strains: (T) ex-type, (ET) ex-epitype, (NT) ex-neotype, (IT) ex-isotype.

[3] GenBank accession numbers for LSU: large subunit (28S) of the nrRNA gene operon.

[4] GenBank accession numbers for ITS: internal transcribed spacers and intervening 5.8S nrDNA.

[5] GenBank accession numbers for *rpb2*: partial RNA polymerase II second largest subunit gene; "–" represents a DNA sequence that was not available.

Table 2. Details of primers used for amplification and sequencing in this study.

Locus[1]	Primer Name	Primer sequence (5'→3')	Annealing temperature (°C)	Orientation	Reference
ITS	V9G	TTA CGT CCC TGC CCT TTG TA	52	Forward	Hoog & Gerrits van den Ende (1998)
	ITS4	TCC TCC GCT TAT TGA TAT GC	52	Reverse	White *et al*. (1990)
LSU	LSU1Fd	GRA TCA GGT AGG RAT ACC CG	52	Forward	Crous *et al*. (2009c)
	LR5	TCC TGA GGG AAA CTT CG	52	Reverse	Vilgalys & Hester (1990)
rpb2	fRPB2-5F	GAY GAY MGW GAT CAY TTY GG	60→58→54	Forward	Liu *et al*. (1999)
	RPB2-5F2	GGG GWG AYC AGA AGA AGG C	60→58→54	Forward	Sung *et al*. (2007)
	Rpb2-F1	GGT GTC AGT CAR GTG YTG AA	60→58→54	Forward	Videira *et al*. (2015a)
	Rpb2-F4	GAY YTB GCI GGI CCI YTI ATG GC	60→58→54	Forward	Videira *et al*. (2016)
	Rpb2-F5	GCN ACI GGI AAY TGG GG	60→58→54	Forward	This study
	Rpb2-F6	AAR GCI GGT GTI AGY CAR GT	60→58→54	Forward	This study
	fRPB2-7cR	CCC ATR GCT TGY TTR CCC AT	60→58→54	Reverse	Liu *et al*. (1999)
	Rpb2-R1	TCC TCN GGV GTC ATG ATR ATC AT	60→58→54	Reverse	Videira *et al*. (2015a)
	Rpb2-R3	ATC ATN GMN GGR TGR ATY TC	60→58→54	Reverse	This study

[1] ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: large subunit (28S) of the nrRNA gene operon; *rpb2:* partial RNA polymerase II second largest subunit gene.

genes were used in the subsequent phylogenetic analyses, with the exception of *Cercospora apii* (CBS 116455), "*Passalora vaginae*" (CBS 140.34), *Phaeoramularia capsicicola* (CBS 156.62), *Prathigada* (MUCC 1088), *Rasutoria pseudotsugae* (rapssd), *Rasutoria tsugae* (ratstk), *Zasmidium biverticillatum* (CBS 335.36) and *Zasmidium parki* (CBS 387.92), which were missing the *rpb2* sequence; in those cases, the missing sequences were treated as missing data in the alignments.

The phylogenetic methods used in this study included a Bayesian analysis performed with MrBayes v. 3.2 (Ronquist *et al.* 2012), a Maximum-Likelihood analysis performed with RAxML v. 7.2.6 (Stamatakis & Alachiotis 2010) and a Parsimony analysis performed with PAUP v. 4.0b10 (Swofford 2003). The phylogenetic analyses were individually applied to four datasets: dataset 1 consisted of a concatenated alignment of LSU and *rpb2* sequences from representative strains of most genera currently known to belong in the *Mycosphaerellaceae*, and from closely related families; datasets 2 to 4 were based on three major clades observed in dataset 1 and consisted of concatenated alignments of LSU, *rpb2* and ITS sequences. MrModeltest v. 2.2 (Nylander 2004) was used to determine the best nucleotide substitution model settings for each data partition in order to perform a model-optimised **Bayesian** phylogenetic reconstruction. The Markov Chain Monte Carlo (MCMC) analysis of four chains started in parallel from a random tree topology, the heat parameter was set at 0.15 and trees were saved every 200 generations until the average standard deviation of split frequencies reached 0.01 (stop value). Burn-in was set to 25 % after which the likelihood values were stationary. The **Maximum Likelihood** phylogenies performed with RAxML executed 1 000 rapid bootstrap inferences using the GAMMA model and the GTR substitution matrix and produced the best-score maximum-likelihood tree. In the **Maximum Parsimony** analysis, alignment gaps were treated as fifth character state and all characters were unordered and of unequal weight. A heuristic search option with 100 random taxon additions and tree bisection and reconnection (TBR) as the branch-swapping algorithm was used. Branches of zero length were collapsed and all multiple, equally most parsimonious trees were saved. The robustness of the trees obtained was evaluated by 1 000 bootstrap replications (Hillis & Bull 1993). Other measures calculated included tree length (TL), consistency index (CI), retention index (RI) and rescaled consistency index (RC).

All resulting trees were printed with Geneious v. 7.0.6 (http://www.geneious.com, Kearse *et al.* 2012). All new sequences generated in this study were deposited in NCBI's GenBank nucleotide database (www.ncbi.nlm.nih.gov) and the accession numbers are listed in Table 1 (GenBank accessions MF951115–MF951743). The alignments and respective phylogenetic trees were deposited in TreeBASE, study number 21537.

Taxonomy

Isolates were cultivated for 15–30 d at 21 °C in a 12 h day/night regime. Morphological observations of reproductive structures were determined using a Nikon Eclipse 80i compound microscope with differential interference contrast (DIC) illumination. Slides were prepared using the inclined coverslip method (Kawato & Shinobu 1959, revised in Nugent *et al.* 2006) and also transparent adhesive tape (Titan Ultra Clear Tape, Conglom Inc., Toronto, Canada) (Bensch *et al.* 2012). Clear lactic acid was used as mounting medium for microscopic observations of both *in vivo* and herbarium specimens. The observed isolates were cultivated in synthetic nutrient-poor agar (SNA), V8-juice agar (V8), malt extract agar (MEA) or oatmeal agar (OA) media to produce conidiogenous structures (recipes according to Crous *et al.* 2009f). The recorded conidial and ascospore measurements represent the minimum and maximum value of 30 individual

measurements, for both length and width. For Scanning Electron Microscopy (SEM) observations, dried herbarium specimens were cut into small pieces and mycelial discs were incubated on MEA (Crous *et al.* 2009f). Both materials were fixed with OsO4 gas at room temperature for 12 h and then coated with gold using an ion-sputter (model E-1010, Hitachi, Tokyo, Japan). Specimens were observed with a SEM (S-4000, Hitachi) at 10–15 kV accelerating voltage. Nomenclatural novelties and descriptions were deposited in MycoBank (Crous *et al.* 2004a).

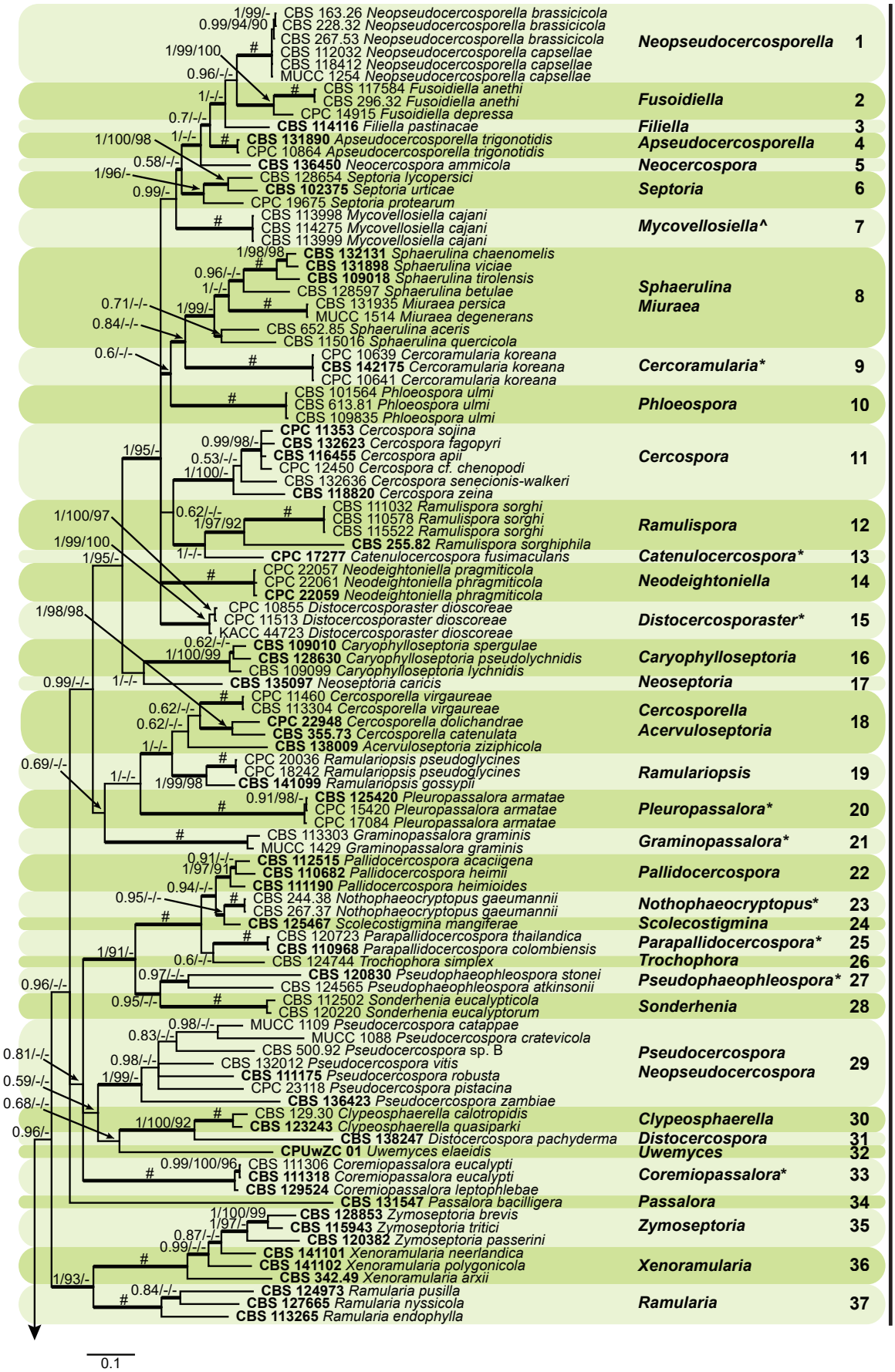
RESULTS

DNA amplification

The partial amplification of LSU and ITS was successful for all isolates (Table 1). The partial amplification of *rpb2* was difficult with the primer combination fRPB2-f5F and fRPB2-7cR (Liu *et al.* 1999), but more successful using the forward primer RPB2-5F2 (Sung *et al.* 2007). Among the used primers, the most successful combination was Rpb2-F4 (Videira *et al.* 2016) and fRPB2-7cR (Liu *et al.* 1999). The remaining primers designed in this study were used only in a small number of isolates for which the previously mentioned combinations failed to amplify the gene.

LSU & rpb2 phylogeny: **Dataset 1** consisted of a concatenated alignment of two loci (LSU, *rpb2*) that contained 262 taxa representing several genera known from culture belonging to the *Mycosphaerellaceae*. A strain of *Cylindroseptoria ceratoniae* (CBS 477.69; *Dothideaceae*) was used as outgroup. The final alignment contained a total of 1 471 characters divided in two partitions containing 750 (LSU) and 716 (*rpb2*) characters respectively, including alignment gaps. From the total alignment five characters that were artificially introduced as spacer between the genes were excluded from the phylogenetic analyses (see alignment in TreeBASE). MrModelTest determined that the Bayesian analysis for both genes (LSU, *rpb2*) should use dirichlet base frequencies and the GTR+I+G model. The **Bayesian** analyses of the concatenated two-locus alignment generated 65 562 trees from which 16 390 trees were discarded (25 % burn-in). The posterior probability values (PP) were calculated from the remaining 49 172 trees (Fig. 1; first value: PP ≤1 shown). The alignment contained a total of 811 unique site patterns: 291 (LSU) and 520 (*rpb2*). The **Maximum Likelihood** analysis detected 810 distinct patterns and reached a final optimization likelihood of −66911.187183. The bootstrap support values (ML-BS) from the best-scoring tree were mapped on the Bayesian tree as the second value in the tree

Fig. 1. Phylogenetic tree (50 % majority rule consensus) resulting from a Bayesian analysis of the combined LSU and *rpb2* sequence alignment (dataset 1). Bayesian posterior probabilities (PP), maximum likelihood bootstrap support values (≥ 90 %; ML-BS) and maximum parsimony bootstrap support values (≥ 90 %; MP-BS) are indicated at the nodes (PP/ML-BS/MP-BS; a hash (#) symbol denotes fully-supported branches and the scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Genera clades are delimited in coloured boxes, with the genus name and clade number indicated to the right. All taxa names are written in black, ex-type strains are represented in bold, novel genera denoted with an asterisk (*) and resurrected genera with a circumflex (^). A vertical bar is used to the right of the coloured boxes and encompasses all genera within their respective families. The family name *Mycosphaerellaceae* is unabbreviated while the rest are abbreviated as follows: *D* = *Dissoconiaceae*, *P* = *Phaeothecoidiellaceae*, *S* = *Schizothyriaceae*, *T* = *Teratosphaeriaceae*, *C* = *Cladosporiaceae*. The tree was rooted to *Cylindroseptoria ceratoniae* (CBS 477.69).


CBS 163.26 Neopseudocercosporella brassicicola
CBS 228.32 Neopseudocercosporella brassicicola
CBS 267.53 Neopseudocercosporella brassicicola
CBS 112032 Neopseudocercosporella capsellae
CBS 118412 Neopseudocercosporella capsellae
MUCC 1254 Neopseudocercosporella capsellae
Neopseudocercosporella 1
CBS 117584 Fusoidiella anethi
CBS 296.32 Fusoidiella anethi
CPC 14915 Fusoidiella depressa
Fusoidiella 2
CBS 114116 Filiella pastinacae
Filiella 3
CBS 131890 Apseudocercosporella trigonotidis
CPC 10864 Apseudocercosporella trigonotidis
Apseudocercosporella 4
CBS 136450 Neocercospora ammicola
Neocercospora 5
CBS 128654 Septoria lycopersici
CBS 102375 Septoria urticae
CPC 19675 Septoria protearum
Septoria 6
CBS 113998 Mycovellosiella cajani
CBS 114275 Mycovellosiella cajani
CBS 113999 Mycovellosiella cajani
Mycovellosiella^ 7
CBS 132131 Sphaerulina chaenomelis
CBS 131898 Sphaerulina viciae
CBS 109018 Sphaerulina tirolensis
CBS 128597 Sphaerulina betulae
CBS 131935 Miuraea persica
MUCC 1514 Miuraea degenerans
CBS 652.85 Sphaerulina aceris
CBS 115016 Sphaerulina quercicola
Sphaerulina
Miuraea 8
CPC 10639 Cercoramularia koreana
CBS 142175 Cercoramularia koreana
CPC 10641 Cercoramularia koreana
Cercoramularia* 9
CBS 101564 Phloeospora ulmi
CBS 613.81 Phloeospora ulmi
CBS 109835 Phloeospora ulmi
Phloeospora 10
CPC 11353 Cercospora sojina
CBS 132623 Cercospora fagopyri
CBS 116455 Cercospora apii
CPC 12450 Cercospora cf. chenopodi
CBS 132636 Cercospora senecionis-walkeri
CBS 118820 Cercospora zeina
Cercospora 11
CBS 111032 Ramulispora sorghi
CBS 110578 Ramulispora sorghi
CBS 115522 Ramulispora sorghi
CBS 255.82 Ramulispora sorghiphila
Ramulispora 12
CPC 17277 Catenulocercospora fusimaculans
Catenulocercospora* 13
CPC 22057 Neodeightoniella pragmiticola
CPC 22061 Neodeightoniella phragmiticola
CPC 22059 Neodeightoniella phragmiticola
Neodeightoniella 14
CPC 10855 Distocercosporaster dioscoreae
CPC 11513 Distocercosporaster dioscoreae
KACC 44723 Distocercosporaster dioscoreae
Distocercosporaster* 15
CBS 109010 Caryophylloseptoria spergulae
CBS 128630 Caryophylloseptoria pseudolychnidis
CBS 109099 Caryophylloseptoria lychnidis
Caryophylloseptoria 16
CBS 135097 Neoseptoria caricis
Neoseptoria 17
CPC 11460 Cercosporella virgaureae
CBS 113304 Cercosporella virgaureae
CPC 22948 Cercosporella dolichandrae
CBS 355.73 Cercosporella catenulata
CBS 138009 Acervuloseptoria ziziphicola
Cercosporella
Acervuloseptoria 18
CPC 20036 Ramulariopsis pseudoglycines
CPC 18242 Ramulariopsis pseudoglycines
CBS 141099 Ramulariopsis gossypii
Ramulariopsis 19
CBS 125420 Pleuropassalora armatae
CPC 15420 Pleuropassalora armatae
CPC 17084 Pleuropassalora armatae
Pleuropassalora* 20
CBS 113303 Graminopassalora graminis
MUCC 1429 Graminopassalora graminis
Graminopassalora* 21
CBS 112515 Pallidocercospora acaciigena
CBS 110682 Pallidocercospora heimii
CBS 111190 Pallidocercospora heimioides
Pallidocercospora 22
CBS 244.38 Nothophaeocryptopus gaeumannii
CBS 267.37 Nothophaeocryptopus gaeumannii
Nothophaeocryptopus* 23
CBS 125467 Scolecostigmina mangiferae
Scolecostigmina 24
CBS 120723 Parapallidocercospora thailandica
CBS 110968 Parapallidocercospora colombiensis
Parapallidocercospora* 25
CBS 124744 Trochophora simplex
Trochophora 26
CBS 120830 Pseudophaeophleospora stonei
CBS 124565 Pseudophaeophleospora atkinsonii
Pseudophaeophleospora* 27
CBS 112502 Sonderhenia eucalypticola
CBS 120220 Sonderhenia eucalyptorum
Sonderhenia 28
MUCC 1109 Pseudocercospora catappae
MUCC 1088 Pseudocercospora cratevicola
CBS 500.92 Pseudocercospora sp. B
CBS 132012 Pseudocercospora vitis
CBS 111175 Pseudocercospora robusta
CPC 23118 Pseudocercospora pistacina
CBS 136423 Pseudocercospora zambiae
Pseudocercospora
Neopseudocercospora 29
CBS 129.30 Clypeosphaerella calotropidis
CBS 123243 Clypeosphaerella quasiparki
Clypeosphaerella 30
CBS 138247 Distocercospora pachyderma
Distocercospora 31
CPUwZC 01 Uwemyces elaeidis
Uwemyces 32
CBS 111306 Coremiopassalora eucalypti
CBS 111318 Coremiopassalora eucalypti
CBS 129524 Coremiopassalora leptophlebae
Coremiopassalora* 33
CBS 131547 Passalora bacilligera
Passalora 34
CBS 128853 Zymoseptoria brevis
CBS 115943 Zymoseptoria tritici
CBS 120382 Zymoseptoria passerini
Zymoseptoria 35
CBS 141101 Xenoramularia neerlandica
CBS 141102 Xenoramularia polygonicola
CBS 342.49 Xenoramularia arxii
Xenoramularia 36
CBS 124973 Ramularia pusilla
CBS 127665 Ramularia nyssicola
CBS 113265 Ramularia endophylla
Ramularia 37
Mycosphaerellaceae
0.1

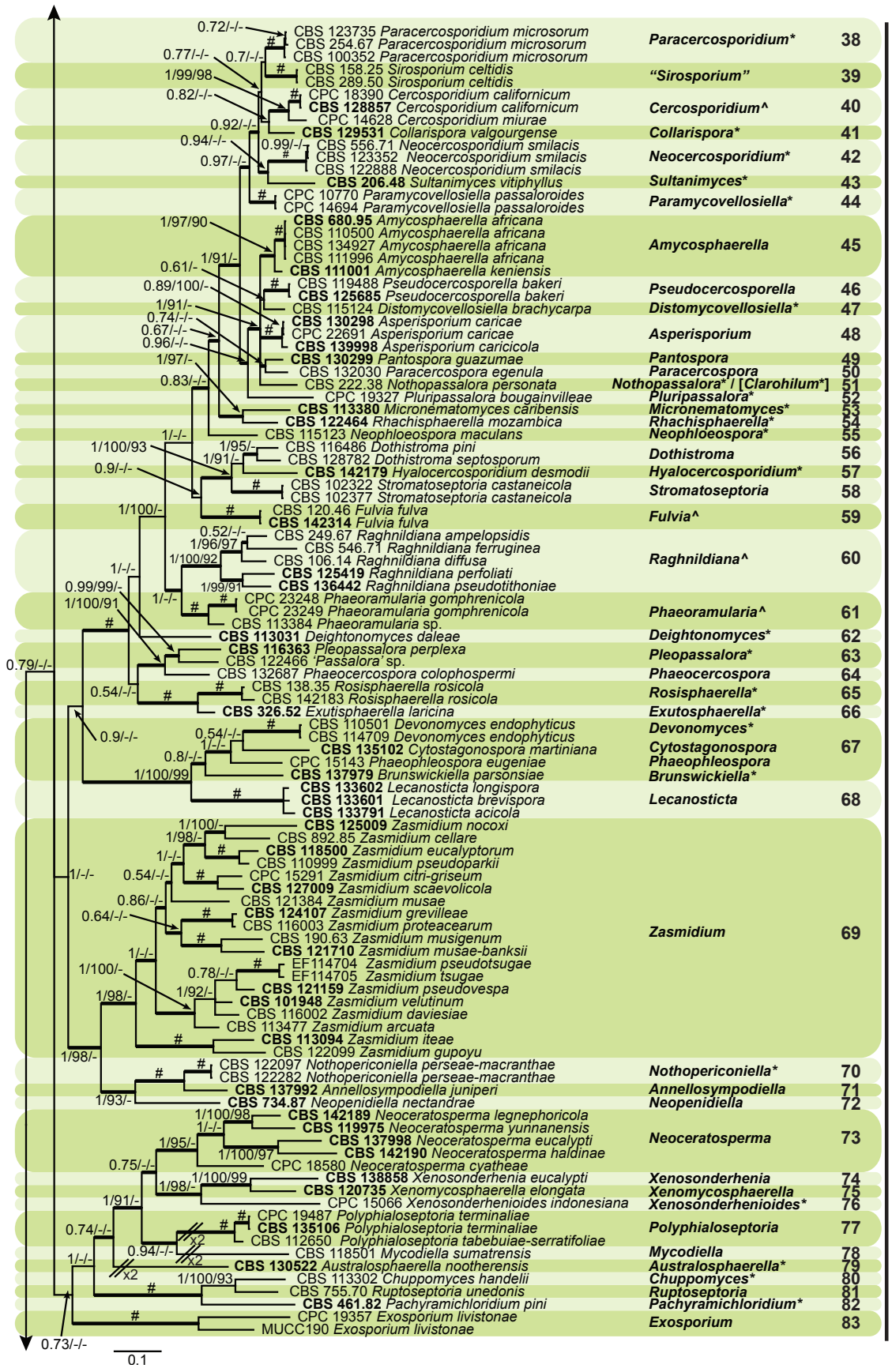


Fig. 1. (Continued).

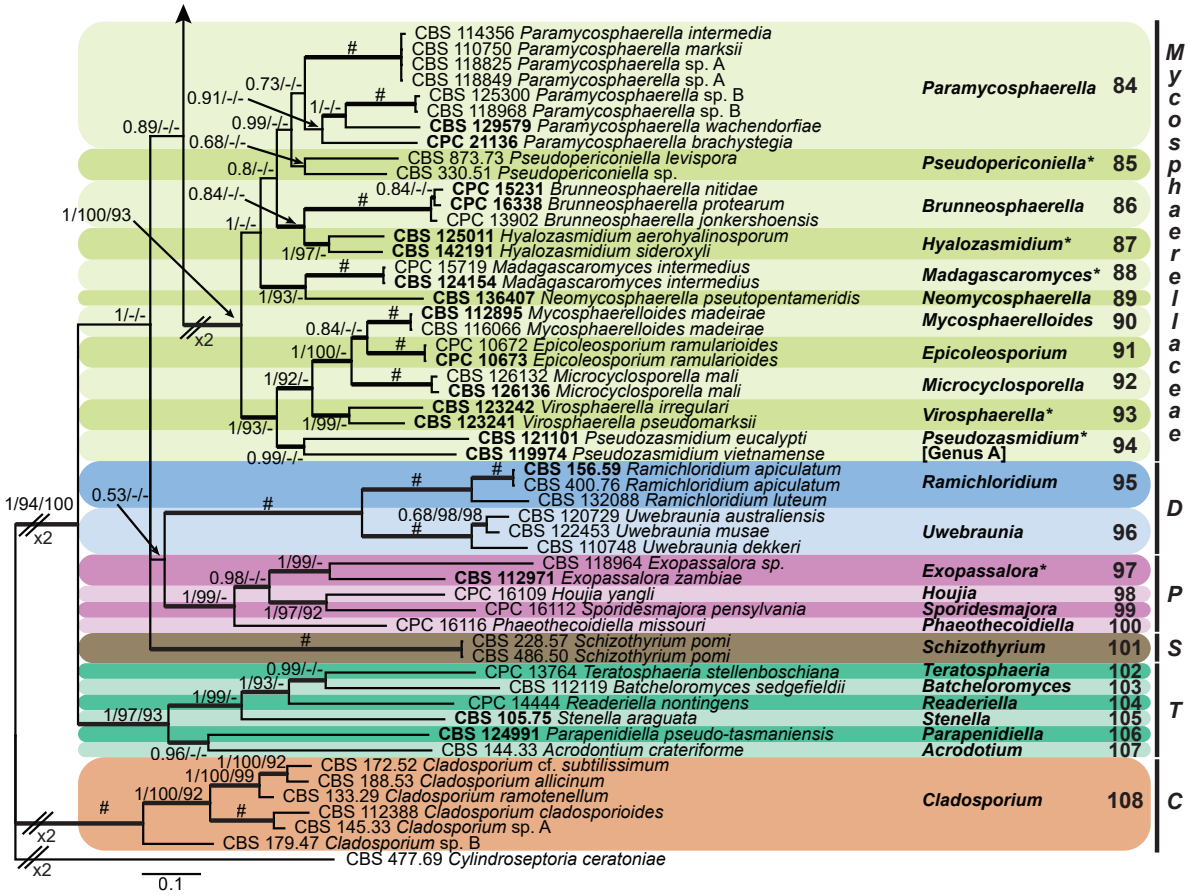


Fig. 1. (Continued).

nodes (Fig. 1; ML-BS ≥ 90 % shown). The **Maximum Parsimony** (MP) analyses generated the maximum of 1 000 equally most parsimonious trees and the bootstrap support values (MP-BS) were mapped on the Bayesian tree as the third value (Fig. 1; MP-BS ≥ 90 % shown). From the analysed characters, 691 were constant, 100 were variable and parsimony-uninformative and 675 were parsimony-informative. A parsimony consensus tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 1; Length = 16678, CI = 0.094, RI = 0.647, RC = 0.061, HI = 0.906). The overall parsimony phylogeny supported the same species clades as those presented in the Bayesian phylogeny (Fig. 1). Likewise, the ML analyses of dataset 1 (Fig. 1) separated the strains into the same genus clades as with Bayesian analyses.

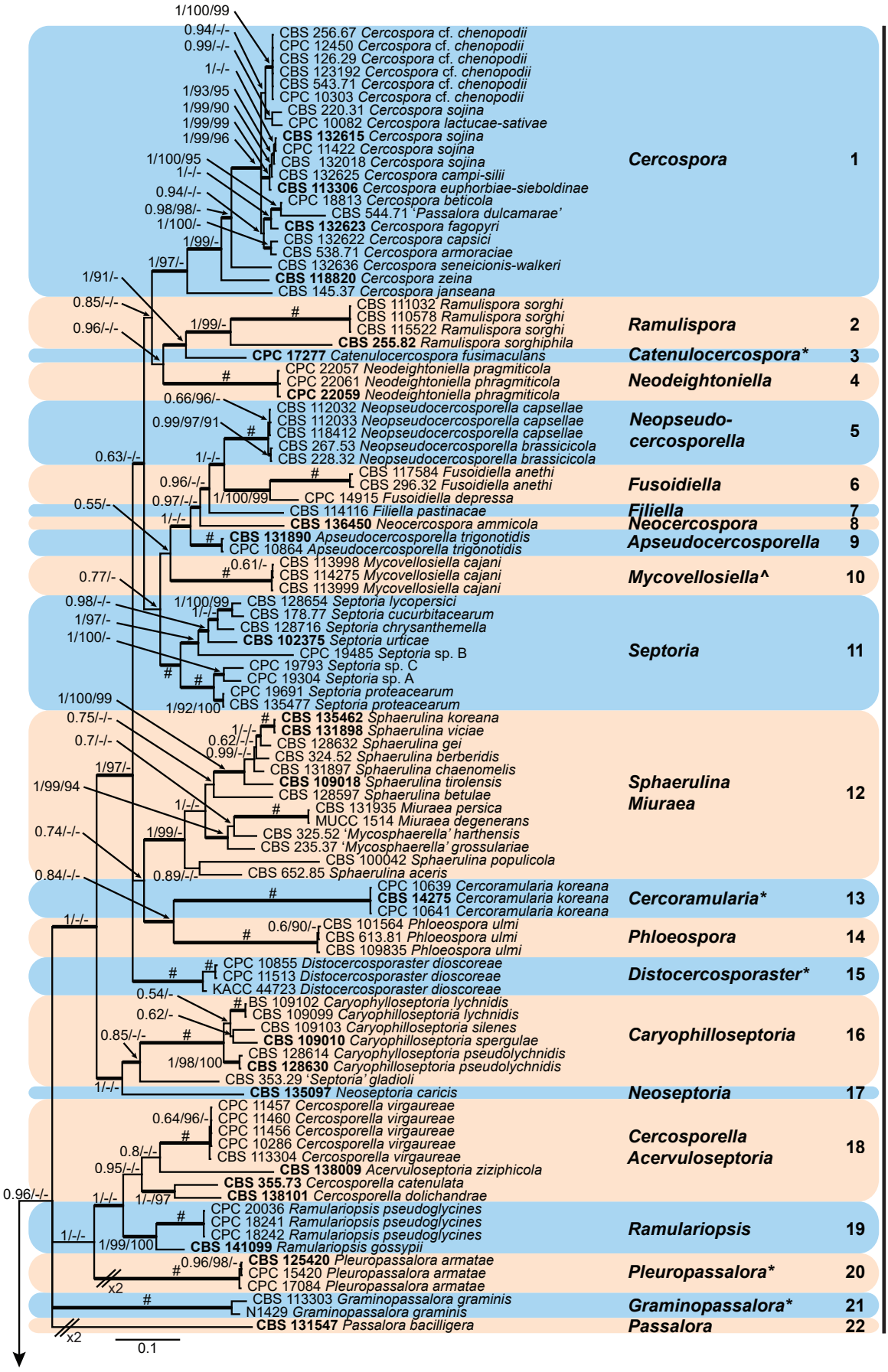
Seven families are represented in the tree (Fig. 1): *Mycosphaerellaceae* (clades 1–94), *Dissoconiaceae* (clades 95, 96), *Phaeothecoidiellaceae* (clades 97–100), *Schizothyriaceae* (clade 101), *Teratosphaeriaceae* (clades 102–107), *Cladosporiaceae* (clade 108) and the single strain used as outgroup belonging to the *Dothideaceae*. The genera included in the *Cladosporiaceae* (*C*), *Dissoconiaceae* (*D*), *Phaeothecoidiellaceae* (*P*) and *Teratosphaeriaceae* (*T*) were used to provide an overview of the phylogenetic position of the *Mycosphaerellaceae*. In addition, some currently include genera that were once considered part of *Mycosphaerellaceae*, namely *Ramichloridium* (clade 95), currently in *Dissoconiaceae* (*D*), and *Stenella* (clade 105), presently in *Teratosphaeriaceae* (*T*).

LSU, *rpb2 and ITS phylogenies (Datasets 2–4)*: For these analyses, DNA sequence data from LSU, *rpb2* and ITS were combined in three datasets (datasets 2–4) corresponding to three large clades from the overview tree with varying outgroup settings. Datasets 2–4 were analysed with the same three phylogenetic methods applied to Dataset 1. The results of the MrModeltest analysis indicated the same priors for the Bayesian analysis for all three partitions (LSU, *rpb2* and ITS), as for Dataset 1.

Dataset 2 consisted of clades 1–37 of Fig. 1 with additional taxa, included a total of 166 taxa and used *Schizothyrium pomi* (CBS 486.50) as outgroup. The final alignment contained a total of 2 113 characters divided in three partitions containing 749 (LSU), 766 (*rpb2*), 588 (ITS) characters respectively, including alignment gaps. From the total alignment, 10 characters previously introduced as spacers between the genes were excluded from the phylogenetic analysis. The **Bayesian** analysis generated 33 282 trees from which 8 320 trees were discarded (25 % burnin). The posterior probability values were calculated from the remaining 24 962 trees (Fig. 2; first value: PP ≤1 shown). The alignment contained a total of 988 unique site patterns: 173 (LSU), 496 (*rpb2*) and 343 (ITS). The **Maximum Likelihood** analysis detected 984 distinct patterns and reached a final ML optimization likelihood of −43958.897307. The bootstrap support values from the best-scoring tree were mapped on the Bayesian tree as the second value in the tree nodes (Fig. 2; ML-BS ≥ 90 % shown). The **Maximum Parsimony** analysis generated the maximum of 1 000 equally most parsimonious trees and the bootstrap support values were mapped on the Bayesian tree as the third value (Fig. 2; MP-BS ≥ 90 % shown). From the 2 103 characters, 1147 were constant, 148 were variable and parsimony-uninformative and 809 were parsimony-informative. A parsimony consensus tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 2; Length = 10381, CI = 0.174, RI = 0.717, RC = 0.125, HI = 0.826).

The phylogenetic trees based on **dataset 2** (Fig. 2) that were generated with Bayesian and maximum likelihood methods, separated strains into the same generic clades. The phylogenetic trees generated using parsimony differed slightly in the clade order (data not shown, trees deposited on TreeBASE). Twenty-two genera represent stable genera since they maintain their positions in the present analysis as they displayed in previous phylogenetic studies, and most of them are based on their respective ex-type cultures: *Cercospora* (clade 1), *Ramulispora* (clade 2), *Neodeightoniella* (clade 4), *Neopseudocercosporella* (clade 5), *Fusoidiella* (clade 6), *Filiella* (clade 7), *Neocercospora* (clade 8), *Apseudocercosporella* (clade 9), *Septoria* (clade 11), *Phloeospora* (clade 14), *Caryophylloseptoria* (clade 16), *Neoseptoria* (clade 17), *Ramulariopsis* (clade 19), *Uwemyces* (clade 25), *Clypeosphaerella* (clade 26), *Pallidocercospora* (clade

Fig. 2. Phylogenetic tree (50 % majority rule consensus) resulting from a Bayesian analysis of the combined LSU, *rpb2* and ITS sequence alignment (dataset 2; representing clades 1–37 of Fig. 1). Bayesian posterior probabilities (PP), maximum likelihood bootstrap support values (≥ 90 %; ML-BS) and maximum parsimony bootstrap support values (≥ 90 %; MP-BS) are indicated at the nodes (PP/ML-BS/MP-BS) and the scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Genera clades are delimited in coloured boxes, with the genus name and clade number are indicated to the right. All taxa names are written in black, ex-type species strains are represented in bold, novel genera with an asterisk (*) and resurrected genera with a circumflex (ˆ). A vertical bar is used to the right of the coloured boxes and encompass all genera within their respective family, the *Mycosphaerellaceae*. The tree was rooted to *Schizothyrium pomi* (CBS 486.50).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CPC 12450 Cercospora cf. chenopodii
CBS 126.29 Cercospora cf. chenopodii
CBS 123192 Cercospora cf. chenopodii
CBS 543.71 Cercospora cf. chenopodii
CPC 10303 Cercospora cf. chenopodii
CBS 220.31 Cercospora sojina
CPC 10082 Cercospora lactucae-sativae
CBS 132615 Cercospora sojina
CPC 11422 Cercospora sojina
CBS 132018 Cercospora sojina
CBS 132625 Cercospora campi-silii
CBS 113306 Cercospora euphorbiae-sieboldinae
CPC 18813 Cercospora beticola
CBS 544.71 'Passalora dulcamarae'
CBS 132623 Cercospora fagopyri
CBS 132622 Cercospora capsici
CBS 538.71 Cercospora armoraciae
CBS 132636 Cercospora seneicionis-walkeri
CBS 118820 Cercospora zeina
CBS 145.37 Cercospora janseana
Cercospora 1
CBS 111032 Ramulispora sorghi
CBS 110578 Ramulispora sorghi
CBS 115522 Ramulispora sorghi
CBS 255.82 Ramulispora sorghiphila
Ramulispora 2
CPC 17277 Catenulocercospora fusimaculans
Catenulocercospora* 3
CPC 22057 Neodeightoniella pragmiticola
CPC 22061 Neodeightoniella phragmiticola
CPC 22059 Neodeightoniella phragmiticola
Neodeightoniella 4
CBS 112032 Neopseudocercosporella capsellae
CBS 112033 Neopseudocercosporella capsellae
CBS 118412 Neopseudocercosporella capsellae
CBS 267.53 Neopseudocercosporella brassicicola
CBS 228.32 Neopseudocercosporella brassicicola
Neopseudo-cercosporella 5
CBS 117584 Fusoidiella anethi
CBS 296.32 Fusoidiella anethi
CPC 14915 Fusoidiella depressa
Fusoidiella 6
CBS 114116 Filiella pastinacae
Filiella 7
CBS 136450 Neocercospora ammicola
Neocercospora 8
CBS 131890 Apseudocercosporella trigonotidis
CPC 10864 Apseudocercosporella trigonotidis
Apseudocercosporella 9
CBS 113998 Mycovellosiella cajani
CBS 114275 Mycovellosiella cajani
CBS 113999 Mycovellosiella cajani
Mycovellosiella^ 10
CBS 128654 Septoria lycopersici
CBS 178.77 Septoria cucurbitacearum
CBS 128716 Septoria chrysanthemella
CBS 102375 Septoria urticae
CPC 19485 Septoria sp. B
CPC 19793 Septoria sp. C
CPC 19304 Septoria sp. A
CPC 19691 Septoria proteacearum
CBS 135477 Septoria proteacearum
Septoria 11
CBS 135462 Sphaerulina koreana
CBS 131898 Sphaerulina viciae
CBS 128632 Sphaerulina gei
CBS 324.52 Sphaerulina berberidis
CBS 131897 Sphaerulina chaenomelis
CBS 109018 Sphaerulina tirolensis
CBS 128597 Sphaerulina betulae
CBS 131935 Miuraea persica
MUCC 1514 Miuraea degenerans
CBS 325.52 'Mycosphaerella' harthensis
CBS 235.37 'Mycosphaerella' grossulariae
CBS 100042 Sphaerulina populicola
CBS 652.85 Sphaerulina aceris
Sphaerulina Miuraea 12
CPC 10639 Cercoramularia koreana
CBS 14275 Cercoramularia koreana
CPC 10641 Cercoramularia koreana
Cercoramularia* 13
CBS 101564 Phloeospora ulmi
CBS 613.81 Phloeospora ulmi
CBS 109835 Phloeospora ulmi
Phloeospora 14
CPC 10855 Distocercosporaster dioscoreae
CPC 11513 Distocercosporaster dioscoreae
KACC 44723 Distocercosporaster dioscoreae
Distocercosporaster* 15
BS 109102 Caryophylloseptoria lychnidis
CBS 109099 Caryophilloseptoria lychnidis
CBS 109103 Caryophilloseptoria silenes
CBS 109010 Caryophilloseptoria spergulae
CBS 128614 Caryophylloseptoria pseudolychnidis
CBS 128630 Caryophilloseptoria pseudolychnidis
CBS 353.29 'Septoria' gladioli
Caryophilloseptoria 16
CBS 135097 Neoseptoria caricis
Neoseptoria 17
CPC 11457 Cercosporella virgaureae
CPC 11460 Cercosporella virgaureae
CPC 11456 Cercosporella virgaureae
CPC 10286 Cercosporella virgaureae
CBS 113304 Cercosporella virgaureae
CBS 138009 Acervuloseptoria ziziphicola
CBS 355.73 Cercosporella catenulata
CBS 138101 Cercosporella dolichandrae
Cercosporella Acervuloseptoria 18
CPC 20036 Ramulariopsis pseudoglycines
CPC 18241 Ramulariopsis pseudoglycines
CPC 18242 Ramulariopsis pseudoglycines
CBS 141099 Ramulariopsis gossypii
Ramulariopsis 19
CBS 125420 Pleuropassalora armatae
CPC 15420 Pleuropassalora armatae
CPC 17084 Pleuropassalora armatae
Pleuropassalora* 20
CBS 113303 Graminopassalora graminis
N1429 Graminopassalora graminis
Graminopassalora* 21
CBS 131547 Passalora bacilligera
Passalora 22
x2
x2
0.1
Mycosphaerellaceae

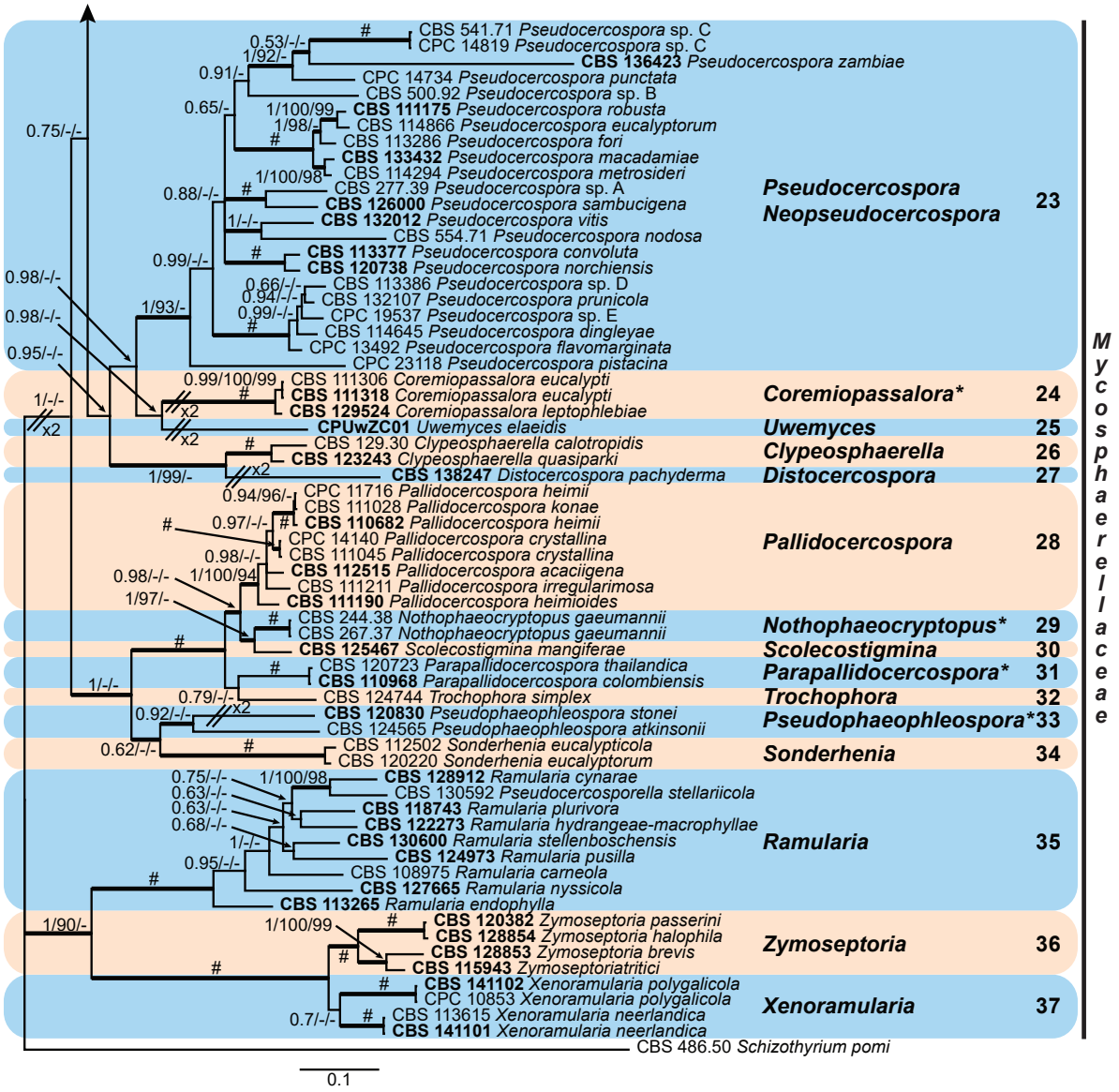


Fig. 2. (Continued).

Fig. 3. Phylogenetic tree (50 % majority rule consensus) resulting from a Bayesian analysis of the combined LSU, *rpb2* and ITS sequence alignment (dataset 3; representing clades 38–66, 79, 84 and 92–94 of Fig. 1). Bayesian posterior probabilities (PP), maximum likelihood bootstrap support values (≥ 90 %; ML-BS) and maximum parsimony bootstrap support values (≥ 90 %; MP-BS) are indicated at the nodes (PP/ML-BS/MP-BS) and the scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Genera clades are delimited in coloured boxes, with the genus name and clade number indicated to the right. All taxa names are written in black, ex-type strains are represented in bold, novel genera with an asterisk (*) and resurrected genera with a circumflex (ˆ). A vertical bar is used to the right of the coloured boxes and encompass all genera within their respective family, the *Mycosphaerellaceae*. The tree was rooted to *Schizothyrium* (CBS 228.57).

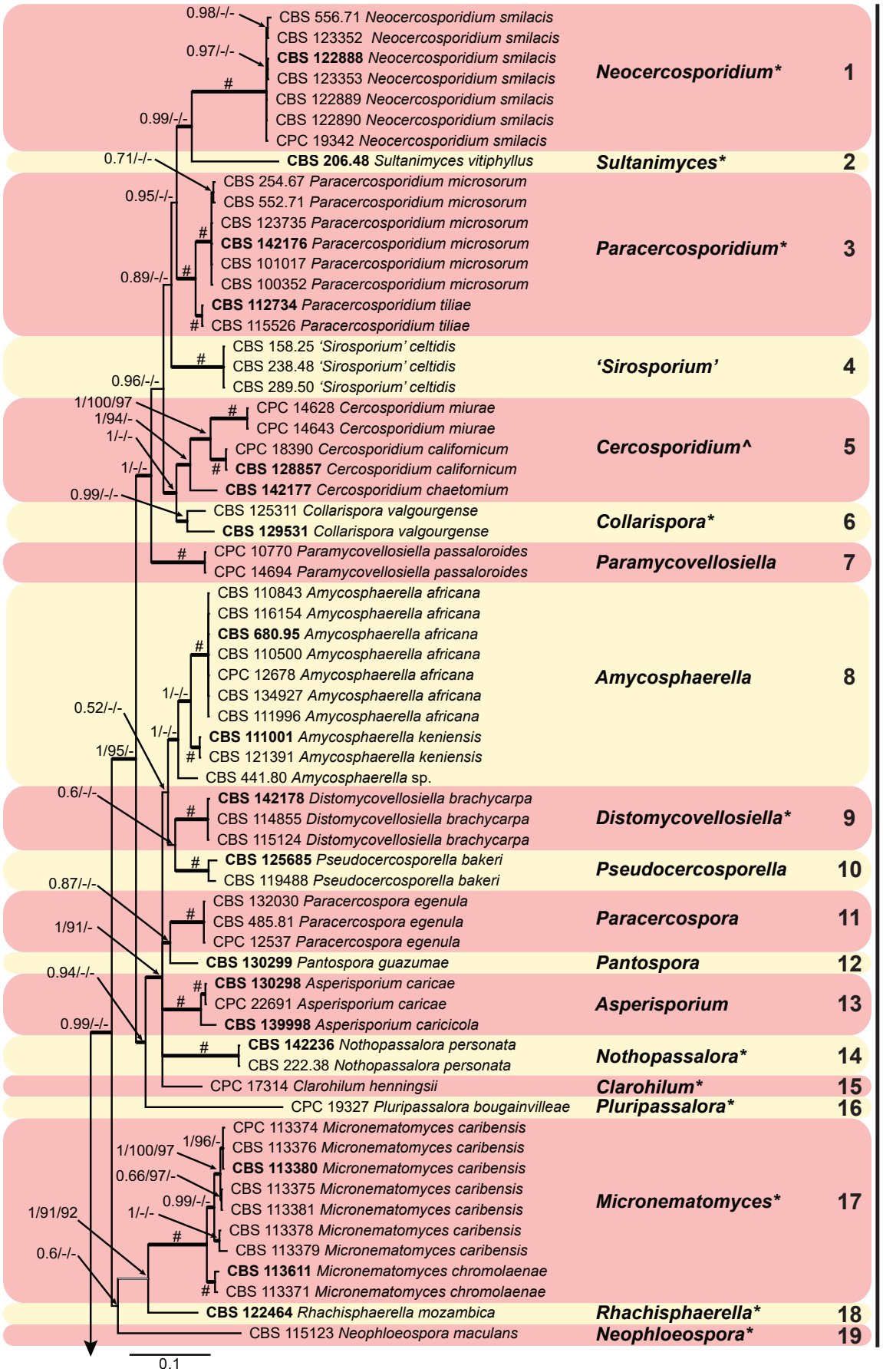

0.98/-/-
CBS 556.71 Neocercosporidium smilacis
CBS 123352 Neocercosporidium smilacis
0.97/-/-
CBS 122888 Neocercosporidium smilacis
CBS 123353 Neocercosporidium smilacis
CBS 122889 Neocercosporidium smilacis
0.99/-/-
CBS 122890 Neocercosporidium smilacis
CPC 19342 Neocercosporidium smilacis
Neocercosporidium* 1
0.71/-/-
CBS 206.48 Sultanimyces vitiphyllus
Sultanimyces* 2
CBS 254.67 Paracercosporidium microsorum
0.95/-/-
CBS 552.71 Paracercosporidium microsorum
CBS 123735 Paracercosporidium microsorum
CBS 142176 Paracercosporidium microsorum
CBS 101017 Paracercosporidium microsorum
0.89/-/-
CBS 100352 Paracercosporidium microsorum
CBS 112734 Paracercosporidium tiliae
CBS 115526 Paracercosporidium tiliae
Paracercosporidium* 3
CBS 158.25 'Sirosporium' celtidis
CBS 238.48 'Sirosporium' celtidis
0.96/-/-
CBS 289.50 'Sirosporium' celtidis
'Sirosporium' 4
1/100/97
CPC 14628 Cercosporidium miurae
1/94/-
CPC 14643 Cercosporidium miurae
1/-/-
CPC 18390 Cercosporidium californicum
1/-/-
CBS 128857 Cercosporidium californicum
CBS 142177 Cercosporidium chaetomium
Cercosporidium^ 5
0.99/-/-
CBS 125311 Collarispora valgourgense
CBS 129531 Collarispora valgourgense
Collarispora* 6
CPC 10770 Paramycovellosiella passaloroides
CPC 14694 Paramycovellosiella passaloroides
Paramycovellosiella 7
CBS 110843 Amycosphaerella africana
CBS 116154 Amycosphaerella africana
CBS 680.95 Amycosphaerella africana
CBS 110500 Amycosphaerella africana
CPC 12678 Amycosphaerella africana
1/-/-
CBS 134927 Amycosphaerella africana
0.52/-/-
CBS 111996 Amycosphaerella africana
1/-/-
CBS 111001 Amycosphaerella keniensis
1/95/-
CBS 121391 Amycosphaerella keniensis
CBS 441.80 Amycosphaerella sp.
Amycosphaerella 8
0.6/-/-
CBS 142178 Distomycovellosiella brachycarpa
CBS 114855 Distomycovellosiella brachycarpa
CBS 115124 Distomycovellosiella brachycarpa
Distomycovellosiella* 9
CBS 125685 Pseudocercosporella bakeri
CBS 119488 Pseudocercosporella bakeri
Pseudocercosporella 10
0.87/-/-
CBS 132030 Paracercospora egenula
CBS 485.81 Paracercospora egenula
1/91/-
CPC 12537 Paracercospora egenula
Paracercospora 11
CBS 130299 Pantospora guazumae
Pantospora 12
0.94/-/-
CBS 130298 Asperisporium caricae
CPC 22691 Asperisporium caricae
0.99/-/-
CBS 139998 Asperisporium caricicola
Asperisporium 13
CBS 142236 Nothopassalora personata
CBS 222.38 Nothopassalora personata
Nothopassalora* 14
CPC 17314 Clarohilum henningsii
Clarohilum* 15
CPC 19327 Pluripassalora bougainvilleae
Pluripassalora* 16
CPC 113374 Micronematomyces caribensis
1/96/-
CBS 113376 Micronematomyces caribensis
1/100/97
CBS 113380 Micronematomyces caribensis
0.66/97/-
CBS 113375 Micronematomyces caribensis
0.99/-/-
CBS 113381 Micronematomyces caribensis
1/91/92
1/-/-
CBS 113378 Micronematomyces caribensis
CBS 113379 Micronematomyces caribensis
0.6/-/-
CBS 113611 Micronematomyces chromolaenae
CBS 113371 Micronematomyces chromolaenae
Micronematomyces* 17
CBS 122464 Rhachisphaerella mozambica
Rhachisphaerella* 18
CBS 115123 Neophloeospora maculans
Neophloeospora* 19
0.1
Mycosphaerellaceae

Fig. 3. (Continued).

28), *Nothophaeocryptopus* (clade 29), *Scolecostigmina* (clade 30), *Trochophora* (clade 32), *Sonderhenia* (clade 34), *Ramularia* (clade 35), *Zymoseptoria* (clade 36), and *Xenoramularia* (clade 37). Three clades have good candidates for epitypification: *Mycovellosiella* (clade 10), *Passalora* (clade 22), and *Distocercospora* (clade 27). Three clades have multiple type species and need to be addressed: *Cercosporella* and *Acervuloseptoria* (clade 18), *Sphaerulina* and *Miuraea* (clade 12), *Pseudocercospora* and *Neopseudocercospora* (clade 23). Seven distinct clades include species that are assigned to new genera: *Cercoramularia* (clade 13), *Distocercosporaster* (clade 15), *Pleuropassalora* (clade 20), *Graminopassalora* (clade 21), *Coremiopassalora* (clade 24), *Parapallidocercospora* (clade 31), *Pseudophaeophleospora* (clade 33).

Dataset 3 consisted of clades 38–66 of Fig. 1 with additional taxa, included a total of 111 taxa and used *Schizothyrium pomi* (CBS 486.50) as outgroup. In addition, a total of 7 strains

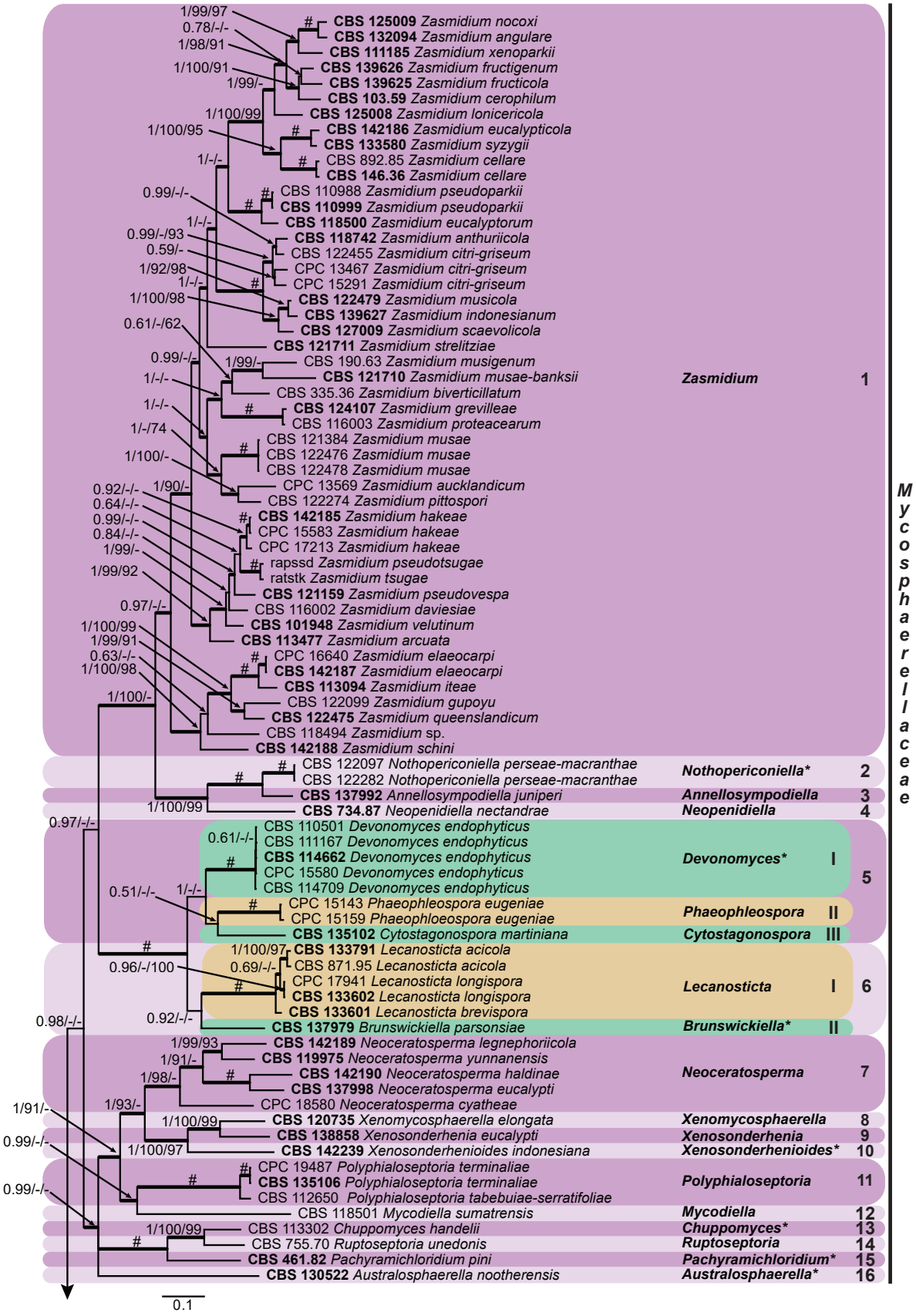
representing 7 taxa from dataset 4 were used for context. The final alignment contained in all 2 067 characters divided in three partitions containing 729 (LSU), 779 (*rpb2*), 548 (ITS) characters respectively, including alignment gaps. From the complete alignment, 10 characters previously introduced as spacers between the genes were excluded from the phylogenetic analysis. The **Bayesian** analysis generated 8 242 trees of which 2 060 trees were discarded (25 % burnin). The posterior probability values were calculated from the remaining 6 182 trees (Fig. 3; first value: PP ≤1 % shown). The alignment contained a total of 824 unique site patterns: 125 (LSU), 478 (*rpb2*) and 233 (ITS). The **Maximum-Likelihood** analysis detected 821 distinct patterns and reached a final ML optimization likelihood of −23304.617065. The bootstrap support values from the best-scoring tree were mapped on the Bayesian tree as the second value in the tree nodes (Fig. 3; ML-BS ≥ 90 % shown). The **Maximum Parsimony** analysis generated the maximum 1 000 equally most parsimonious trees and the bootstrap support values were mapped on the Bayesian tree as the third value (Fig. 3, MP-BS ≥ 90 % shown). From the 2 057 characters, 1 227 were constant, 175 were variable and parsimony-uninformative and 655 were parsimony-informative. A parsimony consensus tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 3; Length = 4806, CI = 0.309, RI = 0.734, RC = 0.227; HI = 0.691). The phylogenetic trees based on **dataset 3** (Fig. 3) that were generated with Bayesian and maximum likelihood methods, separated strains into the same generic clades. The phylogenetic trees generated using parsimony differed slightly in the clade order (data not shown, trees deposited on TreeBASE). Eight genera represent stable genera since they maintain their positions in the present analysis as they displayed in previous phylogenetic studies, and most of them are based on their respective type strain: *Amycosphaerella* (clade 8), *Pseudocercosporella* (clade 10), *Paracercospora* (clade 11), *Pantospora* (clade 12), *Asperisporium* (clade 13), *Dothistroma* (clade 20), *Stromatoseptoria* (clade 22), and *Phaeocercospora* (clade 28). Two clades have good candidates for epitypification: *Fulvia* (clade 23) and *Phaeoramularia* (clade 25). Eighteen clades have species belonging to *Passalora s. lat.* that are reassigned into new genera: *Neocercosporidium* (clade 1), *Sultanimyces* (clade 2), *Paracercosporidium* (clade 3), *Parasirosporium* (clade 4), *Cercosporidium* (clade 5), *Paramycovellosiella* (clade 7), *Distomycovellosiella* (clade 9), *Nothopassalora* (clade 14), *Phanerohilum* (clade 15), *Pluripassalora* (clade 16), *Micronematomyces* (clade 17), *Rhachisphaerella* (clade 18), *Neophloeospora* (clade 19), *Hyalocercosporidium* (clade 21), *Deightonomyces* (clade 26), *Pleopassalora* (clade 27), *Rosisphaerella* (clade 29), and *Exutisphaerella* (clade 30). Four clades have species belonging to *Passalora s. lat.* that are reassigned into resurrected genera: *Cercosporidium* (clade 5), *Fulvia* (clade 23), *Ragnhildiana* (clade 24), and *Phaeoramularia* (clade 25).

Dataset 4 consisted of clades 66–108 of Fig. 1, which included a total of 147 taxa and used *Cylindroseptoria ceratoniae* (CBS 477.69) as outgroup. In addition, the final alignment contained a total of 2 121 characters divided in three partitions containing 767 (LSU), 761 (*rpb2*), 583 (ITS) characters respectively, including alignment gaps. From the total alignment 26 characters were excluded: 10 characters that were previously introduced as spacers between the genes and 16 characters from the ITS that existed only for the outgroup. The **Bayesian** analysis generated 26 202 trees from which 6 550 trees were discarded (25 % burnin). The posterior probability values were calculated from the remaining 19 652 trees (Fig. 4; first value: PP ≤1 shown). The alignment contained altogether 1 209 unique site patterns: 262 (LSU), 557 (*rpb2*) and 390 (ITS). The **Maximum-Likelihood** analysis detected 1187 distinct patterns and reached a final ML optimization likelihood of −57749.224872. The bootstrap support values from the best-scoring tree were mapped on the Bayesian tree as the third value in the tree nodes

Fig. 4. Phylogenetic tree (50 % majority rule consensus) resulting from a Bayesian analysis of the combined LSU, *rpb2* and ITS sequence alignment (dataset 4; representing clades 67–99 of Fig. 1). Bayesian posterior probabilities (PP), maximum likelihood bootstrap support values (≥ 90 %; ML-BS) and maximum parsimony bootstrap support values (≥ 90 %; MP-BS) are indicated at the nodes (PP/ML-BS/MP-BS) and the scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Genera clades are delimited in coloured boxes, with the genus name and clade number indicated to the right. All taxa names are written in black, ex-type strains are represented in bold, novel genera with an asterisk (*) and resurrected genera with a circumflex (^). A vertical bar is used to the right of the coloured boxes and encompass all genera within their respective families. The family name *Mycosphaerellaceae* is unnabreviated while the rest are abbreviated as follows: *D = Dissoconiaceae*, *P = Phaeothecoidiellaceae*, *S = Schizothyriaceae*, *T = Teratosphaeriaceae*, *C = Cladosporiaceae*. The tree was rooted to *Cylindroseptoria ceratoniae* (CBS 477.69).

(Fig. 4; ML-BS ≥ 90 % shown). The **Maximum Parsimony** analysis generated the maximum of 1 000 equally most parsimonious trees and the bootstrap support values were mapped on the Bayesian tree as the third value (Fig. 4, MP-BS ≥ 90 % shown). From the 2 094 characters, 936 were constant, 127 were variable and parsimony-uninformative and 1 031 were parsimony-informative. A parsimony consensus tree was calculated from the equally most parsimonious trees and the branches were mapped with a thicker stroke on the Bayesian tree (Fig. 4; Length = 14 343, CI = 0.177, RI = 0.666, RC = 0.118, HI = 0.823).

The phylogenetic trees based on **dataset 4** (Fig. 4) that were generated with Bayesian and maximum likelihood methods, separated strains into the same generic clades. The phylogenetic trees generated using parsimony differed slightly in the clade order (data not shown, trees deposited on TreeBASE). Seven families are represented in the tree: *Mycosphaerellaceae* (clades 1–29), *Schizothyriaceae* (*S*), *Dissoconiaceae* (*D*), *Phaeothecoidiellaceae* (*P*), *Teratosphaeriaceae* (*T*), *Cladosporiaceae* (*C*) and the single strain used as outgroup belonging to the *Dothideaceae*. Within the *Phaeothecoidiellaceae*, a new genus is described, namely *Exopassalora* (clade 31). Within the *Mycosphaerellaceae*, seventeen genera are stable since they maintain their positions in the present analysis as they displayed in previous phylogenetic studies, and most of them are based on their respective type strain: *Annellosympodiella* (clade 3), *Neopenidiella* (clade 4), *Phaeophleospora* (clade 5), *Lecanosticta* (clade 6), *Neoceratosperma* (clade 7), *Xenomycosphaerella* (clade 8), *Xenosonderhenia* (clade 9), *Polyphialoseptoria* (clade 11), *Mycodiella* (clade 12), *Ruptoseptoria* (clade 14), *Paramycosphaerella* (clade 17), *Brunneosphaerella* (clade 18), *Neomycosphaerella* (clade 20), *Microcyclosporella* (clade 23), *Mycosphaerelloides* (clade 24), *Epicoleosporium* (clade 25), and *Exosporium* (clade 29). The genus *Zasmidium* (clade 1) is redefined as a broader genus and includes species previously belonging to *Ramichloridium*, *Rasutoria*, and *Periconiella* (see also Fig. 5). Eleven clades represent new genera: *Nothopericoniella* (clade 2), *Xenosonderhenioides* (clade 10), *Chuppomyces* (clade 13), *Pachyramichloridium* (clade 15), *Australosphaerella* (clade 16), *Madagascaromyces* (clade 19), *Hyalozasmidium* (clade 21), *Pseudopericoniella* (clade 22), *Mucosphaerella* (clade 26), *Pseudozasmidium* (clade 27), *Saccharosporium* (clade 28). The genera *Ramichloridium* (clade 30) and *Stenella* (clade 32) cluster outside *Mycosphaerellaceae*, in the families *Dissoconiaceae* (*D*) and *Teratosphaeriaceae* (*T*), respectively.


CBS 125009 Zasmidium nocoxi
CBS 132094 Zasmidium angulare
CBS 111185 Zasmidium xenoparkii
CBS 139626 Zasmidium fructigenum
CBS 139625 Zasmidium fructicola
CBS 103.59 Zasmidium cerophilum
CBS 125008 Zasmidium lonicericola
CBS 142186 Zasmidium eucalypticola
CBS 133580 Zasmidium syzygii
CBS 892.85 Zasmidium cellare
CBS 146.36 Zasmidium cellare
CBS 110988 Zasmidium pseudoparkii
CBS 110999 Zasmidium pseudoparkii
CBS 118500 Zasmidium eucalyptorum
CBS 118742 Zasmidium anthuriicola
CBS 122455 Zasmidium citri-griseum
CPC 13467 Zasmidium citri-griseum
CPC 15291 Zasmidium citri-griseum
CBS 122479 Zasmidium musicola
CBS 139627 Zasmidium indonesianum
CBS 127009 Zasmidium scaevolicola
CBS 121711 Zasmidium strelitziae
CBS 190.63 Zasmidium musigenum
CBS 121710 Zasmidium musae-banksii
CBS 335.36 Zasmidium biverticillatum
CBS 124107 Zasmidium grevilleae
CBS 116003 Zasmidium proteacearum
CBS 121384 Zasmidium musae
CBS 122476 Zasmidium musae
CBS 122478 Zasmidium musae
CPC 13569 Zasmidium aucklandicum
CBS 122274 Zasmidium pittospori
CBS 142185 Zasmidium hakeae
CPC 15583 Zasmidium hakeae
CPC 17213 Zasmidium hakeae
rapssd Zasmidium pseudotsugae
ratstk Zasmidium tsugae
CBS 121159 Zasmidium pseudovespa
CBS 116002 Zasmidium daviesiae
CBS 101948 Zasmidium velutinum
CBS 113477 Zasmidium arcuata
CPC 16640 Zasmidium elaeocarpi
CBS 142187 Zasmidium elaeocarpi
CBS 113094 Zasmidium iteae
CBS 122099 Zasmidium gupoyu
CBS 122475 Zasmidium queenslandicum
CBS 118494 Zasmidium sp.
CBS 142188 Zasmidium schini
Zasmidium 1
CBS 122097 Nothopericoniella perseae-macranthae
CBS 122282 Nothopericoniella perseae-macranthae
Nothopericoniella* 2
CBS 137992 Annellosympodiella juniperi
Annellosympodiella 3
CBS 734.87 Neopenidiella nectandrae
Neopenidiella 4
CBS 110501 Devonomyces endophyticus
CBS 111167 Devonomyces endophyticus
CBS 114662 Devonomyces endophyticus
CPC 15580 Devonomyces endophyticus
CBS 114709 Devonomyces endophyticus
Devonomyces* I
CPC 15143 Phaeophleospora eugeniae
CPC 15159 Phaeophloeospora eugeniae
Phaeophleospora II
CBS 135102 Cytostagonospora martiniana
Cytostagonospora III
5
CBS 133791 Lecanosticta acicola
CBS 871.95 Lecanosticta acicola
CPC 17941 Lecanosticta longispora
CBS 133602 Lecanosticta longispora
CBS 133601 Lecanosticta brevispora
Lecanosticta I
CBS 137979 Brunswickiella parsonsiae
Brunswickiella* II
6
CBS 142189 Neoceratosperma legnephoriicola
CBS 119975 Neoceratosperma yunnanensis
CBS 142190 Neoceratosperma haldinae
CBS 137998 Neoceratosperma eucalypti
CPC 18580 Neoceratosperma cyatheae
Neoceratosperma 7
CBS 120735 Xenomycosphaerella elongata
Xenomycosphaerella 8
CBS 138858 Xenosonderhenia eucalypti
Xenosonderhenia 9
CBS 142239 Xenosonderhenioides indonesiana
Xenosonderhenioides* 10
CPC 19487 Polyphialoseptoria terminaliae
CBS 135106 Polyphialoseptoria terminaliae
CBS 112650 Polyphialoseptoria tabebuiae-serratifoliae
Polyphialoseptoria 11
CBS 118501 Mycodiella sumatrensis
Mycodiella 12
CBS 113302 Chuppomyces handelii
Chuppomyces* 13
CBS 755.70 Ruptoseptoria unedonis
Ruptoseptoria 14
CBS 461.82 Pachyramichloridium pini
Pachyramichloridium* 15
CBS 130522 Australosphaerella nootherensis
Australosphaerella* 16
0.1
Mycosphaerellaceae

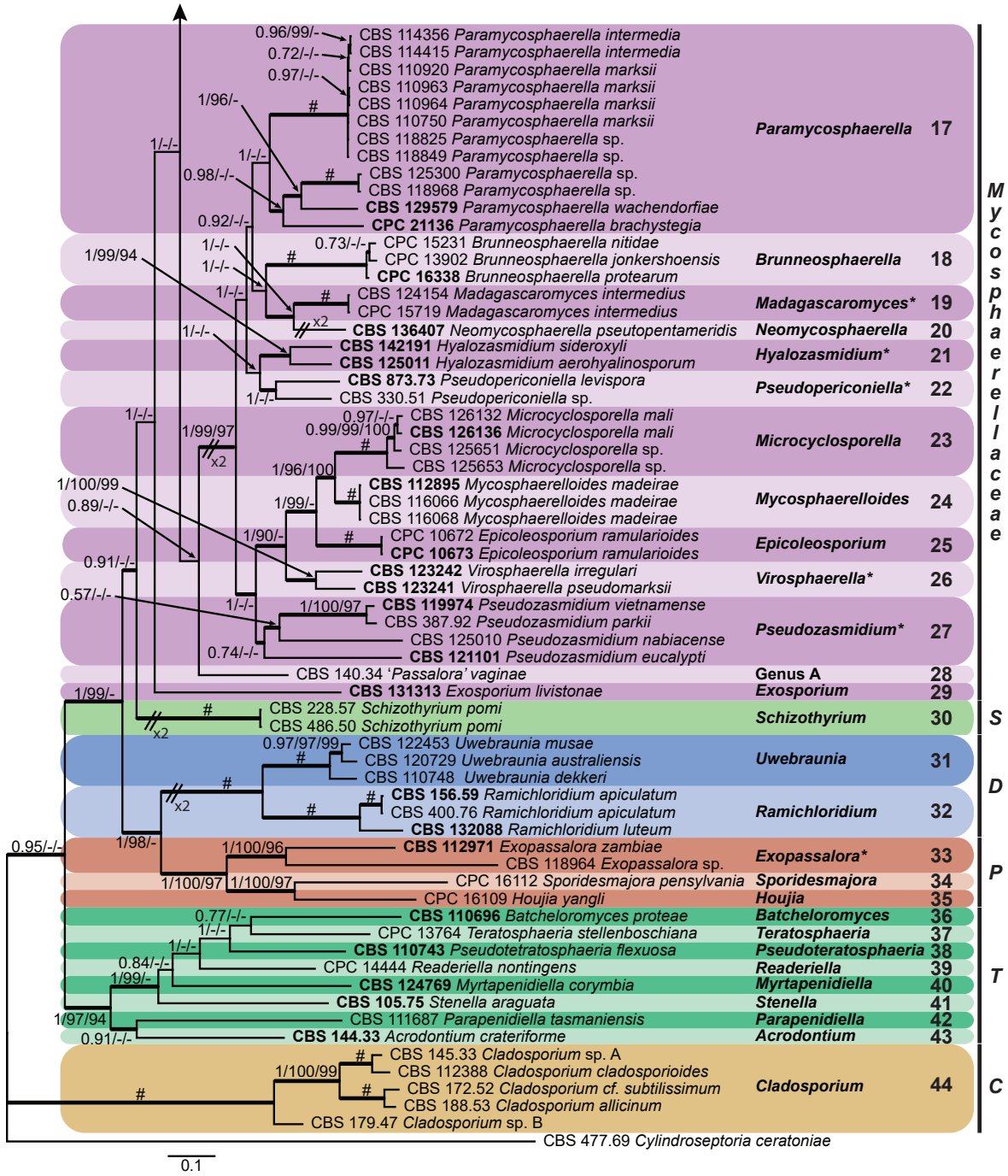


Fig. 4. (Continued).

Taxonomy

The taxonomy section is organized in two parts. The first part is organised by clade number based on the tree depicted in Fig. 1 and covers in detail the genera described in the *Mycosphaerellaceae* for which cultures were available. Untreated taxa whose names are placed under inverted commas are discussed with the genus they were included in, and occur in a coloured box in the trees. The discussed species have a link to the photoplates and trees where they appear. An extra section referring to the genera with uncertain affinity associated with *Mycosphaerellaceae* can

be found at the end of this section. Information about the host and origin of the type specimen is provided along with the most recent reference for a description or illustration in order to motivate the recollection of the species with phylogenetic positions still undetermined. Due to the large number of taxa discussed throughout this manuscript, the taxon names are written in full.

CLADES 1–94: *Mycosphaerellaceae*

Mycosphaerellaceae Lindau, Nat. Pflanzenfam., Teil I, 1(1): 421. 1897.
Basionym: *Sphaerellaceae* Nitschke, Verh. Naturhist. Vereins Preuss. Rheinl. 26: 74. 1869, nom. illeg. (Art. 18.3 and 57.1), non *Sphaerellaceae* (algae).
Synonyms: *Ramularieae* Sacc., Syll. Fung. 4: 188. 1886.
Septocylindrieae Sacc., Syll. Fung. 4: 188. 1886.
Cercosporaceae Nann., Repert. mic. uomo 4: 507. 1934.
Cercosporellaceae Nann., Repert. mic. uomo 4: 473. 1934.
Ramulariaceae (Sacc.) Nann., Repert. mic. uomo 4: 472. 1934.
Septocylindriaceae (Sacc.) Nann., Repert. mic. uomo 4: 188. 1934.
Septoriaceae W.B. Cooke, Revta Biol. (Lisboa) 12(12): 298. 1983.

Clade 1: *Neopseudocercosporella*

Neopseudocercosporella Videira & Crous, Stud. Mycol. 83: 80. 2016.

Description (from Videira *et al.* 2016): Phytopathogenic, causing leaf spots. *Mycelium* internal, hyaline, septate, branched, stromata almost absent to well-developed. *Ascomata* pseudothecial, mycosphaerella-like, single to aggregated, black, immersed, becoming erumpent, globose, with apical ostiole; wall of medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid to narrowly ellipsoid. *Ascospores*, straight to fusoid-ellipsoid, hyaline, guttulate, thin-walled, with subobtuse ends, medianly 1-septate. *Conidiophores* solitary or grouped, erumpent through the cuticle or emerging through stomata, hyaline, sometimes faintly pigmented, smooth, simple, straight, slightly curved or geniculate-sinuous, usually aseptate, i.e. reduced to conidiogenous cells, thin-walled, smooth. *Conidiogenous cells* hyaline, subcylindrical to geniculate-sinuous, with inconspicuous conidiogenous loci, unthickened, neither darkened nor refractive, mostly truncate. *Conidia* solitary, hyaline or rarely slightly pigmented, thin-walled, smooth, straight to flexuous, subcylindrical to obclavate, with apex obtuse to subacute and base truncate, sometimes somewhat obconically, one- to multiseptate, hilum not thickened or darkened.

Type species: *Neopseudocercosporella capsellae* (Ellis & Everh.) Videira & Crous (≡ *Cylindrosporium capsellae* Ellis & Everh.).

Neopseudocercosporella capsellae (Ellis & Everh.) Videira & Crous, Stud. Mycol. 83: 86. 2016.
Basionym: *Cylindrosporium capsellae* Ellis & Everh., J. Mycol. 3(11): 130. 1887.
Synonyms: *Cercoseptoria capsellae* (Ellis & Everh.) H.C. Greene, Trans. Wisconsin Acad. Sci. 47: 127. 1959.
Pseudocercosporella capsellae (Ellis & Everh.) Deighton, Mycol. Pap. 133: 42. 1973.

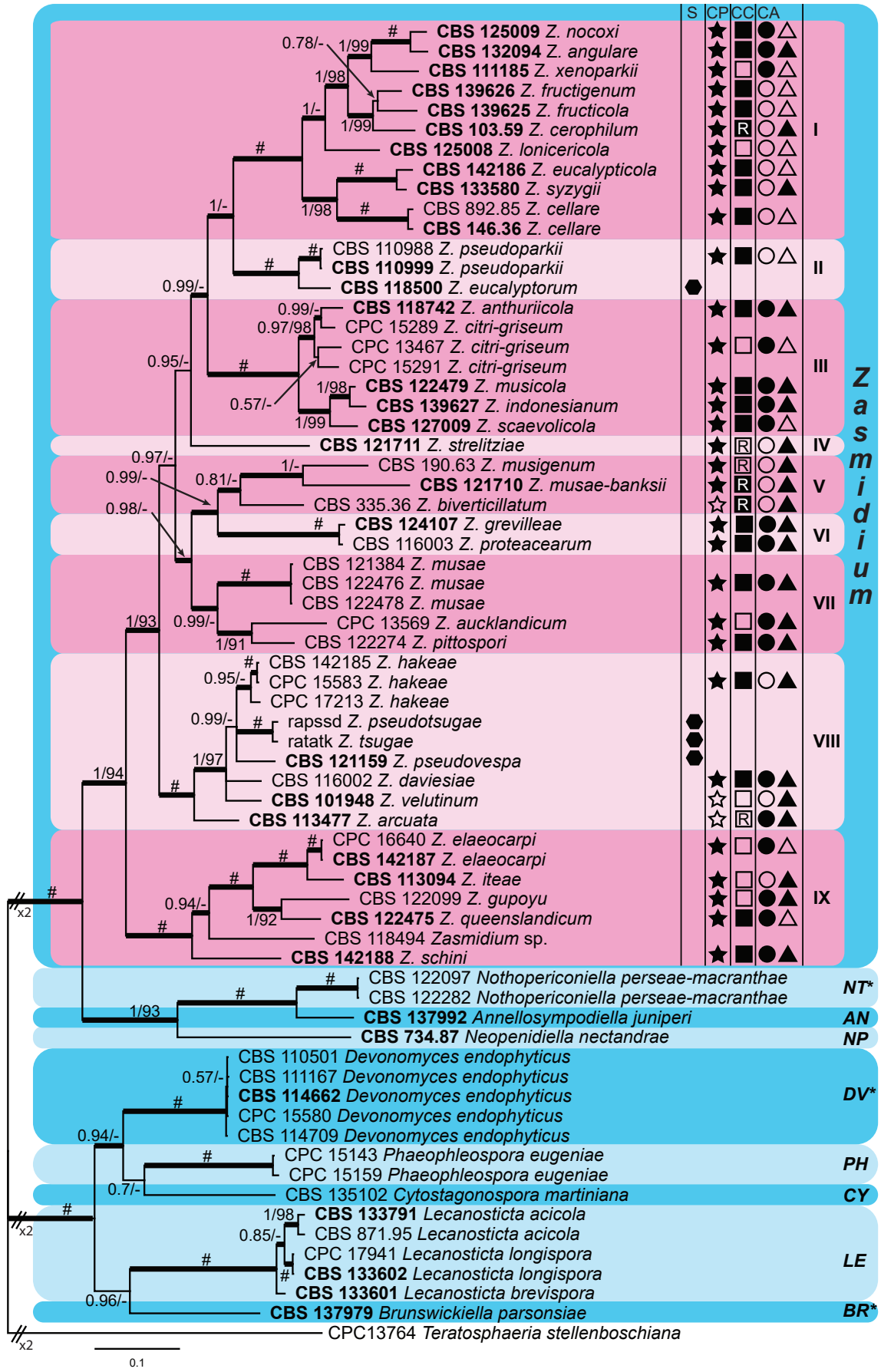
For additional synonyms see Braun (1995) or MycoBank.

Descriptions and illustrations: Braun (1995), Videira *et al.* (2016).

Materials examined: **Japan**, Miyazaki, on *Brassica rapa* var. *oleifera*, unknown date, K. Kishi, culture MAFF 237605 = MUCC 1254. **New Zealand**, Auckland, Mt. Albert, on *Brassica* sp., unknown date and collector, isol. C.F. Hill, Jul. 2005, culture CBS 118412. **Republic of Korea**, Hongcheon, on *Capsella bursa-pastoris*, 4 Nov. 2005, H.D. Shin, culture CPC 12519; on *Draba nemorosa*, 30 Oct. 2004, H.D. Shin, culture CBS 135464 = CPC 11677; Namyangju, on *Raphanus sativus*, 22 Oct. 2007, H.D. Shin, culture CBS 131896 = CPC 14773. **Unknown country**, on *Brassica* sp., unknown date and collector, isol. R. Evans, 28 Aug. 2002, cultures CBS 112032 = HJS 601, CBS 112033 = HJS 600. **USA**, Columbia, Missouri, Boone Co., on *Capsella bursa-pastoris*, May 1887, Galloway 253 (**holotype** NY 883641, **isotype** BPI 399944).

Notes: The genus *Neopseudocercosporella* was recently established to accommodate two species that were initially placed in *Pseudocercosporella*, but were not congeneric with the type species *Pseudocercosporella bakeri* (Videira *et al.* 2016). Both *Neopseudocercosporella capsellae* and *Neopseudocercosporella brassicae* are considered important pathogens of *Brassica* spp. (e.g. broccoli, cauliflower, Brussels sprout, etc.) and have been reported worldwide. In literature, these pathogens are usually distinguished based on their disease symptoms, morphology of their ascospores, and culture characteristics (Inman *et al.* 1991). However, based on the DNA similarities of the currently available strains (Fig. 1, clade 1; Fig. 2, clade 5), these species are so similar that more research is required in order to fully understand their identity and biology (Videira *et al.* 2016).

Fig. 5. Phylogenetic tree (50 % majority rule consensus) resulting from a Bayesian analysis of the combined LSU, *rpb2* and ITS sequence alignment of the strains in the clades 1–6 from Fig. 4 (clades 67–72 of Fig. 1). Bayesian posterior probabilities (PP) and maximum parsimony bootstrap support values (≥ 90 %; MP-BS) are indicated at the nodes (PP/MP-BS) and the scale bar represents the expected number of changes per site. Branches in a thicker stroke represent the branches present in the strict consensus parsimony tree. Genera clades are delimited in dark and light blue boxes, with the genus name indicated to the right. The genus name *Zasmidium* is unnabreviated while the rest are abbreviated as follows: *NT* = *Nothopericoniella*, *AN* = *Annellosimpodiella*, *NP* = *Neopenidiella*, *DV* = *Devonomyces*, *PH* = *Phaeophleospora*, *CY* = *Cytostagonospora*, *LE* = *Lecanosticta*, *BR* = *Brunswickiella*. All taxa names are written in black, ex-type strains are represented in bold and novel genera with an asterisk (*). The dark and light pink coloured boxes, numbered with roman numerals to the right, represent a possible phylogenetic division of the genus *Zasmidium* based on branch support and/or taxonomic history. Within the pink boxes, the generic name of *Zasmidium* was abbreviated (*Z.* = *Zasmidium*) and a grid representing morphological charaters respective of each taxon is displayed to the right of the taxa and should be interpreted as: S – only sexual morph described (filled hexagon); CP – conidiophores unbranched (filled star), conidiophores branched (empty star); CC – conidiogenous cell terminal (filled square), conidiogenous cell terminal forming rachis (filled square with letter R in white), conidiogenous cell terminal and intercalary (empty square), conidiogenous cell terminal and intercalary forming rachis (empty square with letter R in black); CA – conidia long (>30 µm average; full circle), conidia short (<30 µm average; empty circle), single (full triangle), catenate (empty triangle). The tree was rooted to *Teratosphaeria stellenboschiana* (CPC 13764).


S
CP
CC
CA
CBS 125009 Z. nocoxi
CBS 132094 Z. angulare
CBS 111185 Z. xenoparkii
CBS 139626 Z. fructigenum
CBS 139625 Z. fructicola
CBS 103.59 Z. cerophilum
CBS 125008 Z. lonicericola
CBS 142186 Z. eucalypticola
CBS 133580 Z. syzygii
CBS 892.85 Z. cellare
CBS 146.36 Z. cellare
I
CBS 110988 Z. pseudoparkii
CBS 110999 Z. pseudoparkii
CBS 118500 Z. eucalyptorum
II
CBS 118742 Z. anthuriicola
CPC 15289 Z. citri-griseum
CPC 13467 Z. citri-griseum
CPC 15291 Z. citri-griseum
CBS 122479 Z. musicola
CBS 139627 Z. indonesianum
CBS 127009 Z. scaevolicola
III
CBS 121711 Z. strelitziae
IV
CBS 190.63 Z. musigenum
CBS 121710 Z. musae-banksii
CBS 335.36 Z. biverticillatum
V
CBS 124107 Z. grevilleae
CBS 116003 Z. proteacearum
VI
CBS 121384 Z. musae
CBS 122476 Z. musae
CBS 122478 Z. musae
CPC 13569 Z. aucklandicum
CBS 122274 Z. pittospori
VII
CBS 142185 Z. hakeae
CPC 15583 Z. hakeae
CPC 17213 Z. hakeae
rapssd Z. pseudotsugae
ratatk Z. tsugae
CBS 121159 Z. pseudovespa
CBS 116002 Z. daviesiae
CBS 101948 Z. velutinum
CBS 113477 Z. arcuata
VIII
CPC 16640 Z. elaeocarpi
CBS 142187 Z. elaeocarpi
CBS 113094 Z. iteae
CBS 122099 Z. gupoyu
CBS 122475 Z. queenslandicum
CBS 118494 Zasmidium sp.
CBS 142188 Z. schini
IX
Zasmidium
CBS 122097 Nothopericoniella perseae-macranthae
CBS 122282 Nothopericoniella perseae-macranthae
NT*
CBS 137992 Annellosympodiella juniperi
AN
CBS 734.87 Neopenidiella nectandrae
NP
CBS 110501 Devonomyces endophyticus
CBS 111167 Devonomyces endophyticus
CBS 114662 Devonomyces endophyticus
CPC 15580 Devonomyces endophyticus
CBS 114709 Devonomyces endophyticus
DV*
CPC 15143 Phaeophleospora eugeniae
CPC 15159 Phaeophleospora eugeniae
PH
CBS 135102 Cytostagonospora martiniana
CY
CBS 133791 Lecanosticta acicola
CBS 871.95 Lecanosticta acicola
CPC 17941 Lecanosticta longispora
CBS 133602 Lecanosticta longispora
CBS 133601 Lecanosticta brevispora
LE
CBS 137979 Brunswickiella parsonsiae
BR*
CPC13764 Teratosphaeria stellenboschiana
0.1

Clade 2: *Fusoidiella*

Fusoidiella Videira & Crous, Stud. Mycol. 83: 87. 2016.

Description: Phytopathogenic, causing small yellow to olivaceous green spots on leaves. *Mycelium* internal. *Conidiophores* aggregated in dense fascicles, arising through stomata, aseptate, i.e. usually reduced to conidiogenous cells, smooth, brown, subcylindrical to clavate, straight to curved due to thickening of the wall on one side, not geniculate, one to multiple conidiogenous loci located laterally or apically, loci conspicuous, thickened and broad, areolate, darkened and refractive. *Conidia* solitary, smooth to rough, hyaline to pale brown, thin- to thick-walled, fusiform to obclavate-fusiform, straight to somewhat curved, septate, not constricted at the septa, apex obtuse and base truncate, hilum flattened, thickened, darkened and refractive.

Type species: *Fusoidiella depressa* (Berk. & Broome) Videira & Crous (≡ *Cladosporium depressum* Berk. & Broome).

Fusoidiella anethi (Pers.) Videira & Crous, **comb. nov.** MycoBank MB822818.
Basionym: *Sphaeria anethi* Pers., Observ. mycol. 1: 67. 1796.
Synonyms: *Dothidea anethi* (Pers.) Fr., Summa veg. Scand., Sectio Post. 2: 387. 1849.
Azosma punctum Lacroix, Pl. Cryptog. France, Ed. 2, Fasc. XVI, no. 757. 1860.
Mycosphaerella anethi (Pers.) Petr., Ann. Mycol. 25: 229. 1927.
Cercosporidium punctum (Lacroix) Deighton, Mycol. Pap. 112: 48. 1967.
Passalora punctum (Lacroix) Petzoldt (as "*puncta*") Nova Hedwigia, Beih. 87: 192. 1987.
For additional synonyms see Deighton (1967) or MycoBank.

Descriptions and illustrations: Deighton (1967) and Crous & Braun (2003).

Materials examined: **Italy**, unknown host, collector and date, isol. M. Curzi, culture CBS 296.32. **New Zealand**, Auckland, St. John's, on *Foeniculum vulgare*, unknown collector and date, isol. C.F. Hill (1099-B), Dec. 2004, culture CBS 117584.

Notes: This species is the pathogenic agent responsible for cercosporoid leaf blight on *Foeniculum* (fennel), *Petroselinum* (parsley) and *Anethum* (dill) (Davis & Raid 2002). The taxonomic history of this species is complex and has been addressed by multiple authors (Deighton 1967, Arx 1987, Srivastava 1994, Crous & Braun 2003, Nakashima *et al.* 2011). Morphologically the isolates obtained from all three hosts appear to be identical but some varieties may be present. The connection between the sexual morph *Mycosphaerella anethi* and the asexual morph *Passalora punctum* has been experimentally proven by Petzoldt (1989, 1990). The disease has a worldwide distribution (Africa, Asia, Europe, the Middle East, North America) but this is the first time an isolate was reported from New Zealand. The two strains form a well-supported clade within *Fusoidiella* represented in both phylogenetic trees (Fig. 1 clade 2; Fig. 2, clade 6).

Fusoidiella depressa (Berk. & Broome) Videira & Crous, Stud. Mycol. 83: 88. 2016.
Basionym: *Cladosporium depressum* Berk. & Broome, Ann. Mag. Nat. Hist. 7: 99, t. 5: 8. 1851.
Synonyms: *Passalora depressa* (Berk. & Broome) Sacc., Nuovo Giorn. Bot. Ital. 8(2): 187. 1876.

Cercosporidium depressum (Berk. & Broome) Deighton, Mycol. Pap. 112: 37. 1967.
For additional synonyms see Deighton (1967), Crous & Braun (2003) and MycoBank.

Descriptions and illustrations: Deighton (1967), Crous & Braun (2003) and Videira *et al.* (2016).

Material examined: Republic of Korea, Bonghwa, on *Angelica gigas*, 18 Oct. 2007, H.D. Shin, KUS-F23064 = CBS H-22632, culture CBS 141335 = CPC 14915.

Notes: The genus *Fusoidiella* was recently established to accommodate *Passalora depressa*, a species that is not congeneric with *Passalora s. str.* as defined by the type species *Passalora bacilligera*. The type species has fusiform conidia that are morphologically very different from the closest phylogenetic species, *Neopseudocercosporella capsellae*, and fits the description of the authentic specimen (IMI 29181, on *Angelica sylvestris*, Great Britain; Deighton 1967) (Videira *et al.* 2016). Based on the phylogenetic analysis the present strains cluster in a well-supported clade by all three phylogenetic methods employed (Fig. 1 clade 2; Fig. 2, clade 6).

Clade 3: *Filiella*

Filiella Videira & Crous, Stud. Mycol. 83: 88. 2016.

Description (from Videira *et al.* 2016): Phytopathogenic. Mycelium internal, hyphae hyaline, septate, branched, forming well-developed stromata composed of swollen hyphae. *Conidiophores* emerging in dense fascicles from stromata, through the cuticle or through stomata, subcylindrical, straight to flexuous, geniculate-sinuous, aseptate, i.e. usually reduced to conidiogenous cells, rarely 1-septate near the base, hyaline to pale yellow at the base, thin-walled, smooth, with inconspicuous conidiogenous loci, unthickened, neither darkened nor refractive. *Conidia* solitary, acicular, subcylindrical, filiform, narrowly obclavate, hyaline, discretely septate, thin-walled, smooth, apex subacute, base truncate, hila unthickened, not darkened.

Type species: *Filiella pastinacae* (P. Karst.) Videira & Crous (≡ *Cercosporella pastinacae* P. Karst.).

Filiella pastinacae (P. Karst.) Videira & Crous, Stud. Mycol. 83: 88. 2016.
Basionym: *Cercosporella pastinacae* P. Karst., Hedwigia 23: 63. 1884.
Synonyms: *Ramularia pastinacae* (P. Karst.) Lindr. & Vestergr., Acta Soc. Fauna Fl. Fenn. 22(1): 8. 1902.
Pseudocercosporella pastinacae (P. Karst.) U. Braun, Nova Hedwigia 56(3–4): 444. 1993.
For additional synonyms see Braun (1995) and MycoBank.

Description and illustration: Videira *et al.* (2016).

Materials examined: **Finland**, Mustalia, on *Pastinaca sativa*, 7 Jul. 1867, P. Karsten (**holotype** H 3921). **Germany**, Dresden, on *Pastinaca sativa*, 1866, Rabenh., Fungi Eur. Exs. 1262 (HAL, erroneously designated as "neotype" in Braun 1995). **Sweden**, Uppland, Uppsala Näs, Vreta, on *Laserpitium latifolium*, 2 Jun. 1988, K. & L. Holm, culture CBS 114116 = UPSC 2633.

Notes: This monotypic genus was recently established to accommodate *Pseudocercosporella pastinacae*, since it was not congeneric with *Pseudocercosporella s. str*. based on *Pseudocercosporella bakeri* (Videira *et al.* 2016). This genus is represented by a single-strain lineage in the phylogenetic analyses (Fig. 1, clade 3; Fig. 2, clade 7), and it is closely related to *Neopseudocercosporella* and *Fusoidiella*. Morphologically, it can be distinguished by producing acicular-filiform conidia instead of the subcylindrical conidia of *Neopseudocercosporella capsellae*, or pigmented, fusiform conidia of *Fusoidiella depressa*. Braun's (1995) designation of a neotype, based on the assumption that the holotype was not preserved, is now obsolete since holotype material of *Cercosporella pastinacae* has recently been traced at H. The holotype material has been re-examined by U. Braun and found to represent the present species.

Clade 4: *Apseudocercosporella*

Apseudocercosporella Videira & Crous, Stud. Mycol. 83: 89. 2016.

Description (from Videira *et al.* 2016): Phytopathogenic. *Mycelium* composed of hyaline, septate, branched, thin-walled, smooth hyphae. *Conidiophores* arising from hyphae, simple, and occasionally branched, straight and subcylindrical to flexuous, geniculate-sinuous, septate or aseptate, hyaline, thin-walled, smooth. *Conidiogenous cells* integrated, terminal or conidiophores often reduced to conidiogenous cells, subcylindrical to geniculate-sinuous conidiogenous loci slightly thickened and darkened. *Conidia* formed singly, filiform, or subcylindrical, hyaline, thin-walled, smooth, septate or aseptate, base more or less truncate, hilum slightly thickened and darkened.

Type species: *Apseudocercosporella trigonotidis* Videira *et al.*

Apseudocercosporella trigonotidis Videira *et al.*, Stud. Mycol. 83: 89. 2016.

Description and illustration: Videira *et al.* (2016).

Material examined: **Republic of Korea**, Jeju, on *Trigonotis peduncularis*, 12 Nov. 2003, H.D. Shin (**holotype** KUS-F 20054, **isotype** CBS H-22515, culture ex-isotype CBS 131890 = CPC 10864); *idem*., culture CPC 10865.

Notes: This monotypic genus was recently established to accommodate a pseudocercosporella-like species that was not congeneric with *Pseudocercosporella s. str*. based on *Pseudocercosporella bakeri*. Phylogenetically, this genus is closely related to *Filiella* and *Neopseudocercosporella* (Fig. 1, clade 4; Fig. 2, clade 9). Morphologically, it can be distinguished by the conidial hila and conidiogenous loci that are slightly thickened and darkened instead of inconspicuous.

Clade 5: *Neocercospora*

Neocercospora M. Bakhshi *et al.*, Phytotaxa 213: 28. 2015.

Description (from Bakhshi *et al.* 2015a): Foliicolous and caulicolous, phytopathogenic. *Mycelium* internal. *Stromata* substomatal, weakly to moderately developed, brown. *Caespituli* amphigenous, punctiform, brown. *Conidiophores* aggregated in loose to moderately dense fascicles, arising

from the upper cells of sub-stomatal to intraepidermal brown stromata; conidiophores aseptate, reduced to conidiogenous cells. *Conidiogenous cells* unbranched, pale brown to brown, smooth, subcylindrical to cone-shaped, wider at the base, uni- to multilocal, sympodial, sub-denticulate; loci conspicuous, thickened, darkened, somewhat refractive, apical or formed on shoulders caused by geniculation. *Conidia* solitary or catenate, in unbranched chains, hyaline, smooth, guttulate or not, cylindrical, subcylindrical to obclavate-cylindrical, straight to slightly curved, septate; hilum flattened, moderately thickened, darkened and somewhat refractive.

Type species: *Neocercospora ammicola* M. Bakhshi *et al.*

Neocercospora ammicola M. Bakhshi *et al.*, Phytotaxa 213: 28. 2015.

Description and illustration: Bakhshi *et al.* (2015a).

Material examined: **Iran**, West Azerbeijan, Khoy, Firouragh, on leaves and stems of *Ammi majus*, Sep. 2012, M. Arzanlou (**holotype** IRAN 16461 F, culture ex-type CCTU 1186 = CBS 136450).

Notes: The monotypic genus *Neocercospora* was recently introduced by Bakhshi *et al.* (2015a) to accommodate a cercospora-like species that is not congeneric with *Cercospora s. str*. based on *Cercospora apii*. The most distinctive characteristics are the conidiophores reduced to conidiogenous cells and conidia that can occur in chains. Phylogenetically, this genus forms a single lineage (Fig. 1, clade 5; Fig. 2, clade 8) closely related to *Filiella* and *Neopseudocercosporella.*

Clade 6: *Septoria*

Septoria Sacc., Syll. Fung. 3: 474. 1884.

Description (from Quaedvlieg *et al.* 2013): *Mycelium in vitro* slow-growing, pale brown, septate, *in vivo* immersed. *Conidiomata* pycnidial, immersed, separate or aggregated (but not confluent), globose, papillate (or not), brown, wall of thin, pale brown *textura angularis*, inner layer of flattened, hyaline *textura angularis*, frequently somewhat darker and more thick-walled around the ostiole. *Ostiole* single, circular, central. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, either determinate or indeterminate, proliferating sympodially and/or percurrently, hyaline, smooth, ampulliform, doliiform or lageniform to short cylindrical, without thickened loci. *Conidia* hyaline, multiseptate, filiform, solitary, smooth, often constricted at septa. Sexual morphs are mycosphaerella-like.

Type species: *Septoria cytisi* Desm.

Septoria cytisi Desm., Ann. Sci. Nat., Bot., Sér. 3, 8: 24. 1847.

Description and illustration: Quaedvlieg *et al.* (2013).

Material examined: **Slovakia**, on leaves of *Laburnum anagyroides*, 1884, J.A. Baeumler, BPI USO 378994.

Notes: *Septoria* represents a genus of plant pathogenic fungi with a wide geographic distribution, commonly associated with leaf spots and stem cankers of a broad range of plant hosts. Following a proposal accepted by the International Code of Nomenclature for algae, fungi, and plants (ICN), the generic name *Septoria* Sacc. was conserved over the older synonym *Septaria* Fr. (original spelling). *Septoria s. str*. was circumscribed when Quaedvlieg *et al.* (2011) managed to obtain sequence data of both ITS (GenBank accession JF700932) and LSU (GenBank accession JF700954) from a *Septoria cytisi* fungarium specimen (BPI USO 378994). Phylogenetically, *Septoria* forms a well-supported clade (Fig. 1, clade 6; Fig. 2, clade 11) closely related to *Mycovellosiella* and *Neocercospora.*

Clade 7: *Mycovellosiella*

Mycovellosiella Rangel, Arch. Jard. Bot. Rio de Janeiro 2: 71. 1917.
Synonym: *Vellosiella* Rangel, Bol. Agric. (São Paulo) 16: 151. 1915, non Baill. 1887.

Description: Phytopathogenic, causing leaf spots. *Colonies* effuse, greyish olivaceous to olivaceous brown. *Stroma* absent or poorly developed. *Mycelium* pale to moderately deep olivaceous, septate, branched, smooth, stromata absent or small; superficial hyphae arising from internal hyphae or stromatic hyphal aggregations, usually emerging through stomata. *Conidiophores* macronematous, mononematous, solitary, arising from superficial hyphae or in small to medium fascicles, erect, tangled or forming loose ropes resembling synnemata, straight to flexuous, simple or branched, subcylindrical to geniculate-sinuous, thin-walled, continuous to septate, smooth, subhyaline to pigmented. *Conidiogenous cells* integrated, terminal, intercalary or pleurogenous, straight to geniculate-sinuous, polyblastic, sympodial, with conidiogenous loci thickened, darkened and often protuberant. *Conidia* solitary to catenate, sometimes in branched chains, ellipsoid-ovoid, subcylindrical-fusiform, obclavate, straight or curved, aseptate or multiseptate (euseptate), sub-hyaline to pigmented, smooth to slightly verruculose, ends obtuse, rounded, truncate or pointed; hila thickened and darkened; conidial secession schizolytic.

Type species: *Mycovellosiella cajani* (Henn.) Rangel ex Trotter (≡ *Cercospora cajani* Henn.).

Mycovellosiella cajani (Henn.) Rangel ex Trotter, Syll. Fung. 25: 942. 1931. Fig. 6.
Basionym: *Cercospora cajani* Henn., Hedwigia 41: 309. 1902.
Synonyms: *Vellosiella cajani* (Henn.) Rangel, Bol. Agric. (São Paulo) 16(2): 145. 1915.
Passalora cajani (Henn.) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. 1: 93. 2003.

Description in vivo *and illustrations*: Deighton (1974), Seifert *et al.* (2011).

Description in vitro (MEA; CBS 114275): *Mycelium* hyaline to brown, irregular in width, 1.5–3 µm. *Conidiophores* hyaline to brown, smooth, simple or branched, geniculate-sinuous, irregular in width, 10–50 × 2.5–5(–7.5) µm. *Conidiogenous cells* integrated, apical, intercalary, pale brown, rarely hyaline, polyblastic, simple or branched, proliferating sympodially, integrated, sometimes reduced to hyphal loci, aseptate, with thickened, darkened and rim-like loci at the apex and shoulders, 1.5–2.5 µm diam. *Conidia* cylindrical to ellipsoidal, pale brown, solitary to catenate, in single or branched chains, conically truncate at both ends or basal end, rounded at

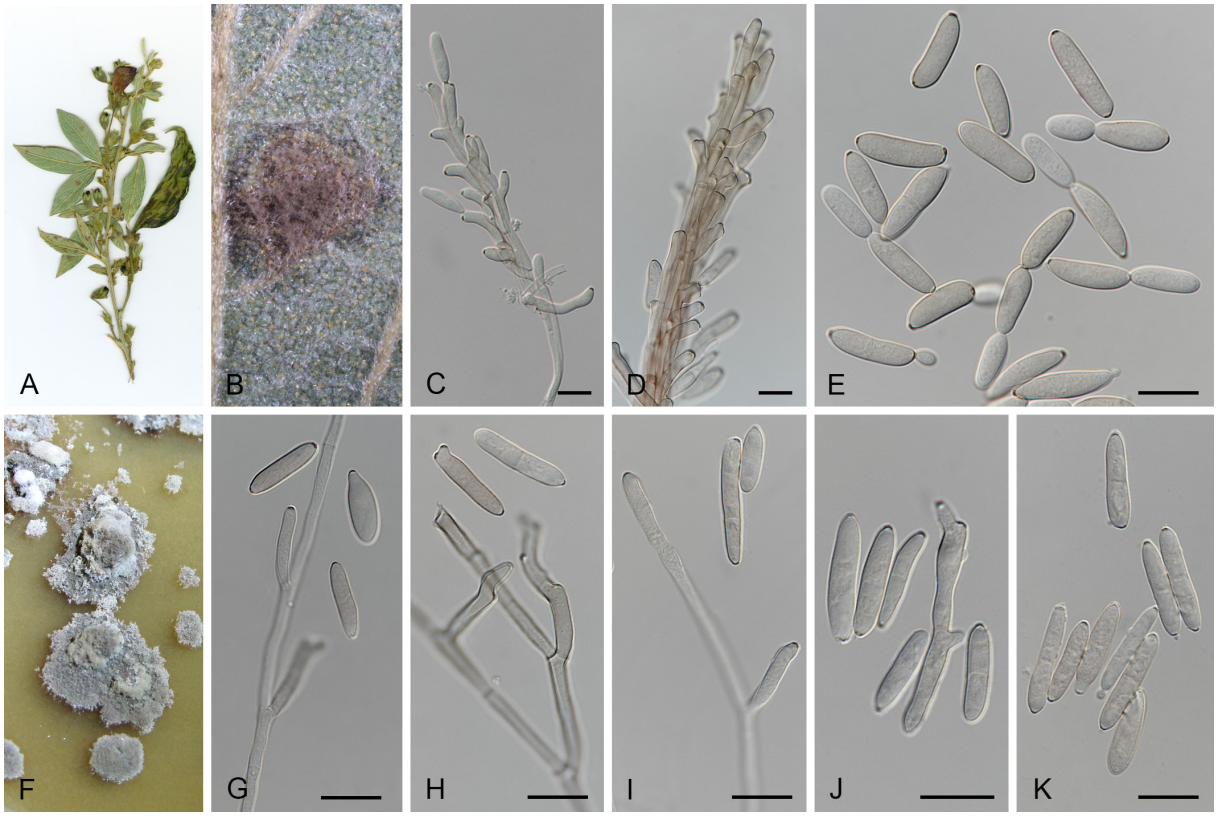


Fig. 6. *Mycovellosiella cajani* (CBS 114275). A–E. Observations *in vivo*. F–K. Observations *in vitro*. A, B. Leaf spot symptoms on the host. C, D, G–I. Conidiophores, conidiogenous cells and conidia. E, J–K. Catenate conidia. F. Culture on V8. Scale bars = 10 µm.

the apex when solitary, 7–25 × 3–7.5 µm, aseptate, with darkened, thickened, and rim-like loci at the both ends or basal end, 1.5–2.5 µm diam.

Materials examined: **Brazil**, Minas Gerais, Viçosa, on *Cajanus cajan*, 2016, R.W. Barreto (**neotype** designated here CBS H-22940, MBT378566, culture ex-neotype CBS 142174 = CPC 30580 = RB 2071A); *idem*. CPC 31579 = RB 2071B. **South Africa**, Mpumalanga, Nelspruit, on *Cajanus cajan*, 17 May 2002, L. van Jaarsveld, cultures CBS 113998 = CPC 5335, CBS 113999 = CPC 5339, CBS 114275 = CPC 5334.

Notes: The type species of *Mycovellosiella*, *Mycovellosiella cajani*, was described from leaves of *Cajanus indicus* (syn. *Cajanus cajan*), on May 1901 (Puttemans 237) in Brazil (Hennings 1902), but the type material is not preserved in B and could not be located elsewhere. Deighton (1974) examined numerous specimens deposited in IMI and TAI and concluded that two varieties could be distinguished: *Mycovellosiella cajani* var. *cajani* (conidia 0–3-septate and 10–35 µm long; South America, West Indies, Mauritius and Africa) and *Mycovellosiella cajani* var. *indica* (conidia 0–9-septate 10–129 µm long; India, Pakistan, Bangladesh and Burma). In this study, we obtained a freshly collected sample of *Cajanus cajan* from Brazil and cultured this fungus. This strain is phylogenetically identical to those from South Africa (Fig. 1, clade 7, Fig. 2, clade 10) and the morphology is identical to the descriptions available in the literature (Deighton 1974, Braun 1998), and therefore the specimen is hereby designated as neotype. *Mycovellosiella cajani* is the causative agent of leaf spot disease of pigeon pea worldwide and,

when defoliation occurs before flowering and podding, it causes severe yield losses (up to 85 % in eastern Africa) (Reddy *et al.* 2012). *Mycovellosiella*, based on phylogenetic data, is a monotypic genus but with more collections new species may emerge. Previous morphological descriptions of *Mycovellosiella s. lat.* (Deighton 1974, Braun 1998) can no longer be applied to this genus in its current circumscription and the application of this generic name depends on the availability of corresponding phylogenetic data. *Mycovellosiella* was previously distinguished from *Passalora* and *Phaeoramularia* by the formation of superficial mycelium with solitary conidiophores formed *in vivo*, but these traits are phylogenetically and taxonomically not significant and appear unreliable. Without detailed knowledge of the phylogenetic affinity, species with mycovellosiella-like morphology should tentatively be maintained in or assigned to *Passalora s. lat*.

Clade 8: *Miuraea* and *Sphaerulina*

Miuraea Hara, Byochugai-hoten: 260 & 779. 1948, emend.
Unconfirmed synonyms: *Rhopaloconidium* Petr. (1952), *Hyalodictys* Subram. (1962).

Description (adapted from Braun 1995): Leaf spot pathogen of vascular plants. *Mycelium* hyaline to lightly pigmented, septate, branched, emerging through stomata, thin-walled. *Conidiophores* little differentiated, semi-macronematous, mononematous, short, sometimes reduced to a conidiogenous cell integrated in the hyphae, with small lateral peg-like protuberances, occasionally subfasciculate and arising from stromatic hyphal aggregations. *Conidiogenesis* holoblastic, monoblastic, determinate, occasionally polyblastic, proliferation sympodial or percurrent; conidiogenous loci more or less truncate, unthickened or slightly thickened, not darkened. *Conidia* solitary or catenate, ellipsoid-ovoid, subcylindrical-vermiform, obclavate, subclavate, sometimes somewhat asymmetrical, eu- or distoseptate, pluriseptate, septa transverse, oblique to longitudinal, hyaline to faintly pigmented, thin-walled, old conidia often slightly to moderately thick-walled, hila rounded to truncate, unthickened or slightly thickened, not darkened, conidial secession schizolytic.

Type species: *Miuraea degenerans* (Syd. & P. Syd.) Hara (≡ *Clasterosporium degenerans* Syd. & P. Syd.).

Miuraea degenerans (Syd. & P. Syd.) Hara, Byochugai-hoten: 260, 1948. Fig. 7.
Basionym: *Clasterosporium degenerans* Syd. & P. Syd., Ann. Mycol. 12(2): 164. 1914.

Description in vivo: Braun (1995).

Description in vitro (on MEA; MAFF 239265): *Mycelium* hyaline, later blackish, aggregated with white-floccose aerial hyphae. *Conidiophores* short, reduced to conidiogenous cells, hyaline to pale brown, 47–71 × 2–5 µm. *Conidiogenous cells* determinate, proliferating sympodially and/or percurrently, holoblastic, with slightly thickened loci. *Conidia* solitary or catenate, oblong to obclavate, hyaline to pale, 10–23 × 6–9 µm, 2–6-eu- or distoseptate, rounded or conically truncate, slightly thickened or unthickened at the base.

Materials examined: **Japan**, Ibaragi, on *Prunus mume*, Sep. 2003, T. Kobayashi (**epitype** designated here TSU MUMH11567, MBT376838, culture ex-type MAFF 239265 = MUCC

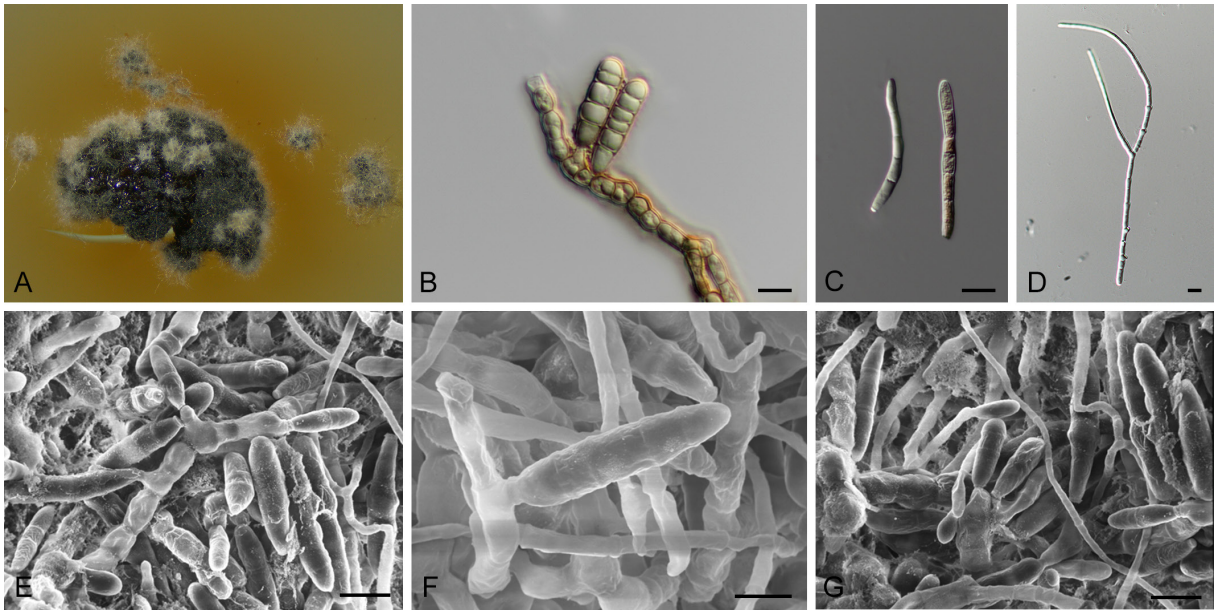


Fig. 7. *Miuraea degenerans* (MUCC 1514). A–D. Observations *in vitro*. A. Culture on MEA. B. Olivaceous conidia and short conidiophore. C. Hyaline (left) and pigmented (right) conidia. D. Microcyclic conidia. E–G. Conidiophores and conidia observed using SEM. Scale bars = 10 µm.

1514); Mutsu (= Aomori), on *Prunus mume*, 1 Nov. 1913, M. Miura (**holotype** S F41753). **Republic of Korea**, Chuncheon, on *Prunus armeniaca*, 7 Oct. 2003, H.D. Shin, CBS H-20840, cultures CBS 131935 = CPC 10828.

Notes: *Miuraea degenerans* and *Miuraea persica* are well-known as the causal agents of white mildew or frosty mildew of *Prunus* spp. in far-east Asian countries. In the present study, the sequences of both *Miuraea persicae* (sexual morph: *Mycosphaerella pruni-persicae*) and *Miuraea degenerans* are quite similar; however, comparison of ITS sequences of several collections identified as either *Miuraea degenerans* or *Miuraea persica* show a limited number of nucleotide differences (data not shown), and pending more collections and multigene data we refrain from synonomising these two species. Subramanian's (1962) description of *Miuraea degenerans* includes *Miuraea persicae*, but Braun (1995) considers them different species based on the conidial characteristics that are generally longer, with less longitudinal septa and only occasionally constricted at septa in *Miuraea persica*, while the conidia of *Miuraea degenerans* are generally broader, with more longitudinal septa and often constricted at septa. Based on the phylogenetic analysis, *Miuraea* strains cluster among *Sphaerulina* species and none of the three phylogenetic methods applied provided strong support for their separation (Fig. 1, clade 8; Fig. 2, clade 12). The introduction of more strains of *Miuraea* species in the future may provide support to the separation of these genera into two independent clades. Morphologically *Miuraea* is considered intermediate between *Pseudocercospora* and *Pseudocercosporella* (Braun 1995), which are hyphomycete genera, while *Sphaerulina* is a coelomycete genus. *Miuraea asiminae*, was recently reallocated to *Pseudocercospora* (Braun & Crous 2008).

Sphaerulina Sacc., Michelia 1(4): 399. 1878.
Unconfirmed synonyms: *Ophiocarpella* Theiss. & Syd. (1915), *Sphaerialea* Sousa da Câmara (1926).

Description (adapted from Quaedvlieg *et al.* 2013): *Ascomata* pseudothecial, immersed, subepidermal, erumpent at the apex, single to clustered, globose, papillate. *Ostiole* central, with hyaline periphyses; wall of *textura angularis*, composed of 2–4 layers of brown cells. *Hamathecium* dissolving at maturity. *Asci* bitunicate, fissitunicate, clustered, cylindrical to obclavate, rounded at apex, with or without a shallow apical chamber, short-stipitate or sessile, with 8 bi- to triseriate ascospores. *Ascospores* subcylindrical to fusiform, rounded at ends, slightly tapered, straight or slightly curved, 1–3-septate, with a primary septum nearly median, hyaline, smooth, without sheath or appendages.

Type species: *Sphaerulina myriadea* (DC.) Sacc. (≡ *Sphaeria myriadea* DC.).

Sphaerulina myriadea (DC.) Sacc., Michelia 1(4): 399. 1878.
Basionym: *Sphaeria myriadea* DC., in de Candolle & Lamarck, Fl. franç., Edn 3 (Paris) 5/6: 145. 1815.

Description and illustration: Crous *et al.* (2011d).

Materials examined: **Germany**, Driesen, Lasch, Rabenhorst, Fungi Eur. Exs. no. 149 (L). **Japan**, Aomori, Tsugaru, Kidukuri, Bense-marsh, on leaves of *Quercus dentata*, 21 Apr. 2007, K. Tanaka 2243, HHUF 29940, single ascospore culture CBS 124646 = JCM 15565. UK, on leaves of *Quercus robur*, J.E. Vize, Microfungi Brit. Ex. No. 195, IMI 57186, (= K(M) 167735). **USA**, California, Sequoia National Park. alt. 2590 m, on leaves of *Castanopsis sempervirens*, 18 Jun. 1931, H.E. Parks, BPI 623686; Lake Co., Hoberg's Resort, on leaves of *Quercus kelloggii*, 15 May 1943, V. Miller, BPI 623707; Maryland, Marlboro, on leaves of *Quercus alba*, 26 Apr. 1929, C.L. Shear, BPI 623705; Texas, Houston, on leaves of *Q. alba*, 8 Apr. 1869, H.W. Ravenel, BPI 623704.

Notes: The genus *Sphaerulina* was traditionally separated from *Mycosphaerella* based on ascospore septation, a trait that was unreliable to infer phylogenetic relatedness (Crous *et al.* 2003, Crous *et al.* 2011d). The currently available strains of *Sphaerulina myriadea* were isolated from several hosts belonging to the *Fagaceae* originating from various locations. These strains were treated in a previous study where the authors proposed that *Sphaerulina myriadea* was a species complex and therefore refrained from designating an epitype pending the collection of authentic European material on *Quercus* from France (Crous *et al.* 2011d). The genus *Sphaerulina* was previously found to be phylogenetically close to *Septoria* (Quaedvlieg *et al.* 2013, Verkley *et al.* 2013). In this work, *Sphaerulina* and *Miuraea* strains cluster together and none of the three phylogenetic methods applied provided strong support for their separation (Fig. 1, clade 8; Fig. 2, clade 12).

Species clustering in the *Sphaerulina* clade that need further material to be collected before a formal combination into *Sphaerulina* can be proposed:

Mycosphaerella grossulariae (Fr.) Lindau, in Engler & Prantl, Nat. Pflanzenfam., Teil I, 1(1): 424. 1897.

Material examined: **Netherlands**, leaf spot on *Ribes nigrum*, col. M.S.J. Ledeboer, isol. H.A. Diddens, dep. 1937, culture CBS 235.37.

Notes: The type of *Mycosphaerella grossulariae* was described from *Ribes grossularia* collected in Sweden (Aptroot 2006). Tomilin (1979) linked this species to two asexual morphs, *Phyllosticta grossulariae* and *Septoria ribis*. According to Eriksson (1992), it is morphologically indistinguishable from *Pleospora herbarum* (= *Stemphylium*). The present species is represented by a single strain in the phylogenetic analysis performed (Fig. 2, clade 12). This species needs to be recollected and its phylogenetic position resolved.

Mycosphaerella harthensis (Auersw.) Mig., Krypt.-Fl. Deutschl., Österr. Schweiz, Pilze Vol 10, Theil 3(1): 289. 1912.

Material examined: **Switzerland**, dead leaves of *Betula* sp., unknown collector and date, isol. E. Müller, 7 Jun. 1952, culture CBS 325.52.

Notes: The type of *Mycosphaerella harthensis* was described llected in Germany and the specimen is probably not preserved (Aptroot 2006). The culture CBS 325.52 is currently sterile. The present species is represented by a single strain in the phylogenetic analysis performed (Fig. 2, clade 12). This species needs to be recollected and neotypified.

Clade 9: *Cercoramularia*

Cercoramularia Videira, H.D. Shin, C. Nakash. & Crous, **gen. nov.** MycoBank MB822581.

Etymology: With cercosporidium-like conidiophores and ramularia-like conidia.

Description: *Mycelium* hyaline to brown. *Conidiophores* brown to pale brown, emerging from brown hyphae or swollen hyphal cells, smooth, euseptate, straight to geniculate-sinuous, simple or branched, sometimes reduced to conidiogenous cell. *Conidiogenous cells* integrated, terminal, hyaline to pale brown, monoblastic or proliferating sympodially, with thickened, darkened and refractive conidiogenous loci. *Conidia* hyaline to pale brown, euseptate, solitary or catenate, holoblastic, fusiform, rounded at the apex when solitary.

Type species: *Cercoramularia koreana* Videira *et al.*

Cercoramularia koreana Videira, H.D. Shin, C. Nakash. & Crous, **sp. nov.** MycoBank MB822710. Fig. 8.

Etymology: In honour of the country it was collected from, Republic of Korea.

Description in vivo (CBS H-22941; herb. spec. CPC 10709): *Leaf spots* small, irregular, 4–10 mm diam, brown to dark brown, distinct. *Stromata* absent to small, brown, globose. *Conidiophores* in loose fascicles of 2–12, dark brown, septate, geniculate-sinuous, 23–78 × 2.5–9 µm. *Conidiogenous cells* integrated, terminal, polyblastic, proliferating sympodially, with thickened, darkened, refractive and rim-like loci at the apex and shoulders, 1.6–2.5 µm diam. *Conidia* hyaline, solitary or catenate in branched chains, obclavate, cylindrical to filiform, 20–62 × 2.5 µm, 2–5-septate, with thickened and darkened rim-like hila, 1.6–2.5 µm diam, rounded at the apex when solitary. *Description* in vitro (SNA; CPC 10639): *Mycelium* hyaline to brown, 2–2.5 µm diam, with swollen brown cells. *Conidiophores* pale brown to brown, emerging

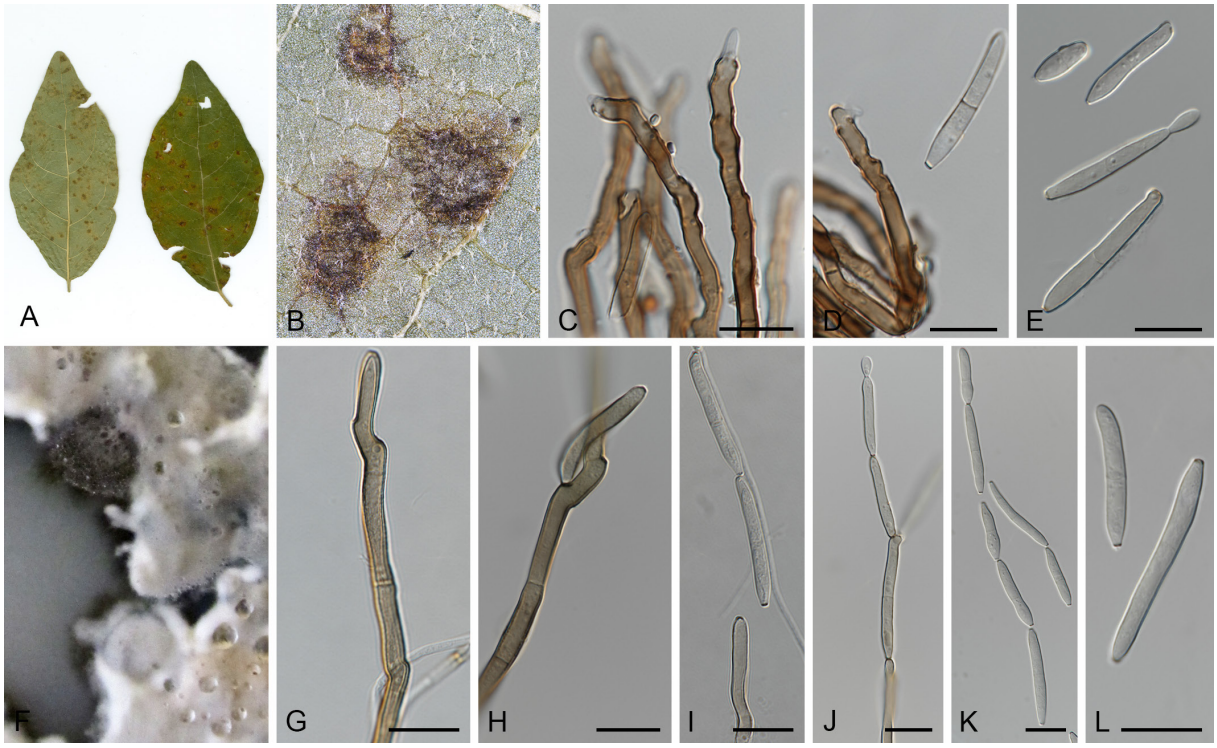


Fig. 8. *Cercoramularia koreana* (CPC 10709). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C, D. Conidiophores, conidiogenous cells and conidia. E. Catenate conidia. F–L. Observations *in vitro*. F. Culture on OA. G. Conidiophore and conidiogenous cell. H. Conidiophore, conidiogenous cell and conidium. I, J. Conidiogenous cell and catenate conidia. K, L. Catenate conidia. Scale bars = 10 µm.

from brown hyphae or swollen hyphal cells, smooth, straight to geniculous-sinuous, simple or branched, euseptate, 12.5–100 × 2.5–3 µm. *Conidiogenous cells* integrated, terminal, hyaline to pale brown, monoblastic or polyblastic, proliferating sympodially, with thickened, darkened and refractive loci, 1.8–2.8 µm diam. *Conidia* hyaline to pale brown, solitary or in chains up to six conidia, fusiform, rounded at the apex when solitary, 1-euseptate, 27–105 × 3–3.7 µm.

Materials examined: **Republic of Korea**, Seoul, on leaves of *Styrax japonica*, 17 Sep. 2003, H.D. Shin (**holotype** CBS H-22941, ex-type culture CBS 142175 = CPC 10709); same location and host, 2003, H.D. Shin, cultures CPC 10639–10641.

Notes: This genus is represented by a single species that is phylogenetically close to *Phloeospora* and *Sphaerulina* (Fig. 1, clade 9; Fig. 2, Clade 13). *Cercoramularia koreana* causes leaf spot symptoms on *Styrax japonica*, a small tree from the *Styracaceae* family commonly planted as ornamental.

Clade 10: *Phloeospora*

Phloeospora Wallr., Fl. Crypt. Germ. 2: 176. 1833.
Synonyms: *Septoria* Fr., Syst. Orb. Veg. 1: 119. 1825.
Helicobolus Wallr., Fl. Crypt. Germ. 2: 751. 1833.
Phloeochora Höhn., Ber. Deutsch. Bot. Ges. 35: 252. 1917.

Description (from Quaedvlieg *et al.* 2013): *Mycelium* immersed, septate, hyaline. *Conidiomata* acervular, subepidermal, circular, discrete or confluent, composed of hyaline to pale brown, thin-walled *textura angularis*; dehiscence irregular. *Conidiophores* reduced to conidiogenous cells or with one or two supporting cells, branched at base or not. *Conidiogenous cells* holoblastic, annellidic, occasionally also sympodial, discrete, indeterminate hyaline, smooth, cylindrical, with several apical inconspicuous annellations, formed from the upper cells of the acervuli. *Conidia* solitary, hyaline, septate, smooth, guttulate or not, cylindrical, curved, attenuated towards the apices, apex obtuse to sub-obtuse, base truncate, with minute marginal frill.

Type species: *Phloeospora ulmi* (Fr.) Wallr. (≡ *Septoria ulmi* Fr.).

Phloeospora ulmi (Fr.) Wallr., Fl. Crypt. Germ. 2: 177. 1833.
Basionym: *Septoria ulmi* Fr. [as 'Septaria'], Novit. Fl. Svec. 5(cont.): 78. 1819.
Synonyms: *Septogloeum ulmi* (Fr.) Died., Krypt. Fl. Brandenburg (Leipzig) 9: 836. 1915.
Cylindrosporium ulmi (Fr.) Vassiljevsky, Fungi Imperfecti Parasitici 2: 580. 1950.
Mycosphaerella ulmi Kleb., Z. PflKrankh. 12: 257. 1902.
Sphaerella ulmi (Kleb.) Sacc. & D. Sacc., Syll. Fung. (Abellini) 17: 642. 1905.

Description and illustration: Quaedvlieg *et al.* (2013).

Materials examined: **Austria**, Innsbruck, near Hungerburg, on leaves of *Ulmus* sp., 21 Sep. 1981, H.A. van der Aa, CBS H-14740, CBS H-14861, culture CBS 613.81; Innsbruck, road to Hungerburg, on leaves of *Ulmus glabra*, 20 Oct. 1996, W. Gams, culture CBS 344.97. **Netherlands**, Baarn, garden of CBS, Oosterstraat 1, on leaves of *Ulmus* sp., 26 Aug. 1998, H.A. van der Aa, CBS H-14739, culture CBS 101564; community of Borsele, Schouwersweel near Lisse, on *Ulmus* sp., 27 Aug. 2001, G. Verkley, culture CBS 109835.

Notes: The generic synonymy has been discussed by Sutton (1977) and the type species described and illustrated by Sutton & Pollack (1974). *Phloeospora* is based on the type species *Phloeospora ulmi*, isolated from *Ulmus glabra* in Europe, but a type specimen could not be located. It can be morphologically distinguished from *Septoria* by the production of conidia in acervuli, whereas conidiomata in the latter genus are pycnidial. A recent phylogenetic analysis performed to delimit *Septoria* and allied genera confirmed that *Phloeospora* (based on *Phloeospora ulmi*) clusters close to, but separate from *Septoria s. str*. (Quaedvlieg *et al.* 2013). This separation is also observed in the phylogenetic analyses performed in this study (Fig. 1, clade 10; Fig. 2, clade 14). The known sexual morphs linked to *Phloeospora* resemble the concepts of *Mycosphaerella*, *Didymella* and *Sphaerulina* supporting the idea that this genus is heterogenous and in need of revision (Verkley & Priest 2000). In this study, we observed that the strain currently known as *Phloeospora maculans* is not congeneric with *Phloeospora ulmi*.

Clade 11: *Cercospora*

Cercospora Fresen. ex Fuckel, Hedwigia 2(15): 91. 1863 and Fungi Rhen. Exs., Fasc. II: no. 117. 1863, nom. cons. prop.
Unconfirmed synonyms: *Virgasporium* Cooke (1875), *Cercosporina* Speg. (1910).

Description (adapted from Braun *et al.* 2013): Mostly plant pathogenic but also saprobic, usually causing distinct lesions (leaf spots) but sometimes symptomless. *Mycelium* internal and only rarely external, hyphae usually pigmented but occasionally hyaline, branched, septate, thin-walled, smooth, rarely faintly verruculose. *Stromata* lacking to well-developed, substomatal, intra-epidermal or immersed, mostly pigmented, composed of *textura angulata* or *globosa*. *Conidiophores* mono- and macro-nematous, solitary or fasciculate, rarely in sporodochial conidiomata, emerging through stomata or erumpent, erect, continuous to multi-septate, hyaline (subgen. *Hyalocercospora*) to pigmented, pale olivaceous to dark brown (subgen. *Cercospora*), wall smooth to slightly rough, thin to moderately thick, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal or intercalary, usually polyblastic but sometimes monoblastic, proliferation sympodial, rarely percurrent, conidiogenous loci (scars) conspicuous, thickened and darkened-refractive, planate with minute central pore. *Conidia* solitary, rarely in short chains, mostly scolecosporous, obclavate-cylindrical, acicular, filiform and multi-euseptate, rarely amero- to phragmosporous, broadly ellipsoid-ovoid to broadly obclavate-cylindrical, but always hyaline or subhyaline, thin-walled, smooth or almost so, hila thickened and darkened, conidial secession schizolytic.

Type species: *Cercospora apii* Fresen. (typ. cons. prop.)

Cercospora apii Fresen., Beitr. Mykol. 3: 91. 1863.

Description: Groenewald *et al.* (2005).

Materials examined: **Austria**, Wien, on *Beta vulgaris*, Jun. 1931, E.W. Schmidt, culture CBS 121.31 = CPC 5073; on *Apium* sp., 28 Aug. 2003, Institut fur Pflanzengesundheit, culture CBS 114416 = CPC 10925. **Germany**, Oestrich, garden, on *Apium graveolens*, Fuckel, Fungi Rhen. Exs. 117 (**lectotype** selected by Groenewald *et al.* 2005: HAL); Landwirtschaftsamt, Heilbron, on *Apium graveolens*, 10 Aug. 2004, K. Schrameyer (**epitype** designated by Groenewald *et al.* 2005: preserved as metabolically inactive culture CBS 116455 = CPC 11556); *idem*. CBS 116504 = CPC 11579, CBS 116507 = CPC 11582. For complete list of existing strains see Groenewald *et al.* (2013).

Notes: The genus *Cercospora* contains numerous important plant pathogenic fungi from a diverse range of hosts. The modern taxonomy of this complex began with Chupp (1954) who included all variants in a broadly circumscribed *Cercospora*. This concept was continuously revised and narrowed by several authors over the years (Deighton 1976a, 1979, Arx 1983, Braun 1995, Crous & Braun 2003). Recent studies based on multi-gene phylogenies have helped to circumscribe *Cercospora* and to identify new species. No single locus has yet been found as an ideal DNA barcode for the genus, and species identification needs to be based on a combination of gene loci and morphological characters (Groenewald *et al.* 2013, Bakhshi *et al.* 2015a, b). The type species of *Cercospora*, *Cercospora depazeoides* (= *Cercospora penicillata*) (see Braun 1995: 41), is a common, widespread cercosporoid fungus on elderberry. Re-examinations of type material and numerous other collections revealed that this species is conspecific with *Pseudocercospora sambucigena* (Braun *et al.* 2015a), which is a proven species of *Pseudocercospora* (Crous *et al.* 2013a). Therefore, *Cercospora* would formally become the oldest available name for *Pseudocercospora*, which would be reduced to synonymy with *Cercospora*. This would be an unpleasant situation with enormous consequences and name changes, which should be avoided.

Therefore, a proposal to conserve *Cercospora* with *Cercospora apii* as conserved type was recently published (Braun & Crous 2016), which will help to maintain the application of the name *Cercospora* in the common, generally accepted circumscription.

Cercospora janseana (Racib.) O. Constant., Cryptog. Mycol. 3: 63. 1982.
Basionym: *Napicladium janseanum* Racib., Parasitische Algen und Pilze Javas 2: 41. 1900.
Synonyms: *Passalora janseana* (Racib.) U. Braun, Schlechtendalia 5: 39. 2000.
Cercospora oryzae Miyake, Bot Mag. Tokyo 23 (267): 139. 1909.
Sphaerulina oryzina Hara, Diseases of the rice plant (Japan): 144. 1918.
Cercospora oryzae var. *rufipogonis* R.A. Singh & Pavgi, Sydowia 21: 176. "1967" 1968.

Description and illustration: Chupp (1954), Braun *et al.* (2015a).

Material examined: **USA**, unknown collector and date, isol. E.C. Tullis, Aug. 1937, culture CBS 145.37 = IMI 303642.

Notes: The present species is represented by a single strain in the phylogenetic analysis performed (Fig. 2, clade 1). See Braun *et al.* (2015a).

Species clustering in the *Cercospora* clade that need further material to be collected before its status as species of *Cercospora* can be confirmed:

Passalora dulcamarae (Peck) U. Braun & Crous, CBS Biodiversity Ser. 1: 167. 2003.
Basionym: *Ramularia dulcamarae* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 33: 30. 1880.
Synonyms: *Cercospora dulcamarae* (Peck) Ellis & Everh., J. Mycol. 1(4): 55. 1885.
Mycovellosiella dulcamarae (Peck) U. Braun, Mycotaxon 48: 284. 1993.
Cercospora dulcamaricola Hollós, Ann. Hist. Nat. Mus. Natl. Hung. 4: 370. 1906.

Description and illustration: Chupp (1954).

Materials examined: **Romania**, Distr. Constanta, Hagieni, on *Solanum dulcamara*, 14 Oct. 1970, O. Constantinescu & G. Negrean, CBS H-9831, CBS H-9832, culture CBS 544.71 = BUCM 2008.

Notes: *Ramularia dulcamarae* was described on *Solanum dulcamara* collected in the USA (New York, Oneida, Verona) and the herbarium specimen is deposited in NYS. The present strain is currently sterile and forms a single strain lineage in the phylogenetic analyses (Fig. 2, clade 1).

Clade 12: *Ramulispora*

Ramulispora Miura, Bull. S. Manchur. Railway Co. Agr. Exp. Sta. Kunchuling 11: 43. 1920.

Description (adapted from Braun 1995): Graminicolous, causing leaf spots, necrosis, foot-rot, and seedling blight. *Mycelium* hyaline to faintly pigmented, smooth, septate, branched; stromata absent to well-developed, substomatal to intra-epidermal, hyaline to pigmented. *Conidiophores* semi-macronematous or macronematous, mononematous, solitary or fasciculate, arising from

inner hyphae or stromata, erumpent through the cuticle or emerging through stomata, simple, rarely branched, continuous or sparsely septate, often reduced to conidiogenous cell, straight, subcylindrical to geniculate-sinuous, smooth, hyaline or subhyaline, rarely faintly pigmented. *Conidiogenous cells* directly arising from hyphae or stromata or integrated, terminal, subcylindrical to geniculate, monoblastic to polyblastic, sympodial, rarely percurrent, with inconspicuous, unthickened, hyaline conidiogenous loci. *Conidia* solitary, scolecosporous, acicular, subcylindrical, filiform, narrowly obclavate, sometimes with lateral branchlets (microcyclic conidiation), continuous or septate (branchlets mainly produced under humid conditions and in culture when grown on wet, poor media under lights, sometimes developing into secondary conidia which are detached), hyaline, euseptate, multi-septate, smooth, apex blunt to acute, base rounded to truncate, hilum unthickened, hyaline, conidial secession schizolytic.

Type species: *Ramulispora sorghi* (Ellis & Everh.) L.S. Olive & Lefebvre (≡ *Septorella sorghi* Ellis & Everh.).

Ramulispora sorghi (Ellis & Everh.) L.S. Olive & Lefebvre, Phytopathology 36: 198. 1946. Fig. 9.
Basionym: *Septorella sorghi* Ellis & Everh., J. Mycol. 9: 164. 1903.
Synonym: *Ramulispora andropogonis* Miura, Bull. S. Manchur. Railway Co. Agr. Exp. Sta. Kunchuling: 43. 1920.

Description in vivo *and illustrations*: Braun (1995).

Description in vitro (SNA, CBS 110578): *Mycelium* composed of hyaline, smooth, septate, branched hyphae, 1.5 µm wide. Stromata absent to small, pseudoparenchymatous, brown. Conidiophores, conidiogenous cells and conidia hyaline and smooth. *Conidiophores* solitary or in fascicles, subcylindrical-filiform, sometimes geniculate-sinuous, simple, septate, sometimes reduced to conidiogenous cell, (10–)12–13(–15) × 1.5(–2) µm. *Conidiogenous cells* terminal, monoblastic or polypblastic, with unthickened and non-refractive loci. *Conidia* formed singly, filiform, acicular, straight to curved, (11–)39–52(–79.5) × 1.5–2(–3) µm, 4–9-septate, hyaline, smooth, with subacute apex and truncate base, frequently with 1–2 lateral branches.

Materials examined: **South Africa**, KwaZulu-Natal Province, on *Sorghum bicolor*, Mar. 1995,

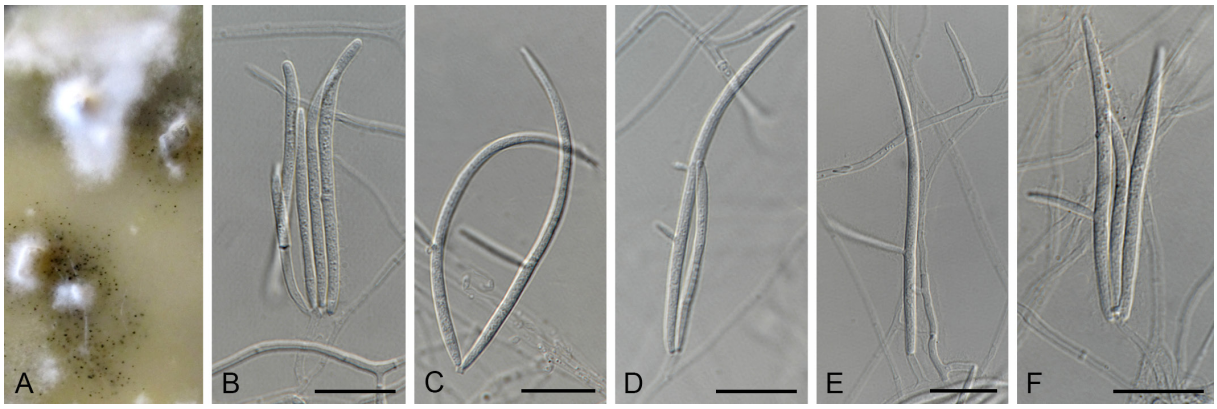


Fig. 9. *Ramulispora sorghi* (CBS 110578). A–F. Observations *in vitro*. A. Culture on OA. B–F. Conidiophore, conidiogenous cell and conidia. Scale bars = 10 µm.

coll. D. Nowell, cultures CBS 110578 = CPC 905, CBS 111032 = IMI 153076 = CPC 899, CBS 115522 = CPC 902.

Notes: The genus *Ramulispora* includes pathogens of gramineous plants (Arx 1983, Braun 1995) and is typified by *Ramulispora sorghi*, the causative agent of sorghum sooty stripe disease (Crous *et al.* 2003, Crous *et al.* 2009e). It produces numerous microsclerotia on the leaf surface and forms sporodochia with hyaline, transversely euseptate, scolecosporous conidia. A total of 14 species of *Ramulispora* are known (MycoBank), but without cultures and molecular analyses, their correct phylogenetic position remains unclear. The type species of *Ramulispora*, *Ramulispora sorghi*, was described from the host *Sorghum halepense*, from Tuskeege (Alabama, USA) but a type specimen could not be located. The cultures included in this study were isolated from sorghum from the KwaZulu-Natal Province of South Africa, where the pathogen was associated with a severe outbreak of sooty leaf stripe (Mchau *et al.* 1996). In a more recent study on the disease, Brady *et al.* (2011) concluded that differences in disease severity was host genotype-dependent and not due to genetic differences in the local pathogen population. The ITS sequence fragments of *Ramulispora sorghi* obtained from Kansas (HQ400740–HQ400745) were 100 % identical to those sequences from South Africa (Mchau *et al.* 1996) which is consistent with the concept that reproduction in *Ramulispora sorghi* is asexual in the field (Brady *et al.* 2011). Phylogenetically, *Ramulispora* forms a well-supported clade (Fig. 1, clade 12; Fig. 2, clade 2), being closely related to *Neodeightoniella*.

Ramulispora sorghiphila U. Braun, C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822717. Fig. 10.

Etymology: Composed of the name of the host genus and the Greek adjectival suffix -philum (loving).

Description in vitro (on V8; CBS 255.82): *Mycelium* composed of hyaline, smooth, septate, branched hyphae, 2–2.5 µm wide. *Conidiophores* micro- to macronematous, sinuous to geniculous-sinuous, hyaline to pale brown, branched, 30–110 × 2–2.5 µm. *Conidiogenous cells* integrated, terminal, mono- or polyblastic, proliferating sympodially or percurrently, smooth to verruculose, with unthickened and non-refractive loci. *Conidia* solitary, rarely catenate,

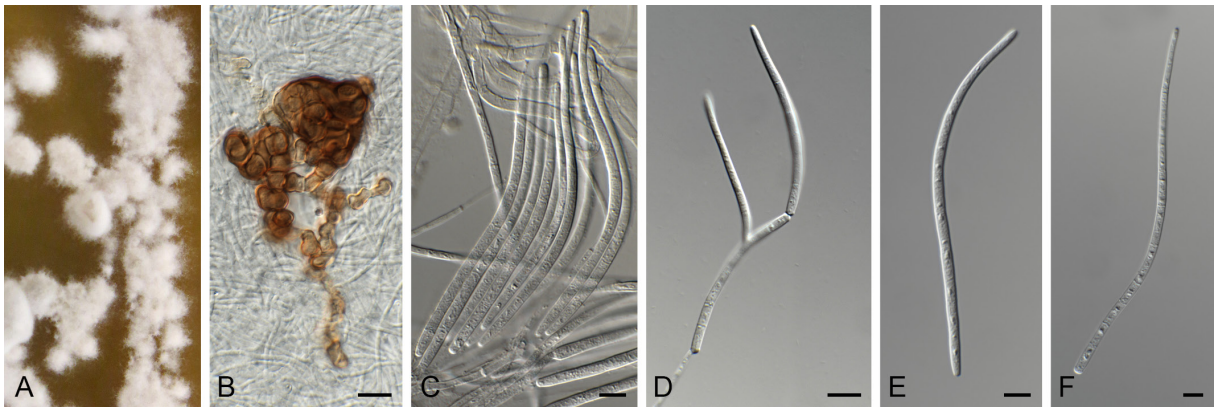


Fig. 10. *Ramulispora sorghiphila* (CBS 255.82). A–F. Observations *in vitro*. A. Culture on V8. B. Stromata. C. Conidiophore and conidia. D–F. Conidia. Scale bars = 10 µm.

holoblastic, hyaline, filiform, 70–250 × 2–2.5 µm, unthickened and truncate at the base, 2–12 septate.

Materials examined: **India**, on *Sorghum vulgare*, Oct. 1969, unknown collector, isol. by G.S. Rawla in 1971, dep. by H.I. Nirenberg in 1982 (**holotype** IMI 153077, culture ex-type CBS 255.82).

Notes: Differs from *Ramulispora sorghi* by producing much longer conidiophores and conidia. It is similar to *Ramulispora sorghicola* by producing very long conidia in culture that are commonly branched but differs by forming sclerotia in culture and not producing conidia in flesh-coloured gelatinous masses. *Ramulispora sorghiphila* forms a single strain lineage within the *Ramulispora* genus clade (Fig. 1, clade 12; Fig. 2, clade 2).

Clade 13: *Catenulocercospora*

Catenulocercospora C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822580.

Etymology: Derived from the similarities to the genus *Cercospora* and the catenulate nature of the conidia.

Description: Phytopathogenic, forming brown rectangular leaf spots. *Caespituli* amphigenous, mainly hypophyllous, hyaline. *Mycelium* internal, hyaline. *Stromata* small to developed, brown, globose. *Conidiophores* pale brown at the base and turning hyaline towards the apex, septate, straight to geniculate-sinuous. *Conidiogenous cells* integrated, mono- or polyblastic, with darkened, thickened and refractive rim-like conidiogenous loci. *Conidia* hyaline, solitary or catenate in branched chains, rounded at the apex when solitary, obclavate or cylindrical to filiform, septate, with rim-like hila that are thickened, darkened and refractive.

Type species: *Catenulocercospora fusimaculans* (G.F. Atk.) C. Nakash. *et al.* (≡ *Cercospora fusimaculans* G.F. Atk.).

Catenulocercospora fusimaculans (G.F. Atk.) C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822745. Fig. 11.
Basionym: *Cercospora fusimaculans* G.F. Atk., J. Elisha Mitchell Sci. Soc. 8(2): 50. 1892.
Synonyms: *Phaeoramularia fusimaculans* (G.F. Atk.) X.J. Liu & Y.L. Guo, Acta Phytopathol. Sin. 12 (4): 9. 1982.
Passalora fusimaculans (G.F. Atk.) U. Braun & Crous, in Crous & Braun, *Mycosphaerella* and Anam.: 192. 2003.
For additional synonyms see Crous & Braun 2003, Braun *et al.* (2015a) or MycoBank.

Descriptions in vivo *and illustrations*: Ellis (1976), Hsieh & Goh (1990).

Description in vivo (CPC 17277): *Leaf spots* formed as small streaks, rectangular, 2–6 × 0.5–1 mm, pale brown to dark brown, distinct. *Caespituli* amphigenous, mainly hypophyllous, white. *Mycelium* internal, hyphae hyaline, 2.5 µm diam. *Stromata* small to developed, brown, globose, 27–71 µm diam. *Conidiophores* in loose fascicles of 2–12, hyaline to pale brown, paler towards the apex, septate, tapered towards the apex, straight to geniculate-sinuous, 23–78

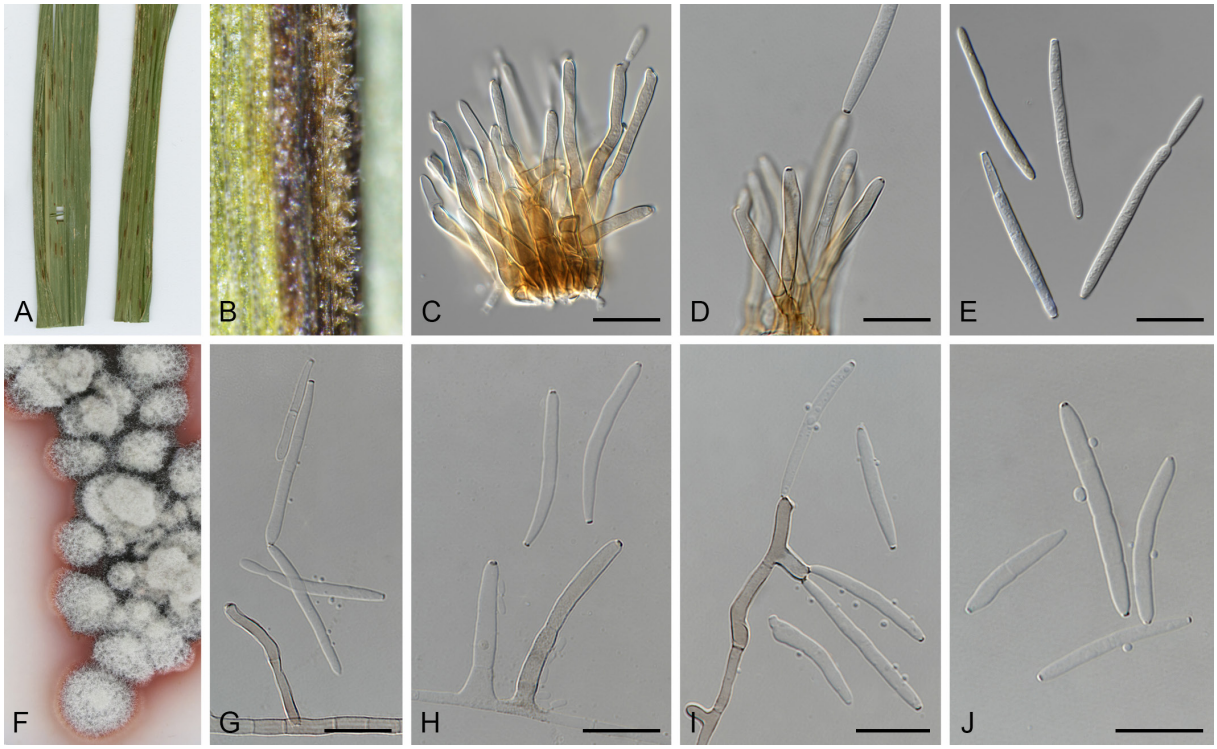


Fig. 11. *Catenulocercospora fusimaculans* (CPC 17277). A–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidia sporulating on the lesion. C, D. Conidiophores, conidiogenous cells and conidia. E. Single and catenate conidia. F–J. Observations *in vitro*. F. Culture on OA. G–I. Conidiophores, conidiogenous cells and conidia. J. Catenate conidia. Scale bars = 10 µm.

× 2.5–9 µm. *Conidiogenous cells* integrated, terminal, polyblastic, proliferating sympodially, with conidiogenous loci rim-like, thickened, darkened and refractive and located at the apex and shoulders, 1.6–2.5 µm diam. *Conidia* hyaline, smooth, solitary or catenate, ocasionaly in branched chains, long-obclavate, cylindrical to filiform, 20–62 × 2.5 µm, 2–5-septate, with thickened and darkened rim-like hila, 1.6–2.5 µm diam.

Description in vitro (on V8; CPC 17277): *Mycelium* hyaline to pale brown, smooth to rough, delicate, uniform in width, 2.5 µm diam. *Conidiophores* micronematous, hyaline to pale brown, smooth to verruculose, simple, cylindrical, straight to geniculate-sinuous, 10–100 × 2.5–5 µm. *Conidiogenous cells* integrated, apical, mono- or polyblastic, proliferating sympodially, with conidiogenous loci thickened, darkened and refractive, 1.5 µm diam. *Conidia* hyaline, smooth, solitary or catenate, occasionaly in branched chains, long-obclavate, cylindrical to filiform, rounded at the apex when solitary, 17–109 × 2–3.5 µm, 1–7-septate, hila thickened, darkened and refractive, 1.5 µm diam.

Materials examined: **Thailand**, on *Agrostis* sp., 15 Sep. 2009, coll. P. Phen, culture CPC 17277. **USA**, Alabama, Lee County, Auburn, on *Panicum dichotomum*, 15 Aug. 1891, B.M. Duggar, det. G.F. Atkinson (**lectotype** designated by Braun *et al.* 2015a: CUP-A-002054#1(AL); isolectotypes CUP-A-2945#2(AL), CUP-A-2945#3(AL)).

Notes: The description of the observed specimen is consistent with the one in literature for the species *Cercospora fusimaculans* (Ellis 1976). The species *Cercospora fusimaculans* was

recently lectotypified and the species *Cercospora agrostidis* removed from its synonyms list and tentatively considered a different species. *Cercospora fusimaculans*, despite the catenate conidia, was tentatively maintained as a *Cercospora* species (Braun *et al.* 2015a). Phylogenetically, the observed strain forms a single-strain lineage closely related to *Ramulispora* (Fig. 1, clade 13; Fig. 2, clade 3), but morphologically they are quite distinct from each other (Fig. 11). Therefore, a new genus was introduced to accommodate this species which has a worldwide distribution and affects numerous grass hosts (*Poaceae*) (Braun *et al.* 2015a). Despite its distribution and host range, it appears to be a mild pathogen susceptible to timely fungicide applications (Smiley 1983).

Clade 14: ***Neodeightoniella***

Neodeightoniella Crous & W.J. Swart, Persoonia 31: 211. 2013.

Description (from Crous *et al.* 2013b): Foliicolous, plant pathogenic. *Conidiophores* fasciculate, 3–6, arising from a weakly developed brown stroma composed of a few brown cells, amphigenous. *Conidiophores* erect, brown, unbranched, finely roughened, straight to slightly flexuous, subcylindrical, septate. *Conidiogenous cells* terminal and integrated, subcylindrical, brown, finely roughened; conidiogenous loci terminal and lateral on conidiogenous cells, darkened, thickened, protruding, tretic with central pore. *Conidia* solitary, pale brown, surface finely roughened, fusoid-ellipsoid, straight or gently curved, 1-septate; apical cell globose, with prominent mucoid cap; basal cell funnel-shaped, widest two thirds from basal hilum, tapering prominently to truncate hilum, thickened, darkened, with central pore.

Type species: *Neodeightoniella phragmiticola* Crous & W.J. Swart.

Neodeightoniella phragmiticola Crous & W.J. Swart, Persoonia 31: 211. 2013.

Description and illustration: Crous *et al.* (2013b).

Materials examined: **South Africa**, Free State, Bultfontein, on leaves of *Phragmites australis*, 31 Jan. 2013, W.J. Swart (**holotype** CBS H-21427, culture ex-type CBS 136418 = CPC 22059); *idem*., cultures CPC 22057, CPC 22061.

Notes: *Neodeightoniella* resembles the genus *Deightoniella* (based on *Deightoniella africana*, on *Imperata* sp., West Africa), in having pale brown, fusoid-ellipsoid, unequally 1-septate conidia arising from brown conidiophores. It is distinct in that conidiophores do not undergo percurrent rejuvenation (seen as nodal swellings in the type of *Deightoniella*), have prominent apical and lateral conidiogenous loci on the conidiogenous cells, conidia have a prominent mucoid cap, and conidiophores are arranged in fascicles. The genus *Deightoniella* presently contains a heterogeneous assemblage of taxa, but the type species, *Deightoniella africana*, probably belongs to the *Pyriculariaceae* (Klaubauf *et al.* 2014). Phylogenetically, *Neodeightoniella* belongs to the *Mycosphaerellaceae* and is closely related to *Ramulispora* (Fig. 1, clade 14; Fig. 2, clade 4).

Clade 15: *Distocercosporaster*

Distocercosporaster Videira, H.D. Shin, C. Nakash. & Crous, **gen. nov.** MycoBank MB822587.

Etymology: Name composed of the hitherto known genus *Distocercospora* + -aster (Latin substantival suffix indicating incomplete resemblance).

Description: Foliicolous, plant pathogenic. *Mycelium* internal, substomatal stromata formed of subhyaline to brown swollen hyphal cells. *Conidiophores* in small to moderately large fascicles, arising from stromata, through stomata, erect, straight, subcylindrical to geniculate-sinuous, unbranched, pale olivaceous to olivaceous brown, thin-walled, smooth, septate, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, with rim-like conidiogenous loci, thickened and darkened. *Conidia* hyaline to pale olivaceous, thin-walled, smooth to rough, solitary or catenate, in simple or occasionally branched chains, subcylindrical to obclavate-cylindrical, rarely subclavate, apex obtuse, subobtuse to truncate, base short obconically truncate, straight to curved, eu- or distoseptate, hila thickened and darkened.

Type species: *Distocercosporaster dioscoreae* (Ellis & G. Martin) Videira, H.D. Shin, C. Nakash. & Crous (≡ *Cercospora dioscoreae* Ellis & G. Martin).

Distocercosporaster dioscoreae (Ellis & G. Martin) Videira, H.D. Shin, C. Nakash. & Crous, **comb. nov.** MycoBank MB822755. Fig. 12.
Basionym: *Cercospora dioscoreae* Ellis & G. Martin, Amer. Naturalist 16: 1003. 1882.

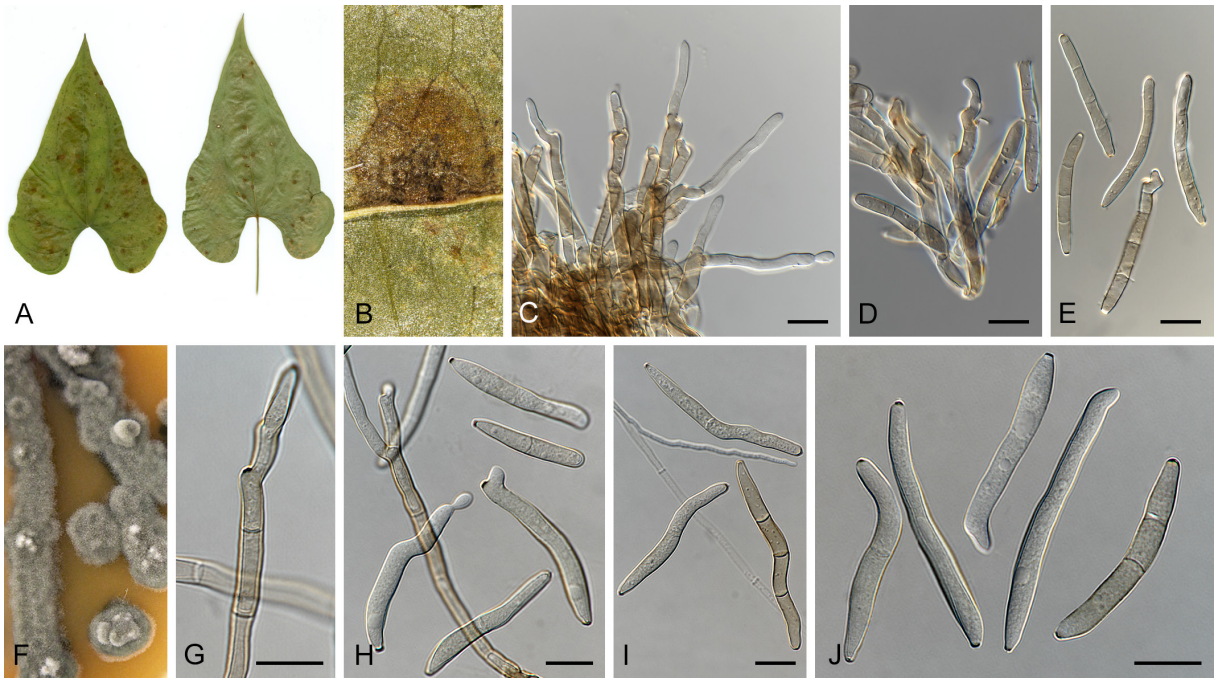


Fig. 12. *Distocercosporaster dioscoreae* (CPC 11513). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C, D. Conidiophores, conidiogenous cells and conidia. E. Catenate conidia. F–L. Observations *in vitro*. F. Culture on V8. G. Conidiophore and conidiogenous cell. H. Conidiophore, conidiogenous cell, single and catenate conidia. I, J. Catenate conidia. Scale bars = 10 µm.

Synonyms: *Phaeoramularia dioscoreae* (Ellis & G. Martin) Deighton, More Dematiaceous Hyphomycetes: 319. 1976.
Cercospora nubilosa Ellis & Everh., J. Mycol. 4 (11): 115. 1888.
Cercospora tokoroi Togashi, Bull. Imp. Coll. Agric. (Morioka): 46. 1936.
Passalora dioscoreae (Ellis & G. Martin) U. Braun & Crous, CBS Biodiversity Ser. 1: 162. 2003.

Description in vivo *and illustrations*: Ellis (1976), Pons & Sutton (1988), Guo *et al.* (2003), Braun *et al.* (2014).

Description in vitro (on SNA; CPC 11513): *Mycelium* pale brown to dark brown. *Conidiophores* micronematous to macronematous, smooth, pale to pale brown, sinuous, irregular in width, 2.5–5(–10) µm, branched. *Conidiogenous cells* apical, intercalary, polyblastic, proliferating sympodially, often branched, integrated, with thickened and darkened, rim-like conidiogenous loci, 2–2.5 µm diam. *Conidia* smooth, hyaline to pale brown, single or often catenate, in sigle or branched chains, holoblastic, long-obovoid when single, cylindrical to obclavate when catenate, conical truncate at both ends, straight to strongly sinuous, 12–120 × 3–7.5 µm, 0–5-eu- or distoseptate and occasionally constricted at septa, with hila rim-like, thickened and darkened, 2–2.5 µm diam.

Materials examined: **Republic of Korea**, on *Dioscorea tokoro*, 16 Oct. 2003, H.D. Shin, culture CBS 135460 = CPC 10855; on *Dioscorea tenuipes*, 2003, H.D. Shin, culture CBS 135463 = CPC 11513; on *Dioscorea* sp., date unknown, H.D. Shin, culture KACC 44723. **USA**, Pennsylvania, Delaware Co., on *Dioscorea villosa*, 1 Aug. 1882, W. Trimble (**holotype** NY 838293, isotype IMI 256891).

Notes: The genus *Distocercosporaster* is newly introduced to accommodate the species *Passalora dioscoreae* which is not congeneric with *Passalora* as defined by the type *Passalora bacilligera*. The existing strains form a well-supported clade in the phylogenetic analyses (Fig. 1 clade 15; Fig. 2, clade 15). Although the examined strains were collected in the Republic of Korea and the type material is originally from the USA, the observed morphology is consistent with the descriptions found in literature (Braun *et al.* 2014) and, therefore, these are considered good representatives of this species. Several species of cercosporoid genera have been described from hosts belonging to the plant genus *Dioscorea* (Crous & Braun 2003, Braun *et al.* 2014). The genus *Distocercosporaster* differs from the genus *Distocercospora*, *in vivo*, by forming stromata composed of subhyaline to brown swollen hyphal cells, rather short conidiophores with rim-like and distinctly thickened conidiogenous loci on terminal conidiogenous cells, and frequently catenate conidia.

Clade 16: *Caryophylloseptoria*

Caryophylloseptoria Verkley *et al.*, Stud. Mycol. 75: 233. 2013.

Description (from Verkley *et al.* 2013): *Conidiomata* pycnidial, epiphyllous or predominantly epiphyllous, globose to subglobose, or slightly depressed, with a central ostiolum; wall composed of *textura angularis* or *globulosa-angularis*. *Conidiogenous cells* hyaline, holoblastic, proliferating percurrently one to multiple times with indistinct annellations, or (in addition)

proliferating sympodially. *Conidia* cylindrical, straight, curved or flexuous, multiseptate, not or somewhat constricted around the septa, hyaline, contents with several oil-droplets and granular material in each cell.

Type species: *Caryophylloseptoria lychnidis* (Desm.) Verkley *et al.* (≡ *Septoria lychnidis* Desm.).

Caryophylloseptoria lychnidis (Desm.) Verkley *et al.*, Stud. Mycol. 75: 234. 2013.
Basionym: *Septoria lychnidis* Desm., Ann. Sci. Nat., Bot., Sér. 3, 11(2): 347. 1849.
For extended synonymy see Shin & Sameva (2004).

Materials examined: **Austria**, Tirol, Inntal, S of Telfs (W of Innsbruck), along road 171, on living leaves of *Silene latifolia* subsp. *alba* (= *Melandrium album*), 4 Aug. 2000, G. Verkley, CBS H-21161, cultures CBS 109098, CBS 109102; *idem.*, G. Verkley 1048, CBS H-21162, cultures CBS 109099, CBS 109101. **Netherlands**, Hilversum, on living leaves of *Silene dioica* (= *Melandrium rubrum*), 22 Jun. 1985, H.A. van der Aa 9524, CBS H-18112.

Notes: The genus *Caryophylloseptoria* was recently established to accommodate four septoria-like species infecting hosts belonging to the *Caryophyllaceae* in Europe and the Republic of Korea (Verkley *et al.* 2013). The type species, *Caryophylloseptoria lychnidis*, was originally described from *Silene dioica* (≡ *Lychnis dioica*) from France. It has been reported from several species of *Silene* and the conidial size given by various authors differs considerably (Verkley *et al.* 2013). In this study, the *Caryophylloseptoria* strains form a well-supported clade in the phylogeny (Fig. 1, clade 16; Fig. 2 clade 16), closely related to *Neoseptoria*.

Clade 17: *Neoseptoria*

Neoseptoria Quaedvlieg *et al.*, Stud. Mycol. 75: 352. 2013.

Description (from Quaedvlieg *et al.* 2013): Foliicolous. *Conidiomata* black, immersed, subepidermal, pycnidial, subglobose with central ostiole, exuding creamy conidial mass; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* 0–2-septate, subcylindrical, hyaline to pale brown at base, smooth, straight to geniculate-sinuous. *Conidiogenous cells* phialidic, hyaline, smooth, aggregated, lining the inner cavity, subcylindrical to ampulliform, straight to geniculate-sinuous; proliferating several times percurrently near apex, rarely sympodially. *Conidia* scolecosporous, hyaline, smooth, flexuous, rarely straight, granular, thin-walled, narrowly obclavate, apex subobtuse, base long obconically truncate, tapering to a truncate hilum, 3- to multi-septate.

Type species: *Neoseptoria caricis* Quaedvlieg *et al.*

Neoseptoria caricis Quaedvlieg *et al.*, Stud. Mycol. 75: 352. 2013.

Description and illustration: Quaedvlieg *et al.* (2013).

Material examined: **Netherlands**, on leaves of *Carex acutiformis*, Aug. 2012, W. Quaedvlieg (**holotype** CBS H-21293, ex-type culture CBS 135097 = S653).

Notes: *Neoseptoria* is a monotypic genus that is morphologically similar to *Septoria* but differs in having conidiogenous cells that are mono- to polyphialidic and proliferate percurrently at the apex. In the phylogenetic analyses, it is represented by a single-strain lineage closely related to *Caryophylloseptoria* (Fig. 1, clade 17; Fig. 2, clade 17).

Clade 18: *Acervuloseptoria* and *Cercosporella*

Acervuloseptoria Crous & Jol. Roux, Persoonia 32: 275. 2014.

Description (from Crous *et al.* 2014a): Plant pathogenic, foliicolous. *Conidiomata* black, amphigenous, exuding a creamy-white conidial cirrhus, subepidermal, erumpent, multilocular, with upper layer breaking open irregularly and leaving conidioma to have acervular appearance; wall of 3–6 layers of brown *textura angularis* to *textura intricata*, basal layers pale brown, roof of conidioma dark brown; in culture conidiomata acervular with elements of conidiomatal roof remaining like brown strands along the sides of conidioma. *Conidiophores* subcylindrical, straight to once geniculate, pale brown, verruculose, septate, branched or not. *Conidiogenous cells* terminal and lateral, subcylindrical, pale brown to subhyaline, verruculose to smooth, proliferating sympodially and percurrently. *Conidia* narrowly obclavate to subcylindrical, flexuous, guttulate, smooth, hyaline, apex subacutely rounded, base obconically truncate, septate.

Type species: *Acervuloseptoria ziziphicola* Crous & Jol. Roux.

Acervuloseptoria ziziphicola Crous & Jol. Roux, Persoonia 32: 275. 2014.

Description and illustration: Crous *et al.* (2014a).

Materials examined: **South Africa**, Northern Cape, Richtersveld National Park, Potjiespram Rest Camp, on leaf spots of *Ziziphus mucronata*, Sep. 2013, J. Roux (**holotype** CBS H-21723, culture ex-type CPC 23707 = CBS 138009).

Notes: *Acervuloseptoria* differs from *Septoria* and allied genera (Quaedvlieg *et al.* 2013) in the peculiar conidiomatal morphology, with black, erumpent conidiomata, from which the top layer disintegrates, leaving a conidiomatal body that appears acervular (Crous *et al.* 2014a, 2015c). The conidiophores are also slightly pigmented and verruculose in their lower part. Phylogenetically, *Acervuloseptoria* is represented by a single-strain lineage that is closely related to *Cercosporella* and *Ramulariopsis* (Fig. 1, clade 18; Fig. 2, clade 18). However, its phylogenetic position is not yet clear since it clustered near *Cercosporella* in dataset 1 (Fig. 1, clade 18) but clustered among the *Cercosporella* species when using dataset 2 (Fig. 2, clade 18). In the single-gene Bayesian trees of dataset 2 (data not shown), *Acervuloseptoria ziziphicola* clusters outside both the *Cercosporella* and the *Ramulariopsis* clade with high posterior probability value for LSU (PP = 0.94), with a low support in the case of ITS (PP = 0.54). In the single-gene Bayesian tree of *rpb2*, *Acervuloseptoria ziziphicola* sits in a highly supported polytomy (PP = 0.84) including the *Cercosporella* strains. In both the RAxML and PAUP analyses of dataset 2, *Acervuloseptoria ziziphicola* appears as a single-strain lineage sister to both *Cercosporella* and *Ramulariopsis*. The genus *Acervuloseptoria* currently includes an additional species, *Acervuloseptoria capensis* (Crous *et al.* 2015c). The differences in morphology are significant

enough for retaining *Acervuloseptoria* (a coelomycete) as distinct from *Cercosporella* (a hyphomycete), pending further collections. The situation of *Acervuloseptoria ziziphicola* is reminiscent of *Pseudocercospora pistacina*, which after much debate was placed in the genus *Pseudocercospora*, although it had pycnidial conidiomata (Crous *et al.* 2013a).

Cercosporella Sacc., Michelia 2(6): 20. 1880.

Description (from Videira *et al.* 2016): Phytopathogenic, mostly causing leaf spots. *Hyphae* restricted to intercellular spaces and forming cup- or bowl-shaped appressoria, 7–17 µm diam that attach to walls of mesophyll cells. *Conidiophores* emerging through stomata or erumpent through the cuticle, straight, subcylindrical to geniculate-sinuous, hyaline, sometimes lightly pigmented near the base, more or less thin-walled and smooth. *Conidiogenous cells* integrated, terminal, polyblastic, sympodial, mostly conspicuously geniculate, conidiogenous loci conspicuous, hyaline but refractive, thickened and raised in the shape of a truncated cone (ultrastructure). *Conidia* formed singly, hyaline, subcylindrical to obclavate, sometimes fusiform, 1- to multi-septate, usually thin-walled and smooth, apex obtuse, base often rounded to truncate or obconically truncate, hilum thickened, not darkened but refractive. Description adapted from Braun (1995) and Kirschner (2009).

Type species: *Cercosporella virgaureae* (Thüm.) Allesch (≡ *Ramularia virgaureae* Thüm.).

Cercosporella virgaureae (Thüm.) Allesch., Hedwigia 34: 286. 1895.
Basionym: *Ramularia virgaureae* Thüm., Fungi Austr. Exs., Cent. 11: no. 1072. 1874.
Synonyms: *Cylindrosporium virgaureae* (Thüm.) J. Schröt., in Cohn, Krypt.-Fl. Schles. 3: 489. 1897.
Cercosporella cana (Sacc.) Sacc., Michelia 2(6): 20. 1880.
For additional synonymy see Braun (1995) or MycoBank.

Descriptions and illustrations: Braun (1995), Kirschner (2009), Videira *et al.* (2016).

Materials examined: **Austria**, Krems, on *Solidago virgaurea*, 1871 [Thüm., Fungi Austr. Exs. 1072] (**lectotype** K, designated by Deighton 1973). **Brazil**, Guimarania, Minas Gerais, on *Conyza canadensis*, unknown date, B.S. Vieira, culture CPC 19492. **Republic of Korea**, Jinju, on *Erigeron annuus*, 1 Jul. 2004, H.D. Shin, cultures CPC 11456, CPC 11457, CPC 11460, CPC 11461; Namyangju, on *Erigeron annuus*, 9 Oct. 2002, H.D. Shin, cultures CPC 10286–10288; Chuncheon, on *Erigeron annuus*, 21 May 2003, H.D. Shin, culture CBS 113304.

Notes: The taxonomic confusion between *Cercosporella* and *Ramularia* has been addressed by several authors (Braun 1995, 1998, Kirschner 2009, Videira *et al.* 2016). *Cercosporella* and *Ramularia* are phylogenetically distinct since the LSU sequences of freshly collected isolates of the type species of both genera clustered separately (Kirschner 2009). A later study using. Both LSU and *rpb2* sequences corroborated these results (Videira *et al.* 2016). Morphologically, *Cercosporella* can be distinguished from *Ramularia* by forming an appressorium structure to adhere to the plant cells and by having a distinct ultrastructure of conidiogenous scars that is flat like a truncate cone. The type species, *Cercosporella virgaureae*, was described from the host *Solidago virgaureae* collected in Austria. Although the currently available strains of this species are of Brazilean and Korean origin, their morphology is identical to the descriptions

available in literature (Braun 1995) and their LSU sequence is 100 % identical to that of a freshly collected isolate of *Cercosporella virgaureae* from Germany (GenBank EU710894) (Kirschner 2009). Two new species of *Cercosporella* have recently been introduced, namely *Cercosporella dolichandrae* (Crous *et al.* 2014a) and *Cercosporella catenulata* (Videira *et al.* 2016), that cluster together with *Cercosporella virgaureae* (Fig. 1, clade 18; Fig. 2, clade 18).

Clade 19: *Ramulariopsis*

Ramulariopsis Speg., Anales Mus. Nac. Buenos Aires 20(13): 421 [ser. 3, 13]. 1910.

Description (from Braun 1998): Parasitic on vascular plants, foliicolous, usually forming leaf spots. *Mycelium* internal, septate, branched, hyaline or almost so, smooth; stromata absent to well-developed, immersed, hyaline to faintly pigmented. *Caespituli* amphigenous, whitish. *Conidiophores* macronematous, mononematous, fasciculate, arising from internal hyphae or stromata, through stomata or erumpent, hyaline, septate, smooth, simple or branched. *Conidiogenous cells* integrated, terminal, intercalary as well as pleurogenous (as short nodulose protuberances or subcylindrical branchlets), polyblastic, sympodial, with cicatrized, thickened and darkened loci. *Conidia* catenate, in simple as well as branched chains, ellipsoid-ovoid, subcylindrical-fusiform, 0–1- to multi-euseptate, hyaline, with thickened and darkened hila. Conidial secession schizolytic.

Type species: *Ramulariopsis cnidoscoli* Speg.

Ramulariopsis cnidoscoli Speg., Anales Mus. Nac. Buenos Aires 20: 422. 1911.

Descriptions and illustrations: Braun (1998), Videira *et al.* (2016).

Material examined: **Argentina**, Salta, Orán, on *Cnidoscolus vitifolius* var. *cnicodendron*, Apr. 1905, C. Spegazzini (**lectotype**, designated by Deighton, 1972, LPS 12.851).

Notes: *Ramulariopsis* was described by Spegazzini (1910) and emended by Deighton (1972). *Ramulariopsis* differs from *Ramularia* by producing conidiophores that are frequently branched and conidiogenous cells that are often intercalary or pleurogenous. The type species, *Ramulariopsis cnidoscoli*, was collected on *Cnidoscolus vitifolius* in Argentina, and is thus far only known from herbarium material. Five species are currently recognised in this genus (Braun 1998) but only two are known from culture, namely *Ramulariopsis gossypii* and *Ramulariopsis pseudoglycines* (Videira *et al.* 2016). Phylogenetically, these two species cluster in a well-supported clade closely related to *Cercosporella* (Fig. 1, clade 19; Fig. 2, clade 19). Unfortunatelly, it is still unproven whether *Ramulariopsis gossypii* is congeneric with *Ramulariopsis cnidoscoli*. Morphologically, there are slight differences in the structure of the conidiogenous loci between the two species: the loci in *Ramulariopsis gossypii* are conspicuously thickened and darkened, whereas in *Ramulariopsis cnidoscoli* these structures are less conspicuous.

Clade 20: *Pleuropassalora*

Pleuropassalora U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822610.

Etymology: Derived from the sporulating arrangement, pleurosporous + its resembling genus, *Passalora.*

Description: Phytopathogenic. *Mycelium* internal, smooth, branched, pale brown. *Caespituli* hypophyllous, fasciculate to synnematous, arising from a pale brown stroma. *Conidiophores* subcylindrical, unbranched, flexuous, guttulate, pale to medium brown, smooth, septate. *Conidiogenous cells* terminal, subcylindrical, guttulate, pale to medium brown, finely verruculose, becoming slightly swollen, appearing clavate, with multiple conidiogenous loci, round, darkened, thickened, refractive, prominent, proliferation sympodial. *Conidia* solitary, pale to medium brown, smooth to finely verruculose, granular to guttulate, thin-walled, ellipsoidal to obovoid, obpyriform, wider basal cell and apical cell elongating into a beak, transversely multiseptate, hilum thickened, darkened and refractive.

Type species: *Pleuropassalora armatae* (Crous & A.R. Wood) U. Braun *et al.* (≡ *Passalora armatae* Crous & A.R. Wood).

Pleuropassalora armatae (Crous & A.R. Wood) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822777.
Basionym: *Passalora armatae* Crous & A.R. Wood, Stud. Mycol. 64: 35. 2009.

Description in vivo *and illustrations*: Crous *et al.* (2009c).

Description in vitro (on SNA; CBS 125420): *Mycelium* composed of hyaline to pale hyphae, uniform in width, 2–2.5 µm. *Conidiophores* semimacronematous to macronematous, pale brown to pale olivaceous brown, multiseptate, straight or mildly curved, smooth, 200–740 × 3.8–7.5 µm. *Conidiogenous cells* integrated, terminal, cylindrical, straight or slightly curved, polyblastic, proliferating sympodially without geniculation, with numerous lateral conidiogenous loci, rim-like, thickened and darkened, 2–2.5 µm. *Conidia* subhyaline to pale brown, holoblastic, solitary, acropleurogenous, obpyriform with a beak-shape at the apex, obclavate or ellipsoidal, 25–45 × 10–12.5 µm, 1–3-euseptate, not constricted at septa, with distinctly protuberant, thickened, and refractive hilum, 2–2.5 µm diam.

Materials examined: **South Africa**, KwaZulu-Natal Province, South Coast, Mpenjati Nature Reserve, between Ramsgate and Port Edward, on leaves of *Dalbergia armata*, 28 May 2008, A.R. Wood (**holotype** CBS H-20337, culture ex-type CBS 125420 = CPC 15419); *idem*. cultures CPC 15420, CPC 15421; Kloof Nature Reserve area, on *Dalbergia obovata*, 15 Jun. 2009, A. Wood, herb. 7/7/ 2009 (4), culture CPC 17084.

Notes: This genus is proposed in order to accommodate the species *Passalora armatae* that is not congeneric with *Passalora* as defined by the type *Passalora bacilligera*. *Pleuropassalora* is a monotypic genus that forms a well-supported clade in this study (Fig. 1, clade 20; Fig. 2, clade 20). At the time it was described (Crous *et al.* 2009c), it was observed that, when in culture, conidia remain attached to conidiogenous cells, giving conidiophores the appearance of small tufts which is very characteristic, but not observed in *Passalora s. str.*

Clade 21: *Graminopassalora*

Graminopassalora U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822591.

Etymology: Derived from the host family (*Poaceae* = *Gramineae*) and similarity to the genus *Passalora*.

Description: Plant pathogenic, causing leaf spotting symptoms. *Mycelium* internal, forming stromata of variable shape and size, usually well-developed, substomatal to immersed, brown. *Conidiophores* in small to very large fascicles, arising from stromata, through stomata or erumpent, erect, subcylindrical, straight to curved, sinuous, slightly geniculate, unbranched, septate, pale to dark brown, thin-walled, smooth to rough-walled, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, with a single to several conspicuous conidiogenous loci, circular in outline, thickened and darkened, usually barely protuberant. *Conidia* formed singly, ellipsoid-ovoid, obovoid, short obclavate, 0–3-septate, occasionally slightly constricted at the septa, subhyaline to pale brownish, thin-walled, smooth to rough-walled, hila rounded, thickened and darkened.

Type species: *Graminopassalora graminis* (Fuckel) U. Braun, C. Nakash., Videira & Crous (≡ *Scolicotrichum graminis* Fuckel).

Graminopassalora graminis (Fuckel) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822760. Fig. 13.
Basionym: *Scolicotrichum graminis* Fuckel, Hedwigia 2(15): 134. 1863.
Synonym: *Passalora graminis* (Fuckel) Höhn., Zentrabl. Bakteriol., 2. Abt., 60: 6. 1923.
For additional synonyms see Braun *et al.* (2015a).

Description and illustrations: Braun *et al.* (2015a).

Materials examined: **Germany**, Rheinland-Pfalz: Mt. Rabenkopf, on grass leaves (exact identity unclear), Fuckel, Fungi Rhen. Exs. 130 (**lectotype** designated by Braun *et al.* 2015a, HAL; isolectotypes: Fuckel, Fungi Rhen. Exs. 130, e.g. FH, G). **Japan**, Chiba, on *Dactylis*

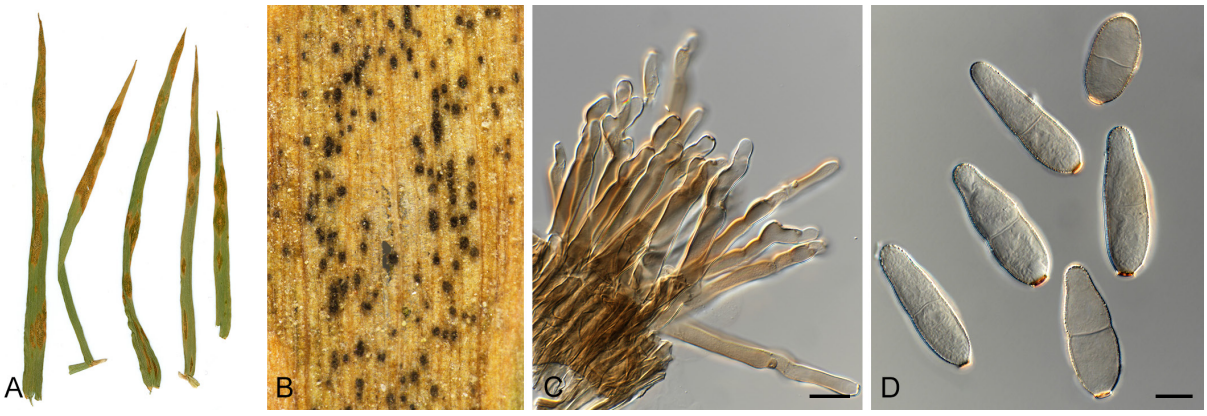


Fig. 13. *Graminopassalora graminis* (CBS 113303). A–D. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Conidiophores. D. Conidia. Scale bars = 10 µm.

glomerata, N. Nishihara, culture MAFF510604 = MUCC 1429. **Republic of Korea**, Yangyang, on *Alopecurus aequalis* var. *amurensis*, 24 May 2003, H.D. Shin, culture CBS 113303.

Notes: The genus *Graminopassalora* is newly introduced to accommodate *Passalora graminis*, which is not congeneric with the type of *Passalora* as defined by the type *Passalora bacilligera* (Fig. 1, clade 35; Fig. 2, clade 22). The lectotype of *Passalora graminis* was described from grass leaves of uncertain identity originating from Germany. *Passalora graminis* is considered a widespread pathogen able to infect a wide range of grass hosts (*Poaceae*). The existing collections on various hosts are morphologically uniform suggesting this is a single plurivorous species, but more detailed analyses including an ex-type strain are required to ascertain this hypothesis. In this study, two Asian isolates isolated from different hosts were also analysed. Their morphology is identical to the description available in literature (Braun *et al.* 2015a) and they are deemed as good representatives of this species. These isolates formed a well-supported clade by all three phylogenetic methods employed (Fig. 1, clade 21; Fig. 2, clade 21).

Clade 22: *Pallidocercospora*

Pallidocercospora Crous, Stud. Mycol. 75: 73. 2013.

Description (from Crous *et al.* 2013a): Foliicolous, phytopathogenic, causing discrete leaf spots. *Ascomata* single, black, immersed, globose, glabrous; wall of 3–4 layers of medium brown *textura angularis*. *Asci* fasciculate, bitunicate, aparaphysate, subsessile, 8-spored, ellipsoid to obclavate or cylindrical, straight or curved, numerous. *Ascospores* 2- to multi-seriate, oblique, overlapping, straight ellipsoidal to obovoid, hyaline, smooth, 1-septate. *Mycelium* predominantly immersed, consisting of olivaceous brown hyphae, smooth, branched, septate, 2–4 µm diam. *Conidiophores in vivo* fasciculate, or occurring singly on superficial mycelium as lateral projections, unbranched or branched, septate, cylindrical, straight to geniculate-sinuous, olivaceous brown. *Conidiogenous cells* integrated, terminal, cylindrical, straight to geniculate-sinuous, olivaceous brown, proliferating sympodially or percurrently, with unthickened loci, not darker than the surrounding conidiogenous cell. *Conidia* solitary, straight to irregularly curved, guttulate, pale olivaceous to olivaceous brown, subcylindrical to narrowly obclavate, multi-septate; hila neither thickened nor darkened.

Type species: *Pallidocercospora heimii* (Crous) Crous (≡ *Pseudocercospora heimii* Crous).

Pallidocercospora heimii (Crous) Crous, Stud. Mycol. 75: 74. 2013.
Basionym: *Pseudocercospora heimii* Crous, S. African Forest. J. 172: 4. 1995.
Synonyms: *Mycosphaerella heimii* Crous, S. African Forest. J. 172: 2. 1995.
Mycosphaerella heimii Bouriquet, Encycl. Mycol. 12: 418. 1946, nom. nud.

Description and illustration: Crous *et al.* (2013a).

Materials examined: **Brazil**, Bahia, Teixeira de Freitas, on leaves of *Eucalyptus* sp., 2004, A.C. Alfenas, culture CPC 11716. **Madagascar**, Moramanga, on leaves of *Eucalyptus* sp., 16 Apr. 1994, P.W. Crous (PREM 51749, **holotype** of sexual morph; PREM 51748, **holotype** of asexual morph, cultures ex-type CPC 760–761 = CBS 110682).

Notes: The genus *Pallidocercospora* was established to accommodate the species previously belonging to the *Mycosphaerella heimii* complex. *Pallidocercospora* species are morphologically similar to *Pseudocercospora s. str.* but can be distinguished by the pale olivaceous and smooth conidia and the red crystals they form when cultivated in agar (Crous *et al.* 2013a). The strains used in this study clustered in a well-supported clade by all three phylogenetic methods employed (Fig. 1, clade 22; Fig. 2, clade 28). At the time this genus was introduced (Crous *et al.* 2013a), the authors observed two pseudocercospora-like species clustering in the same clade, namely *Pseudocercospora thailandica* (foliar pathogen of *Acacia*; Crous *et al.* 2004c) and *Pseudocercospora colombiensis* (foliar pathogen of *Eucalyptus*; Crous 1998), also with mycosphaerella-like sexual morphs. Morphologically, *Pseudocercospora thailandica* and *Pseudocercospora colombiensis* were indistinguishable from *Pseudocercospora* species. In that study (Crous *et al.* 2013a), the multigene phylogeny strongly supported the clade that included *Pallidocercospora*, *Trochophora*, *Scolecostigmina* and the two mentioned species, but poorly supported their separation, despite their strikingly different morphologies. Based on the morphological differences and poor phylogenetic support, the authors refrained from proposing a formal combination of *Pseudocercospora thailandica* and *Pseudocercospora colombiensis* into *Pallidocercospora* at the time (Crous *et al.* 2013a). In a recent study, a formal proposal for the combination of these two species into *Pallidocercospora* was presented on the basis of a multigene phylogeny based on a LSU and ITS alignment (Hyde *et al.* 2016). In this study, with the introduction of a wider range of species sequences and the *rpb2* gene, we find good support for the separation of these two species into their own clade.

Clade 23: *Nothophaeocryptopus*

Nothophaeocryptopus Videira, C. Nakash. & Crous, **gen. nov.** MycoBank MB822698.

Etymology: From the greek notho-, meaning false, and the similarity to the genus *Phaeocryptopus*.

Description: Phytopathogenic. *Mycelium* internal and superficial, pseudothecia, internal and superficial, emerging through stomata on the lower surface of leaves, black. *Ascospores* hyaline, ellipsoidal with obtuse ends, 1-septate, slightly constricted at the septa, the basal cell slightly narrower and tapering toward its base. Germinating ascospores develop germ hyphae from polar ends of both cells.

Type species: *Nothophaeocryptopus gaeumannii* (T. Rohde) Videira *et al.* (≡ *Adelopus gaeumannii* T. Rohde).

Nothophaeocryptopus gaeumannii (T. Rohde) Videira, C. Nakash., U. Braun & Crous, **comb. nov.** MycoBank MB822768.
Basionym: *Adelopus gaeumannii* T. Rohde, Silva: 51. 1936.
Synonyms: *Adelopus balsamicola* f. *douglasii* J. Steiner, Z. Pflanzenkrankh. 47: 184. 1937.
Phaeocryptopus gaeumannii (T. Rohde) Petr., Ann. Mycol. 36(1): 22. 1938.

Description (adapted from Stone *et al.* 2008): *Ascomata* pseudothecial, internal, emerging from stomata, on the lower surface of living leaves and dead leaves, less than 0.1 mm diam, black. Superficial, radiating hyphae emerging from developing ascocarps, spreading across the needle surface and re-entering the needle through unoccupied stomata. *Ascospores* hyaline, ellipsoidal

with obtuse ends, 1-septate, slightly constricted at the septa, the basal cell slightly narrower and tapering toward its base, 11–17 × 4–5 µm. Germinating ascospores develop germ hyphae from polar ends of both cells. Germinating hyphae initially hyaline, becoming pale olive brown when up to 20 µm long, then becoming dark brown to black.

Materials examined: **Austria**, unknown host, date and collector, isol. H. Steiner, dep. in 1938, culture CBS 244.38. **Germany**, on needles of *Pseudotsuga menziesii*, unknown date and collector, isol. T. Rohde, deposited in 1937 (**lectotype** designated here, MBT378568, preserved as metabolically inactive culture CBS 267.37).

Notes: The genus *Nothophaeocryptopus* is introduced to accommodate the species *Phaeocryptopus gaeumannii* which is not congeneric with the type of *Phaeocryptopus*, *Phaeocryptopus nudus* (*Dothideales*). The systematic position of *Phaeocryptopus gaeumannii* was originally determined based on a phylogeny of combined LSU and SSU sequences that placed it within the *Mycosphaerellaceae* (*Capnodiales*), followed by a phylogeny of ITS sequences that placed it in the *Mycosphaerella heimii* complex (Winton *et al.* 2007). In this study, the phylogenetic results agreed with the previous results of Winton *et al.* (2007), placing this species in a well-supported clade (Fig. 1, clade 23; Fig. 2, clade 29), closely related with *Pallidocercospora*. *Nothophaeocryptopus gaeumannii* is the causal agent of Swiss needle cast disease on *Pseudotsuga menziesii* (Douglas-fir). The disease symptoms include severe defoliation that leads to reduced height and diameter growth. Publications by Rohde (1937) and Steiner (1937) provided the first insights into the pathogen life-cycle and how it differed from *Phaeocryptopus nudus*. Although *Nothophaeocryptopus gaeumannii* grows well on artificial culture media, it behaves as an obligate parasite, reproducing only on living needles of *Pseudotsuga menziezii*, and no asexual morph has been observed thus far (Stone *et al.* 2008). Isolates of *Nothophaeocryptopus gaeumannii* also have been observed to produce diffusing red pigments in culture (Winton *et al.* 2007), which is a feature also observed in *Pallidocercospora*.

Clade 24: *Scolecostigmina*

Scolecostigmina U. Braun, New Zealand J. Bot. 37: 323. 1999.

Description (from Braun *et al.* 1999): Foliicolous, phytopathogenic, associated with leaf spots. *Mycelium* immersed, consisting of septate, branched, pigmented hyphae. *Sporodochia* immersed to erumpent; stromata subglobose to applanate, composed of brown, angular to subglobose cells. *Conidiophores* numerous, densely aggregated, arising from a stroma, subcylindrical or somewhat tapered towards the apex, occasionally ampulliform, continuous or septate, pigmented, wall somewhat thickened, usually verruculose. *Conidiogenous cells* integrated, terminal or at times conidiophores reduced to conidiogenous cells, holoblastic, proliferating percurrently via conspicuous annellations. *Conidia* solitary, scolecosporous, usually subcylindrical-obclavate, transversely pluriseptate, occasionally with few longitudinal or oblique septa, euseptate, rarely with few intermixed distosepta, thick-walled, pigmented, dark, smooth to verrucose, apex obtuse to subacute, base truncate or obconically truncate, hila unthickened, not darkened; secession schizolytic.

Type species: *Scolecostigmina mangiferae* (Koord.) U. Braun & Mouch. (≡ *Cercospora mangiferae* Koord.).

Scolecostigmina mangiferae (Koord.) U. Braun & Mouch., New Zealand J. Bot. 37: 323. 1999.
Basionym: *Cercospora mangiferae* Koord., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 13(4): 236. 1907.
Synonyms: *Stigmina mangiferae* (Koord.) M.B. Ellis, Mycol. Pap. 72: 49. 1959.
Sciniatosporium mangiferae (Koord.) Morgan-Jones, Canad. J. Bot. 49: 999. 1971.

Descriptions and illustrations: Ellis (1959), Crous *et al.* (2013a).

Materials examined: **Australia**, Queensland, Mareeba, S16°58075.500 E145°20060.800 on leaves of *Mangifera indica*, 10 Aug. 2009, P.W. Crous & R.G. Shivas (**neotype** designated here CBS H-20846, MBT378567, ex-neotype culture CBS 125467 = CPC 17351); *idem*. CPC 17352. **New Caledonia**, Port Laguerre (Ec. Agr.), on *Mangifera indica*, 20 Nov. 1959, Bugnicourt, NC 59.061 a, b (PC).

Notes: The genus *Scolecostigmina* was introduced by Braun *et al.* (1999) to accommodate foliicolous stigmina-like hyphomycetes such as the type species *Scolecostigmina mangiferae*, characterised by producing sporodochial conidiomata with firm stromata, verruculose conidiophores and conidiogenous cells with conspicuous coarse annellations and scolecosporous, pluriseptate, thick-walled conidia. The type material of *Cercospora mangiferae* could not be traced (Indonesia, Java, on leaves of *Mangifera indica*, 21 Sep. 1905; Koorders 1907), but various other collections have been examined (Braun *et al.* 1999). Therefore, we propose the specimen CBS H-20846 as neotype and the strain CBS 125467 = CPC 17351 as ex-neotype culture. In this study, *Scolecostigmina* is represented by a single-train lineage in the phylogenetic analysis (Fig. 1, clade 24; Fig. 2, clade 30) and is closely related to *Trochophora* and *Pallidocercospora*. Numerous other morphologically similar species assigned to *Scolecostigmina* are hitherto not known in culture and the affinity of the species concerned to *Scolecostigmina mangiferae* remains to be proven. Therefore, they are currently only tentatively retained in *Scolecostigmina.*

Clade 25: *Parapallidocercospora*

Parapallidocercospora Videira, Crous, U. Braun, C. Nakash., **gen. nov.** MycoBank MB822604.

Etymology: Similar to the genus *Pallidocercospora*.

Description: Plant pathogenic. *Leaf spots* amphigenous, irregular to subcircular. *Ascomata* pseudothecial, predominantly hypophyllous, black, subglobose to globose, with apical ostiole, walls of 2–3 layers of medium brown *textura angularis*. *Asci* fasciculate, bitunicate, subsessile, cylindrical to narrowly ellipsoidal, straight or slightly incurved. *Ascospores* bi- to multiseriate, overlapping, hyaline, guttulate, thin-walled, straight to slightly curved, fusoid-ellipsoidal, obovoid, medianly 1-septate, not constricted at septum or only slightly constricted, tapering toward both ends but more prominently toward the base. *Spermogonia* intermixed with the ascomata or with the asexual morph, hyaline and rod-shaped. *Mycelium* internal and external, hyphae light brown, septate, branched, smooth. *Conidiophores* arising from superficial mycelium, from the upper cells of a brown stroma; conidiophores light brown, smooth, aseptate or septate, subcylindrical, straight to variously curved, unbranched. *Conidiogenous cells* terminal, unbranched, light brown, smooth, tapering to flat-tipped apical loci, proliferating sympodially, rarely percurrently near apex. *Conidia* solitary, light brown, smooth to finely

verruculose, septate, guttulate, narrowly obclavate or subcylindrical, tapering towards the base, straight to curved.

Type species: *Parapallidocercospora colombiensis* (Crous *et al.*) Videira & Crous (≡ *Pseudocercospora colombiensis* Crous & M.J. Wingf.).

Parapallidocercospora colombiensis (Crous & M.J. Wingf.) Videira & Crous, **comb. nov.** MycoBank MB822774.
Basionym: *Pseudocercospora colombiensis* Crous & M.J. Wingf., Mycol. Mem. 21: 42. 1998.
Synonym: *Mycosphaerella colombiensis* Crous & M.J. Wingf., Mycol. Mem. 21: 41. 1998.

Description and illustration: Crous (1998).

Materials examined: **Colombia**, Pinal Farm, on leaves of *Eucalyptus urophylla*, May 1995, M.J. Wingfield (**holotype** PREM 54397, ex-type culture CBS 110968 = CPC 1105).

Notes: The genus *Parapallidocercospora* is hereby introduced in order to accommodate two species, *Pseudocercospora colombiensis* (foliar pathogen of *Eucalyptus*; Crous 1998), and *Pseudocercospora thailandica* (foliar pathogen of *Acacia*; Crous *et al.* 2004c). Morphologically, these taxa appear typical members of *Pseudocercospora s. str.* and are difficult to identify without the use of DNA sequence data. In this study both species clustered in a well-supported clade in the phylogenetic analyses (Fig. 1, clade 25; Fig. 2, clade 31) and are closely related to *Pallidocercospora*, *Scolecostigmina* and *Trochophora*.

Parapallidocercospora thailandica (Crous, Himaman & M.J. Wingfield) Videira & Crous, **comb. nov.** MycoBank MB822775.
Basionym: *Mycosphaerella thailandica* Crous *et al.*, Stud. Mycol. 50: 465. 2004.
Synonyms: *Pseudocercospora thailandica* Crous *et al.*, Stud. Mycol. 50: 465. 2004.
Pallidocercospora thailandica (Crous *et al.*) Phook. *et al.*, Fungal Diversity 80: 21. 2016.

Descriptions and illustrations: Crous *et al.* (2004c), Hyde *et al.* (2016).

Materials examined: **Thailand**, Chachoengsao Prov., Sanamchaikhet, on leaves of *Acacia mangium*, 28 May 2003, K. Pongpanich (**holotype** CBS H-9875, of both *M. thailandica* and *P. thailandica*, cultures ex-type CBS 116367 = CPC10547–10549); Thatakiab District, on living leaves of *Eucalyptus camaldulensis*, Oct. 2006, W. Himaman, culture CBS 120723 = CPC 13478.

Note: See notes on *Parapallidocercospora colombiensis* and *Pallidocercospora*.

Clade 26: *Trochophora*

Trochophora R.T. Moore, Mycologia 47: 90. 1955.

Description (from Crous *et al.* 2013a): Foliicolous, but pathogenicity unproven. *Colonies* hypophyllous, medium to dark brown, consisting of fasciculate conidiophores or numerous synnemata. *Stroma* absent, but with a superficial network of hyphae linking the various

synnemata. *Conidiophores* fasciculate to synnematous, mostly unbranched and straight, or with 1–2 short branches, straight or curved, cylindrical, individual conidiophores tightly aggregated, but separating near the apex, pale to medium brown, smooth. *Conidiogenous cells* polyblastic, integrated, terminal, determinate to sympodial, with visible unthickened loci, clavate. *Conidia* solitary, terminal or lateral on conidiogenous cells, prominently curved to helicoid, pale to medium brown, smooth, transversely euseptate with a darkened, thickened band at the septa.

Type species: *Trochophora fasciculata* (Berk. & M.A. Curtis) Goos (≡ *Helicoma fasciculatum* Berk. & M.A. Curtis).

Trochophora fasciculata (Berk. & M.A. Curtis) Goos, Mycologia 78: 759. 1986.
Basionym: *Helicoma fasciculatum* Berk. & M.A. Curtis, Proc. Amer. Acad. Arts Sci. 4: 127. 1858.
Synonyms: *Helicosporium fasciculatum* (Berk. & M.A. Curtis) Sacc., Syll. Fung. 4: 560. 1886.
Helicomyces fasciculatus (Berk. & M.A. Curtis) Pound & Clem., Minn. Bot. Stud. 9: 658. 1896.
Helicostilbe simplex Petch, Ann. Royal Bot. Gard. Peradeniya 7: 321. 1922.
Trochophora simplex (Petch) R.T. Moore, Mycologia 47: 90. 1955.

Description and illustrations: Ellis (1971), Zhao *et al.* (2007), Crous *et al.* (2013a).

Materials examined: **India**, Sri Lanka, on *Daphniphyllum glaucescens*, collector unknown, Apr. 1917 (**holotype** of *Helicostilbe simplex*, IMI 87262). **Japan**, under side of dead leaves, date unknown, C. Wright 142 (**holotype** of *Helicoma fasciculatum*, NY 00945981); Shimane, Matsue, on *Daphniphyllum macropodum*, 26 Apr. 2008, C. Nakashima & I. Araki (**epitype** designated here TSU MUMH11134, MBT377074, ex-epitype culture MUCC 952). **Republic of Korea**, Jeju, Halla arboretum, on leaves of *Daphniphyllum macropodum*, 29 Oct. 2005, H.D. Shin, KACC 42362 = CBS H-20847, culture CBS 124744 = SMKC 21713; Pusan, on leaves of *Daphniphyllum macropodum*, 13 Nov. 2002, H.D. Shin, KUS-F19414, cultures CPC 10280–10282.

Notes: The genus *Trochophora* is currently monotypic based on *Trochophora fasciculata*, a pathogen of *Daphniphyllum* shrubs and trees in several Asian countries (Zhao *et al.* 2007). Based on the LSU sequence, the phylogenetic position has been shown to be closely related to *Pallidocercospora* and *Scolecostigmina* (Crous *et al.* 2013a). The phylogenetic results in this study, with the addition of *rpb2* and ITS sequences, agreed with the previous observations (Fig. 1, clade 26; Fig. 2, clade 32). Despite the low support, the distinctive morphology observed in *Trochophora* justifies that it is retained as separate, pending more collections to be added to this clade.

Clade 27: *Pseudophaeophleospora*

Pseudophaeophleospora C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822700.

Etymology: Composed of 'pseudo' (resembling but not equalling) + the similar genus, *Phaeophleospora*.

Description (adapted from Crous *et al.* 2007c and Wu *et al.* 1996): Phytopathogenic. *Conidiomata* amphigenous, globose, wall with up to four layers of dark brown *textura angularis*, subepidermal,

scattered, rarely aggregated, with a central ostiole from where conidia exude in a cirrhus. *Conidiophores* absent or reduced to only two cells. *Conidiogenous cells* pale brown, smooth to finely verruculose, ampulliform to doliiform, subcylindrical, proliferating percurrently near apex. *Conidia* formed singly, pale to dark brown, smooth to slightly verruculose, guttulate, subcylindrical to narrowly obclavate, slightly fusiform, straight, multiseptate, with apical cell tapering into an obtuse apex, widest at basal septum and tapering to a subtruncate base, hilum flattened with minute marginal frill.

Type species: *Pseudophaeophleospora stonei* (Crous) C. Nakash. *et al.* (≡ *Phaeophleospora stonei* Crous).

Pseudophaeophleospora atkinsonii (Syd.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822781.
Basionym: *Scoleciasis atkinsonii* Syd., Annls. Mycol. 22(3–6): 312. 1924.
Synonyms: *Phaeophleospora atkinsonii* (Syd.) Pennycook & McKenzie, Mycotaxon 82: 145. 2002.
Septoria exotica sensu Grove, Brit. Leaf-fung. 1: 415. 1935.
Kirramyces hebes W.P. Wu, B. Sutton & Gange, Mycol. Res. 100: 1208. 1996.
Phaeophleospora hebes (W.P. Wu, B. Sutton & Gange) Crous, F.A. Ferreira & B. Sutton, S. Afr. J. Bot. 63: 113. 1997.

Description and illustration: Wu *et al.* (1996).

Materials examined: **New Zealand**, Wellington, York Bay, on *Hebe stricta* var. *atkinsonii*, Oct. 1920, E.H. Atkinson (**holotype** PDD 968); St Johns, Morrin Road, Auckland University Campus, on *Hebe* sp., unkown date and collector, isol. C.F. Hill, 27 Jan. 2009, PDD 95173, cultures ICMP 17860 = CBS 124565; Grey Lynn, Western Springs Park, Jan. 2007, C.F. Hill, PDD 95176, culture ICMP 17862 = CBS 124566.

Notes: Despite the repeated attempts to induce the available cultures to sporulate on different types of agar medium, no reproductive structures characteristic of this species were formed. This species is transferred to *Pseudophaeophleospora* based on phylogenetic inference (Fig. 1, clade 27; Fig. 2, clade 33). According to Wu *et al.* (1996), the conidiophores are reduced to conidiogenous cells that are pale brown, and the conidia are obclavate to cylindrical, which correlate with the type species of *Pseudophaeophleospora.*

Pseudophaeophleospora stonei (Crous) C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822782.
Basionym: *Phaeophleospora stonei* Crous, Fungal Diversity 26: 169. 2007.

Description and illustration: Crous *et al.* (2007c).

Description in vitro (on V8; CBS 13330): *Mycelium* composed of hyaline to pale blackish brown hyphae, uniform in width, 2–2.5 µm diam. *Conidiomata* absent. *Conidiophores* micronematous to macronematous, emerging from hyphae, sometimes reduced to conidiogenous cells, pale blackish brown, 10–25 × 2.5–3.8 µm. *Conidiogenous* cells apical, intercalary, integrated, sometimes reduced to hyphae, proliferating percurrently, with unthickened loci, 2–2.5 µm

diam. *Conidia* solitary, pale blackish brown, smooth, holoblastic, schizolytic, cylindrical to short obclavate, rounded at the apex, 15–32.5 × 3.5–7.5 µm, 1–4-septate, with unthickened and truncate hilum at the base.

Materials examined: **Australia**, Queensland, Cairns, Kuranda, Karoomba River Walk, S 16° 490 08.800, E 145° 380 24.700, on leaves of *Eucalyptus* sp., 19 Aug. 2006, P.W. Crous & J. Stone (**holotype** CBS H-19835, culture ex-type CBS 120830 = CPC 13330); *idem*. CPC 13331, CPC 13332.

Notes: The genus *Phaeophloeospora*, based on the ITS sequence of its type species *Phaeophloeospora eugeniae*, belongs to *Mycosphaerellaceae* (Crous *et al.* 2001a, b). Since the ITS sequence of *Phaeophloeospora stonei* did not cluster with the type of *Phaeophleospora*, the genus was considered polyphyletic (Crous *et al.* 2007c). In the present study, the phylogenetic analysis performed based on the sequences of LSU, *rpb2* and ITS agrees with the previous work and the strain of *Pseudophaeophleospora stonei* forms a single strain lineage (Fig. 1, clade 27; Fig. 2, clade 33) that is closely related to *Pseudophaeophleospora atkinsonii*. The species *Phaeophloeospora concentrica* (not included in this study), a pathogen of *Protea* spp., clusters close to *Brunneosphaerella* (Crous *et al.* 2009c). Morphologically, *Pseudophaeophleospora* is very similar to *Phaeophleospora*, and the two genera can only safely be distinguished by means of DNA data.

Clade 28: *Sonderhenia*

Sonderhenia H.J. Swart & J. Walker, Trans. Brit. Mycol. Soc. 90: 640. 1988.

Description (from Crous 1998): Foliicolous, phytopathogenic, causing discrete leaf spots. *Leaf spots* amphigenous, round to confluent and irregular, surrounded by a purple border when young, which becomes dark red to brown and raised with age. *Ascomata* pseudothecial, amphigenous, on one side of each lesion, often 1–3, intermingled with conidiomata, immersed, black, punctiform, globose to subglobose; apical ostiole substomatal; wall olive brown, of 3–4 layers of *textura angularis*, subhymenium of 1–2 layers of hyaline cells. *Asci* fasciculate, bitunicate, subsessile, 8-spored, ovoid to obclavate, straight to incurved. *Ascospores* 2–3-seriate, hyaline, guttulate, straight or slightly curved, fusiform, 1-septate, widest just above median septum, slightly constricted at septum. *Conidiomata* pycnidial, amphigenous, subepidermal with central non-projecting ostiole, scattered, black, globose; wall of 2–3 layers of brown cells. *Conidiogenous cells* minute, olivaceous, proliferating enteroblastically and percurrently, lining the inner pycnidial wall layer. *Conidia* ellipsoidal to cylindrical or ovoid, straight or bent, brown, 3-distoseptate, not constricted, verruculose, apex obtuse, base truncate with marginal frill.

Type species: *Sonderhenia eucalyptorum* (Hansf.) H.J. Swart & J. Walker (≡ *Hendersonia eucalyptorum* Hansf.).

Sonderhenia eucalyptorum (Hansf.) H.J. Swart & J. Walker, Trans. Brit. Mycol. Soc. 90: 640. 1988.
Basionym: *Hendersonia eucalyptorum* Hansf., Proc. Linn. Soc. N.S.W. 79(3-4): 135. 1954.
Synonym (sexual morph): *Mycosphaerella swartii* R.F. Park & Keane, Trans. Brit. Mycol. Soc. 83: 99. 1984.

Descriptions and illustrations: Swart & Walker (1988), Crous (1998).

Materials examined: **Australia**, Mt. Gambier, on leaves of *Eucalyptus leucoxylon*, 9 Dec. 1982, R.F. Park (**holotype** of *Mycosphaerella swartii* DAR 45719, isotype IMI 280474, sexual morph); Clare, on leaves of *E. leucoxylon*, Aug. 1922, T. Osborne (**holotype** of *Hendersonia eucalyptorum*, K(M) 137253, WARI 2007, asexual morph); **Tasmania**, on leaves of *Eucalyptus coccifera*, Jan. 2006, C. Mohammed, cultures CBS 120220 = CPC 12553, CPC 12554–12555.

Notes: *Sonderhenia* includes taxa with mycosphaerella-like sexual morphs and pycnidial asexual morphs. The brown conidiogenous cells proliferate percurrently and give rise to brown conidia that are transversely distoseptate. Only two species, *Sonderhenia eucalypticola* and *Sonderhenia eucalyptorum* are presently known (Crous *et al.* 2013a), and they cluster together in a well-supported clade (Fig. 1, clade 28; Fig. 2, clade 34) closely related to *Pseudophaeophleospora*.

Clade 29: *Pseudocercospora*, *Neopseudocercospora* and pseudocercospora-like

Pseudocercospora Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires, Ser. 3, 20: 437. 1910.
Synonym: *Neopseudocercospora* Crous, Persoonia 31: 219. 2013.
Additional synonyms: See Crous & Braun (2003), Braun *et al.* (2013), Crous *et al.* (2013a).

Description (from Crous *et al.* 2013a): Foliicolous, chiefly phytopathogenic, but also endophytic; commonly associated with leaf spots, but also occurring on fruits. *Mycelium* internal and external, consisting of smooth, septate, subhyaline to brown branched hyphae. *Stroma* absent to well-developed. *Conidiophores in vivo* arranged in loose to dense fascicles, sometimes forming distinct synnemata or sporodochia, emerging through stomata or erumpent through the cuticle, often arising from substomatal or subcuticular to intraepidermal stromata, or occurring singly on superficial hyphae, short to long, septate or continuous, i.e. conidiophores may be reduced to conidiogenous cells, simple to branched and straight to geniculate-sinuous, subhyaline, pale to dark olivaceous to brown, smooth to finely verruculose. *Conidiogenous cells* integrated, terminal, occasionally intercalary, polyblastic, sympodial, or monoblastic, proliferating percurrently via inconspicuous or darkened, irregular annellations, subhyaline, olivaceous, pale to dark brown, with inconspicous, or only thickened along the rim, or flat, and unthickened or almost so but refractive or even slightly darkened-refractive loci, but never pronounced. *Conidia* solitary, rarely in simple chains or disarticulating, subhyaline, olivaceous, pale to dark brown, usually scolecosporous, i.e. obclavate-cylindrical, filiform, acicular, and transversely multi-euseptate, occasionally also with oblique to longitudinal septa, conidia rarely amero- to phragmosporous, short subcylindrical or ellipsoidal-ovoid, aseptate or only with few septa, apex subacute to obtuse, base obconically truncate to truncate, or bluntly rounded, with or without a minute marginal frill, straight to curved, rarely sigmoid, smooth to finely verruculose; hila usually unthickened, not darkened, at most somewhat refractive, occasionally slightly thickened along the rim, or rarely flat, unthickened or almost so, but slightly refractive or even slightly darkened-refractive, but never pronounced.

Type species: *Pseudocercospora vitis* (Lév.) Speg. (≡ *Septonema vitis* Lév.).

Pseudocercospora dingleyae U. Braun & C.F. Hill (as '*dingleyii*'), Mycol. Progress 1(1): 23. 2002.

Replaced synonym: *Cercospora haloragis* Dingley, New Zealand J. Agric. Res. 8(4): 913. 1965, non *Pseudocercospora haloragidis* (Hansf.) U. Braun 1995.

Materials examined: **New Zealand**, Auckland, Piha, White's Stream, on *Haloragis erecta* 31 Jan. 1954, J.M. Dingley (**holotype** PDD 20086); Auckland, Grey Lynn, Western Springs, on *Haloragis erecta*, 21 Jan. 2001, C.F. Hill 367, HAL 3239 F, PDD 73036, culture CBS 114645.

Note: The present name was introduced by Braun & Hill (2002) for the species *Cercospora haloragidis* which had unthickened and undarkened conidiogenous loci and hila, a characteristic of *Pseudocercospora*.

Pseudocercospora convoluta (Crous & Breeÿen) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822778.
Basionym: *Passalora convoluta* Crous & Den Breeÿen, Fungal Diversity 23: 96. 2006.

Description and illustrations: Den Breeÿen *et al.* (2006).

Materials examined: **Costa Rica**, San Isidro between San José and Golfito, on leaves of *Chromolaena odorata*, 15 Oct. 1997, M.J. Morris (**holotype** CBS H-19752, ex-type culture CBS 113377 = MJM 1533 = C488).

Notes: The phylogenetic analysis in this study showed that this species clustered within the *Pseudocercospora* clade (Fig. 1, clade 29; Fig. 2, clade 23). Although in the original description of the species the loci and hila were described as 'darkened, thickened and refractive' (Breeÿen *et al.* 2006), observation of the type specimen and culture led to the conclusion that these are within the acceptable range of this genus.

Pseudocercospora metrosideri U. Braun, Fungal Diversity 8: 44. 2001.

Material examined: **New Zealand**, Auckland, on *Metrosideros excelsa*, 17 Oct. 2003, C.F. Hill 929, culture CBS 114294.

Note: The present strain was introduced by Braun & Hill (2004) and, although the conidia were shorter and narrower than average, they were still within the range from the original description by Braun (2001).

Pseudocercospora nodosa (Constant.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822779.
Basionym: *Cercospora nodosa* Constant., Mycotaxon 3: 122. 1975.
Synonym: *Passalora nodosa* (Constant.) L.G. Br. & Morgan-Jones, Mycotaxon 4: 303. 1976.

Description and illustration: Brown & Morgan-Jones (1976).

Materials examined: **Romania**, Bucuresti, on *Psoralea bituminosa*, 23 Sep. 1966, O. Constantinescu (**holotype** BUCM 41472, ex-type culture CBS 554.71, wrongly cited as "555.71" in protologue).

Notes: Based on the phylogenetic analyses in this study, this species clustered within *Pseudocercospora* (Fig. 1, clade 29; Fig. 2, clade 23). Although we did not study the holotype specimen, we examined the ex-type culture. When Constantinescu (1975) proposed this species, his detailed line drawings illustrated "thin", discrete conidial scars (loci)". In addition, Brown & Morgan-Jones (1976), who observed the holotype, mentioned that the thin scars, swollen conidiophore apices and basal conidial cells were indicative of its placement in *Passalora*. However, these characters are also typical characters of *Pseudocercospora*.

Pseudocercospora vitis (Lév.) Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires 20(13): 438. 1910.
Basionym: *Septonema vitis* Lév., Ann. Sci. Nat., Bot., Sér. 3, 9: 261. 1848.
For additional synonyms see MycoBank.

Description and illustrations: Deighton (1976a).

Materials examined: **Republic of Korea**, Namyangju, on *Vitis vinifera*, 30 Sep. 2004, H.D. Shin, CBS H-20848, CBS 132012 = CPC 11595; on *V. vinifera*, 1 Oct. 2007, H.D. Shin, cultures CBS 132112 = CPC 14661.

Notes: Type material of *Septonema vitis* is not preserved, as already noted by Harvey & Wenham (1972), and the designation of a neotype is required, but fresh collections from the type host and location are necessary (France, Bordeaux, on *Vitis vinifera*). *Pseudocercospora* is a large cosmopolitan genus of plant pathogenic fungi that is commonly associated with leaf spots and blights on a wide range of plant hosts. Species occur in arid as well as wet environments and in a wide range of climates. The phylogenetic placement of *Pseudocercospora* has previously been determined and many new species have since been described (Crous *et al.* 2013a). In this study, the *Pseudocercospora* clade is well-supported by the phylogenetic analysis (Fig. 1, clade 29; Fig. 2, clade 23) and *Pseudocercospora pistacina* is basal to the clade. In addition, the type species of *Neocercospora*, *Neocercospora zambiae*, is observed to cluster within the *Pseudocercospora* clade and, therefore, Sutton's reallocation of *Sporidesmium zambiense* to *Pseudocercospora* is resurrected as current name.

Pseudocercospora zambiensis (Deighton) B. Sutton, Mycopathologia 125: 61. 1994.
Basionym: *Sporidesmium zambiense* Deighton, Mycol. Pap. 117: 27. 1969.
Synonyms: *Repetophragma zambiense* (Deighton) Subram., Proc. Indian Acad. Sci., B, 58: 185. 1992.
Neopseudocercospora terminaliae Crous, Persoonia 31: 219. 2013.
Neopseudocercospora zambiensis (Deighton) Crous & U. Braun, IMA Fungus 5: 204. 2014.

Descriptions and illustrations: Crous *et al.* (2013a), Braun *et al.* (2014).

Materials examined: **Zambia**, on *Terminalia* sp., 24 Feb. 2013, M. van der Bank (**holotype** of *Neopseudocercospora terminaliae* CBS H-21431, culture ex-type CBS 136423 = CPC 22686); *idem*., culture CPC 22685.

Notes: When *Neopseudocercospora* was described (Crous *et al.* 2013a) the phylogenetic analysis performed placed it close to zasmidium-like species based on LSU and ITS sequences. In the present study, when the *rpb2* gene is introduced in the phylogenetic analysis,

Neopseudocercospora clusters within the genus *Pseudocercospora* (Fig. 1, clade 29; Fig. 2, clade 23). Conidiogenous cells and conidia of *Neopseudocercospora* are similar to those of *Pseudocercospora* in being unthickened and non-pigmented. However, unlike most *Pseudocercospora* species, it produces solitary conidiophores with conidiogenous cells that proliferate percurrently and conidia with longitudinal septa (sporidesmium-like) (Crous *et al.* 2013a, Braun *et al.* 2014).

Species clustering in the *Pseudocercospora* clade that need further material to be collected before a formal combination into *Pseudocercospora* can be proposed:

Passalora bolleana (Thüm.) U. Braun, Mycotaxon 55: 228. 1995.
Basionym: *Septosporium bolleanum* Thüm., Oesterr. Bot. Z. 27 (1): 12.1877.
Synonyms: *Cercospora bolleana* (Thüm.) Speg., Michelia 1(5): 475. 1879.
Pseudocercospora bolleana (Thüm.) Sivan., The Bitunicate Ascomycetes and their anamorphs: 206. 1984.
For additional synonyms see MycoBank.

Descriptions and illustrations: Ellis (1976), Sivanesan (1984).

Materials examined: **Romania**, on *Ficus carica*, 21 Oct. 1970, O. Constantinescu, culture CBS 541.71. **Republic of Korea**, on *F. carica*, 14 Nov. 2007, H.D. Shin, culture CPC 14819.

Notes: "*Passalora bolleana*" is widely distributed throughout the world and is known as a typical species of *Passalora s. lat*. The conidial loci of "*Passalora bolleana*" are conspicuous, almost unthickened to slightly thickened and somewhat darkened. The present strains, since they cluster in the *Pseudocercospora* clade, will be treated as *Pseudocercospora* sp. until more information is available (Table 1).

Passalora robiniae (Shear) S. Hughes, Canad. J. Bot. 31: 572. 1953.
Basionym: *Fusicladium robiniae* Shear, Bull. Torrey Bot. Club 29: 452. 1902.
Synonyms: *Camptomeris robiniae* (Shear) Cif., Mycopathol. Mycol. Appl. 6: 25. 1951.
Phaeoisariopsis robiniae (Shear) Deighton, in Ellis, More Dematiaceous Hyphomycetes: 234. 1976.
For additional synonyms see MycoBank.

Description and illustration: Hughes (1953a), Ellis (1976).

Material examined: **USA**, on *Robinia pseudoacacia*, unknown date and collector, isol. and dep. R.W. Davidson, deposited in 1939, culture CBS 277.39.

Notes: The type specimen of *Fusicladium robiniae* can be found in BPI, together with several isotypes. The specimen from which the culture CBS 277.39 was isolated is likely BPI 424556, based on the specimen metadata agreeing with the culture metadata (USA, Tennessee, Gatlinburg, Great Smoky Mountains National Park, *Robinia pseudoacacia*, 21 Aug. 1939, R.W. Davidson). Unfortunately, we were unable to study any of the previously mentioned specimens and the examined strain refused to sporulate on various media. Hughes (1953a) redescribed *Passalora robiniae*, which typically forms 1(–2)-septate conidia, the lower cell being wider

than the upper one. The present strain, since it clusters in the *Pseudocercospora* clade, will be treated as *Pseudocercospora* sp. until more information is available (Table 1).

Clade 30: *Clypeosphaerella*

Clypeosphaerella Guatimosim *et al.*, Persoonia 37: 121. 2016, emend.

Description: Phytopathogenic. *Ascomata* pseudothecial, epiphyllous, solitary, subcuticular to erumpent, globose, walls of 2–3 layers of brown to dark brown *textura angularis*, ostiole central. *Asci* bitunicate, aparaphysate, fasciculate, subsessile, 8-spored, obpyriform to ovoid, hyaline, smooth. *Ascospores* inordinate, overlapping, fusoid, straight, 1-septate, slightly constricted at the septum, biguttulate, hyaline, thin-walled, smooth; germinating at both ends, remaining hyaline, germ tubes following the main axis of the spore. *Conidiophores* fasciculate, pale olivaceous, septate, usually curved, rarely branched, geniculate at the apex, conidiogenous cells with *conidiogenous loci* (scars) thickened and darkened. *Conidia* solitary, pale brown to olivaceous brown, cylindrical to obclavate, obconic base, bluntly rounded tip, septate, sometimes constricted at the septa, hilum at the base thickened and darkened.

Type species: *Clypeosphaerella sticheri* Guatimosim *et al.*

Clypeosphaerella calotropidis (Ellis & Everh.) Videira & Crous, **comb. nov.** MycoBank MB822749.
Basionym: *Cercospora calotropidis* Ellis & Everh., Rep. (Annual) Missouri Bot. Gard.: 120. 1898.
Synonyms: *Phaeoramularia calotropidis* (Ellis & Everh.) Kamal, A.S. Moses & R. Chaudhary, Mycol. Res. 94: 716. 1990.
Pseudocercospora calotropidis (Ellis & Everh.) Haldar & J.B. Ray, J. Mycopathol. Res. 39(1): 43. 2001.
Passalora calotropidis (Ellis & Everh.) U. Braun, Schlechtendalia 5: 60. 2000.
For additional synonyms see Crous & Braun (2003) and MycoBank.

Descriptions and illustrations: Chupp (1954), Ellis (1976), Wilkinson *et al.* (2005).

Material examined: **Egypt**, on *Calotropis procera*, unknown date and collector, culture CBS 129.30.

Notes: Braun (2000) transferred *Cercospora calotropidis* to the genus *Passalora* based on the observation of numerous specimens, including the type specimen (Bahamas, Fortune Island (Long Cay), on *Calotropis procera*, Nov. 1890, A.S. Hitchcock, BPI 433953, 433956, NY, IMI 7752, slide). The isolate of *Cercospora calotropidis* used in our study was sterile and the specimen was unfortunately not preserved. The strain used in the present study has an ITS sequence that is 99 % similar to GenBank AY303969, a *Passalora calotropidis* strain used by Wilkinson *et al.* (2005). In Wilkinson *et al.* (2005), the isolate's morphology has similar diagnostic characters to those of *Passalora calotropidis* (Braun 2000) and the phylogenetic analysis based on ITS placed the species in a single-strain lineage closely related to *Pseudocercospora*. In the present study, based on a multigene analysis, the strain CBS 129.30 clusters in *Clypeosphaerella* (Fig. 1, clade 30; Fig. 2, clade 26), which is closely related to *Pseudocercospora*. Based on a BLAST comparison against the alignment, the

present species shares 97 % (425/438) similarity based on ITS and 96 % (733/763) similarity based on *rpb2* with *Clypeosphaerella quasiparkii* CBS 123243. Similar values of percentage similarity can be observed, for example, between *Zymoseptoria brevis* and *Zymoseptoria tritici*. Therefore, proposing a new genus to include this species would be unreasonable. The main issue is that the previously described species in this genus, *Clypeosphaerella sticheri* and *Clypeosphaerella quasiparki*, are only known by their sexual morph and *Passalora calotropidis* is only known from its asexual morph. Nevertheless, based on the molecular similarities, we propose a tentative combination of the present species in *Clypeosphaerella* until further morphological studies can be performed.

Clypeosphaerella quasiparkii (Cheew. *et al.*) Guatimosim *et al.*, Persoonia 37: 121. 2016.
Basionym: *Mycosphaerella quasiparkii* Cheew. *et al.*, Persoonia 21: 85. 2008.

Description and illustration: Cheew. *et al.* (2008).

Material examined: **Thailand**, Burirum, on leaves of *Eucalyptus* sp., Jul. 2007, P. Suwannawong (**holotype** CBS H-20132, culture ex-type CBS 123243 = CPC 15409); *idem*., cultures CPC 15433, CPC 15434.

Note: *Clypeosphaerella sticheri* is similar to *Clypeosphaerella quasiparki* but produces smaller ascospores that germinate in a type D pattern (Crous 1998, Guatimosim *et al.* 2016).

Clypeosphaerella sticheri Guatimosim *et al.*, Persoonia 37: 121. 2016.

Description and illustration: Guatimosim *et al.* (2016).

Materials examined: **Brazil**, Rio de Janeiro, Nova Friburgo, Fazenda Barreto II, Riograndina, ruderal, on fronds of *Sticherus bifidus*, 11 Feb. 2014, R.W. Barreto (**holotype** CBS H-22088, isotype VIC 42607, culture ex-type CPC 24705); Minas Gerais, Araponga, Parque Estadual da Serra do Brigadeiro, path to Pico do Pato, Atlantic rainforest, on fronds of *S. bifidus*, 21 Feb. 2014, E. Guatimosim, CBS H-22089, VIC 42516, culture CPC 24733.

Notes: Morphologically, the genus *Clypeosphaerella* is reminiscent of *Mycosphaerella s. lat*. (sexual morph) but differs by having the thicker upper wall of the ascomata resembling a pseudoclypeus. The phylogenetic analyses in this study places *Clypeosphaerella* in a well-supported clade (Fig. 1, clade 30; Fig. 2, clade 26) closely related to *Distocercospora*.

Clade 31: *Distocercospora*

Distocercospora N. Pons & B. Sutton, Mycol. Pap. 160: 60. 1988.

Description (from Braun *et al.* 2013): Foliicolous, plant pathogenic, leaf spotting hyphomycetes (asexual morphs), sexual morphs unknown. *Mycelium in vivo* internal; hyphae branched, septate, subhyaline to pigmented, thin-walled, smooth. *Stromata* lacking to well-developed, pigmented, *textura angulata* to *textura globosa*. *Conidiophores* macronematous, mononematous, simple to branched, often strongly branched, septate, pigmented, thin-walled, smooth to rough-walled. *Conidiogenous cells* integrated, terminal, occasionally intercalary, proliferation sympodial, conidiogenous loci conspicuous, almost unthickened to somewhat thickened and darkened. *Conidia*

formed singly, rarely in short chains, scolecosporous, mostly obclavate to cylindrical, with a single to several transverse distosepta or a mixture of eu- and distosepta, subhyaline to pigmented, wall smooth to rough, hila somewhat thickened and darkened, conidial secession schizolytic.

Type species: *Distocercospora pachyderma* (Syd. & P. Syd.) N. Pons & B. Sutton (≡ *Cercospora pachyderma* Syd. & P. Syd.).

Distocercospora pachyderma (Syd. & P. Syd.) N. Pons & B. Sutton, Mycol. Pap. 160: 60. 1988. Fig. 14.
Basionym: *Cercospora pachyderma* Syd. & P. Syd., Ann. Mycol. 12: 203. 1914.
Synonyms: *Cercosporina pachyderma* (Syd. & P. Syd.) Sacc., Syll. Fung. 25: 900. 1931.
Cercospora dioscoreae-bulbiferae J.M. Yen & Gilles, Cah. Maboké 9: 105. 1973.

Description and illustration: Braun *et al.* (2014).

Description in vivo (on V8; CPC 24144): *Mycelia* composed of hyaline to pale olivaceous, uniform in width, 2.5–3.8 µm, often forming large brown swollen cells, up to 10 µm in size. *Conidiophores* micro- or macronematous, pale olivaceous, arising from hyphae or swelling cells, smooth, septate, irregular in width, 2.5–7 µm, straight or geniculate, 50–165 × 2.5–7.5 µm. *Conidiogenous cells* integrated, apical, polyblastic, proliferating percurrently following

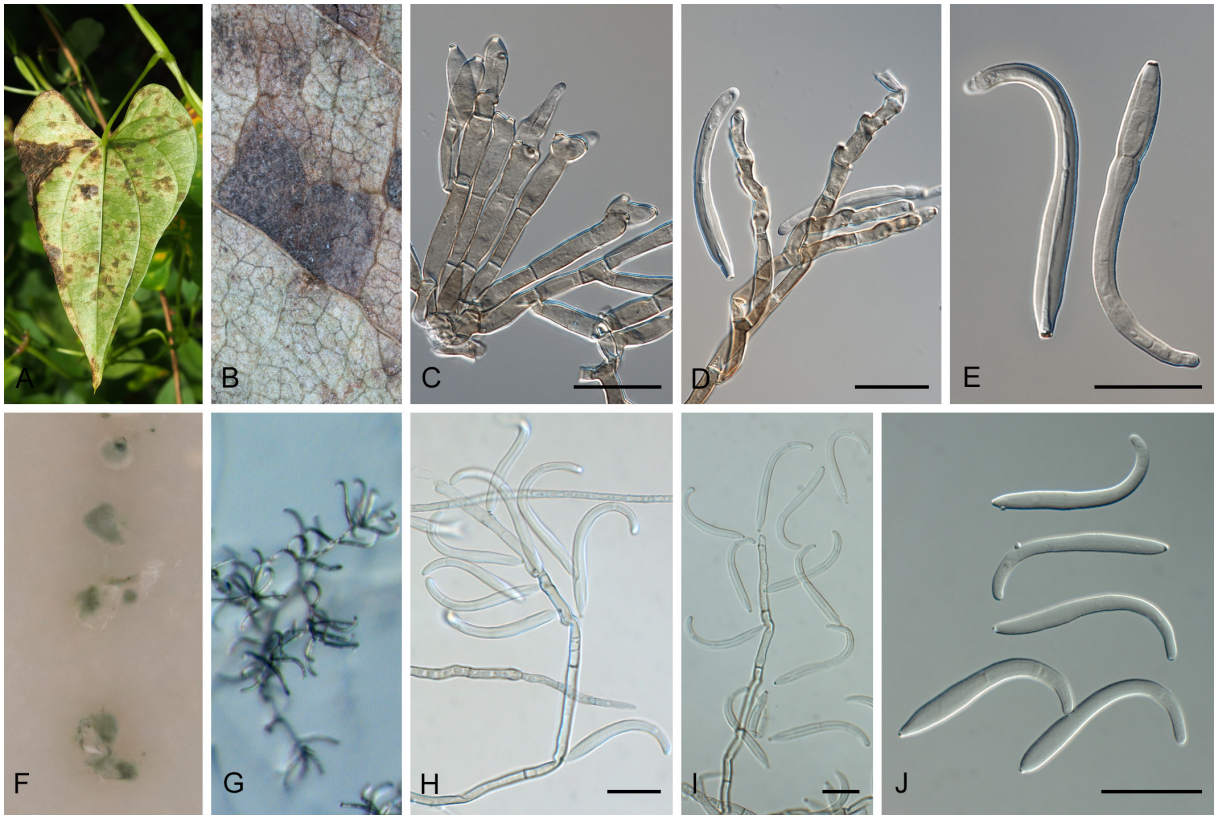


Fig. 14. *Distocercospora pachyderma* (CBS 138247). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Conidiophores and conidiogenous cells. D. Conidiophores, conidiogenous cells and conidia. E. Conidia. F–J. Observations *in vitro*. F. Culture on OA. G. Conidiophores erect and emerging from hyphae. H–I. Conidiophore, conidiogenous cell and conidia. J. Conidia. Scale bars = 10 µm.

sympodial sporulation, with darkened, rim-like and thickened loci, 1.25–2.5 µm diam. *Conidia* solitary, rarely catenate, hyaline to pale olivaceous brown, cylindrical to obclavate, straight, apex rounded and often elongated (beak-like), base long obconically truncate, 28–55 × 2.5–7.5 µm, 2–3- eu- or distoseptate, hila thickened, darkened and refractive.

Materials examined: **Japan**, Iwate, Morioka, Koma, on *Dioscorea* sp., 13 Sep. 2010, C. Nakashima & K. Motohashi (**epitype** designated by Braun *et al.* 2014, TSU MUMH11476, isotype CBS H-21733, ex-epitype culture CBS 138247 = CPC 24144); Ibaragi, on *Dioscorea* sp., T. Kobayashi, slide specimen MUCC-PL-185. **Fiji**, Taveuni, Tabakau, on *Dioscorea bulbifera*, 22 Dec. 2002, E.H.C. McKenzie, PDD 77375. **Philippines**, Prov. Laguna, Luzon, Morong Valley, on *Dioscorea alata*, 9 Nov. 1913, M. B. Raimundo, C.F. Baker 2051 (**neotype** S F37683); Luzon, Los Banos, on *Dioscorea alata*, Nov. 1913, C.F. Baker 522 (**topotypes**: B; BPI 439183, BPI 439184; IMI 256649, S F37682).

Notes: Morphologically, *Distocercospora* is similar to *Passalora* with almost unthickened to somewhat thickened, darkened loci and hila and pigmented conidia, but differs in having conidia with a mixture of eu- and distosepta (Fig. 14). The formation of distoseptate conidia occasionally occurs in other genera (e.g. in *Pseudocercospora cryptomeriicola*) (Nakashima *et al.* 2007), and may have gone undetected among other cercosporoid fungi due to the difficulty in observing such septa in taxa with thin walls (Braun *et al.* 2013). The meaning of distoseptation (= pseudoseptation) as character at generic level within the cercosporoid fungi is still unclear (Braun *et al.* 2015a). Morphologically, the genus *Distocercospora* was evidently characterised by the mode of proliferation of its conidiophores, which are composed of two distinct layers. During proliferation of its conidiogenous cells, first the outer layer of conidiophore is broken by the percurrent proliferation of the inner layer, and secondly, many conidia are formed sympodially. At this point, septa of conidiophores and most of the conidia of *Distocercospora pachyderma* show the pseudoseptation. The cultures and molecular data based on the type species of *Distocercospora* (*Distocercospora pachyderma*) used in this study showed that this species clusters within the *Mycosphaerellaceae* in a separate clade supported by all the phylogenetic analyses performed (Fig. 1, clade 31; Fig. 2, clade 27). These results support *Distocercospora* as a separate genus, distinguished from *Passalora s. str.*

Clade 32: *Uwemyces*

Uwemyces Hern.-Restr., G.A. Sarria & Crous, Persoonia 36: 455. 2016.

Description (from Crous *et al.* 2016b): *Mycelium* immersed and superficial, hyphae branched, septate, hyaline and brown, smooth-walled. *Conidiophores* fasciculate, simple, dark brown at the base and subhyaline at the apex. *Conidiogenous cells* cylindrical, sympodial, polytretic, with dark conidiogenous loci, terminal and intercalary, brown. *Conidia* solitary, straight or curved, cylindrical to obclavate, pale brown to brown, apex subhyaline, verruculose-walled, with a thick, dark brown, truncate scar at the base, septate. Sexual morph unknown.

Type species: *Uwemyces elaeidis* (Steyaert) M. Hern.-Restr. *et al.* (≡ *Cercospora elaeidis* Steyaert).

Uwemyces elaeidis (Steyaert) M. Hern.-Restr. *et al.* Persoonia 36: 455. 2016.
Basionym: *Cercospora elaeidis* Steyaert, Bull. Soc. R. Bot. Belg., 80: 35. 1948; as "*elaedis*".
Synonym: *Pseudospiropes elaeidis* (Steyaert) Deighton, Trans. Brit. Mycol. Soc. 85: 739. 1985.

Descriptions and illustrations: Ellis (1976), Deighton (1985), Braun *et al.* (2014), Crous *et al.* (2016b).

Material examined: **Colombia**, Barrancabermeja, CENIPALMA, on leaves of *Elaeis oleifera*, May 2013, coll. G.A. Sarria, culture CPUwZC-01.

Notes: The taxonomic position of *Cercospora elaedis* was recently discussed by Braun *et al.* (2014). This species has a wide distribution and seems to be restricted to *Elaeis guineensis*, (*Arecaceae*). Phylogenetically, this species is represented by a single-strain lineage closely related to *Distocercospora* (Fig. 1, clade 31) or to *Coremiopassalora* (Fig. 2, clade 24). The type material of *Cercospora elaeidis* (Democratic Republic of the Congo, on *Elaeis guineensis*) could not be traced and the species needs to be neotypified (Braun *et al.* 2014). The present strain is unsuitable for neotypification due to its geographical origin (Crous *et al.* 2016b).

Clade 33: *Coremiopassalora*

Coremiopassalora U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822585.

Etymology: Derived from the arrangement of conidiophores, coremium + resembling the genus *Passalora.*

Differs from the genus *Passalora* by synnematous conidiophores and catenate, hyaline to pale olivaceous conidia with distinct, slightly thickened and not darkened loci.

Type species: *Coremiopassalora eucalypti* (Crous & Alfenas) U. Braun *et al.* (≡ *Mycovellosiella eucalypti* Crous & Alfenas).

Coremiopassalora eucalypti (Crous & Alfenas) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822750
Basionym: *Mycovellosiella eucalypti* Crous & Alfenas, Mycol. Mem. 21: 105. 1998.
Synonym: *Passalora eucalypti* (Crous & Alfenas) Crous & U. Braun, in Crous & Braun, CBS Biodiversity Ser. 1: 452. 2003.

Description and illustration: Crous (1998).

Description in vitro (on V8; CBS 111318): *Mycelium* composed of hyaline to pale brown, delicate hyphae, uniform in width, 2.5 µm, often showing a synnematous or cushion-shaped arrangement. *Conidiophores* straight to sinuous or geniculate, solitary to tightly fasciculate, sometimes appearing as synnemata, simple, 10–33 × 2–2.5 µm. *Conidiogenous cells* integrated, terminal, polyblastic, proliferating sympodially, conidiogenous loci at the apex and shoulders, protruding and conically truncate, slightly thickened and refractive, 1–2 µm diam. *Conidia* catenate, occurring in unbranched or branched chains, hyaline, cylindrical, sometimes obclavate,

obconically truncate at both ends, 8–40 × 2–2.5 µm, 0–1-septate, sometimes constricted at the centre, hila thickened but not darkened, 1–2 µm diam.

Materials examined: **Brazil**, São Paulo, on leaves of *Eucalyptus saligna*, Jun. 1995, P.W. Crous & A.C. Alfenas (**holotype** PREM 55302, culture ex-type CBS 111306 = CPC 1455); *idem*., CBS 111318 = CPC 1457; Suzano, on leaves of *Eucalyptus saligna*, 8 Aug. 1996, P.W. Crous, culture CBS 111306 = CPC 1455.

Note: The genus *Coremiopassalora* (Fig. 1 clade 33; Fig. 2, clade 24) includes two species that morphologically can be characterised as *Passalora s. lat.*, but phylogenetically are not congeneric with the type *Passalora bacilligera* (Fig. 1 clade 34; Fig. 2, clade 22).

Coremiopassalora leptophlebae (Crous *et al.*) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822751.
Basionym: *Passalora leptophlebae* Crous *et al.* (as "*leptophlebiae*"), Persoonia 26: 131. 2011.

Description and illustrations: Crous *et al.* (2011a).

Material examined: **Brazil**, Minas Gerais, Viçosa, University Forestry Nursery, on leaves of *Eucalyptus leptophleba*, 23 Aug. 2010, P.W. Crous, A.C. Alfenas, R. Alfenas & O.L. Pereira (**holotype** CBS H-20585, culture ex-type CBS 129524 = CPC 18480).

Notes: *Coremiopassalora leptophlebae* is the second species in this genus (Fig. 1, clade 33; Fig. 2, clade 24). The host range and geographic distribution of this taxon are thus far restricted to the type collection.

Clade 34: *Passalora*

Passalora Fr., Summa Veg. Scand. 2: 500. 1849, emend.

Description: Hyphomycetous, phytopathogenic. *Mycelium* internal, consisting of hyaline, branched, septate hyphae. *Stromata* absent or small. *Conidiophores* emerging through stomata, in fascicles, unbranched or branched, straight to flexuous, at times with a single basal septum, usually up to 3-septate, medium brown, somewhat swollen in the conidiogenous region. *Conidiogenous cells* integrated, terminal, with flat, somewhat thickened and darkened loci. *Conidia* solitary, olivaceous to pale brown, thin-walled, smooth, straight or gently curved, mostly didymosporous, constricted at septum, with somewhat thickened, darkened and refractive hila.

Type species: *Passalora bacilligera* (Mont. & Fr.) Mont. & Fr. (≡ *Cladosporium bacilligerum* Mont. & Fr.).

Passalora bacilligera (Mont. & Fr.) Mont. & Fr., in Montagne, Sylloge generum specierumque cryptogamarum: 305. 1856. Fig. 15.
Basionym: *Cladosporium bacilligerum* Mont. & Fr., in Montagne, Ann. Sci. Nat., Bot., Sér. 2, 6: 31. 1836.

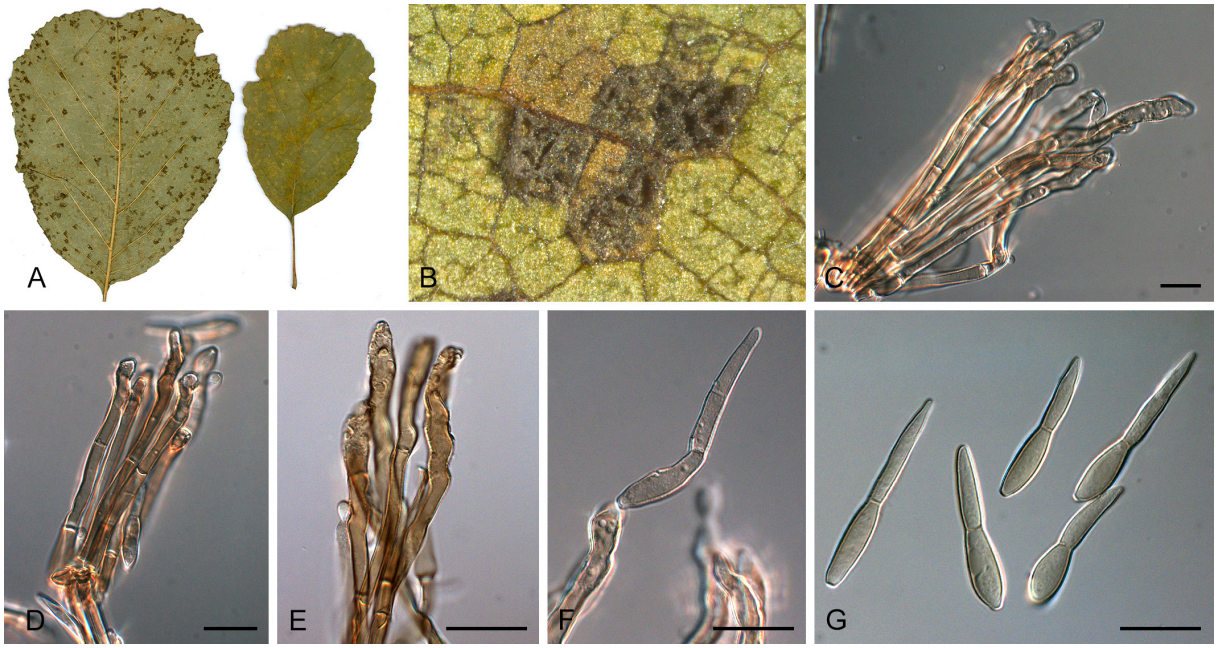


Fig. 15. *Passalora bacilligera* (CBS 131547). A–G. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C–E. Conidiophores and conidiogenous cells. F. Conidiogenous cell and conidium. G. Single conidia. Scale bars = 10 µm.

Description in vivo (CBS H-20777): *Leaf spots* absent or yellowish green, angular, 1–2 mm diam, delimited by leaf veins. *Caespituli* hypophyllous, olivaceous to pale brown. *Mycelium* internal, consisting of hyaline, branched, septate, 1–2 µm diam hyphae. *Stromata* absent or only formed as small aggregations of a few swollen substomatal hyphal cells. *Conidiophores* medium brown, arising from stomata, in fascicles of up to 12, unbranched or occasionally branched, straight to flexuous, usually up to 3-septate, occasionally with a single basal septum, 40–180 × 3–3.5 µm, geniculate at the apex. *Conidiogenous cells* integrated, terminal, somewhat swollen, 3–6.5 µm in width, polyblastic, proliferating sympodially, with conidiogenous loci flat, somewhat thickened and darkened, 1–2 µm diam. *Conidia* solitary, olivaceous to pale brown, thin-walled, smooth, straight or gently curved, basal cell ellipsoid-doliiform and obconical truncate without protruding, apical cell narrowly long-ellipsoid to subcylindrical, 21–68 × 4.5–8.5 µm, (0–)1(–3)-euseptate, constricted at basal septum, with hilum somewhat thickened, darkened and refractive, 1.5–2 µm diam.

Description in vitro (on V8; CBS 131547): *Mycelium* composed of hyaline to pale olivaceous brown, delicate hyphae, 2–2.5 µm width. *Conidiophores* macronematous, pale olivaceous brown to brown, simple or branched, straight to sinuous, smooth, paler towards the apex, 25–300 × 2.5–3.3 µm. *Conidiogenous cells* integrated, terminal, proliferating sympodially, polyblastic, conidiogenous loci located on the shoulders and the apex, slightly thickened and darkened, 2.5 µm diam. *Conidia* solitary, pale olivaceous brown to brown, cylindrical to obclavate, obconical truncate at the base, rounded or pointed at the apex, 13–37.5 × 2.5–5 µm, (0–)1-euseptate, constricted at the septum, hilum slightly thickened, darkened and refractive, 2.5 µm diam.

Material examined: **Poland**, Hwozna Protected Area, Bialowieza National Park, on *Alnus glutinosa*, 20 Sep. 2011, D. Karasinski (**epitype** designated here CBS H-20777, MBT378570,

ex-epitype culture CBS 131547). **France**, Lyon, on *Alnus glutinosa*, 1828, Montagne 568 (**lectotype** designated here, Montagne 568, Ann. Sci. Nat., Bot., Sér. 2, 6: pl. 12, fig. 5. 1836, original illustration, MycoBank, MBT378569).

Notes: *Passalora* was the first genus introduced for cercosporoid hyphomycetes (Fries 1849) and a review of the taxonomical history of the genus has recently been published by Braun *et al.* (2013). In one of the most comprehensive examinations on this generic complex, Crous & Braun (2003) concluded that various genera (e.g. *Mycovellosiella*, *Phaeoramularia*, *Fulvia*) should be merged under the oldest name *Passalora*. After this revision *Passalora* included cercosporoid species with solitary, fasciculate to synnematous conidiophores and conidia formed singly or in chains, but in all cases with conspicuous (thickened and darkened) conidiogenous loci (scars) and mostly non-scolecosporous, pigmented conidia. This new concept was also supported by first molecular sequence analyses (Crous *et al.* 2000, 2001b). However, with the addition of more species and more phylogenetic markers, *Passalora s. lat.* has proven to be para- or polyphyletic (Thomma *et al.* 2005, Crous *et al.* 2009b, d, 2013a). In addition, the type species has not been subjected to DNA sequence analyses before, and the passalora-like clades distributed throughout the *Mycosphaerellaceae* are not clearly connected with morphological groups within *Passalora* (e.g. mycovellosiella-like). In this study, we propose a good candidate for the epitypification of the type species of *Passalora* (CBS 131547). Phylogenetically, this strain forms a single species clade in all phylogenetic analyses performed (Fig. 1, clade 34; Fig. 2, clade 22), but without a strong link to other genera. With the additional epitypification of the type species of *Fulvia* (*Fulvia fulva*; Fig. 1, clade 59), *Mycovellosiella* (*Mycovellosiella cajani*; Fig. 1, clade 7) and *Phaeoramularia* (*Phaeoramularia gomphrenicola*; Fig. 1, clade 61), these names are resurrected and applied to different monophyletic clades and are no longer regarded as synonyms of *Passalora s. str*. The value of features such as mycelium internal and/or external, conidia solitary or in chains, remains doubtful and barely applicable for the discrimination of cercosporoid genera. Morphologically, *Passalora s. str*. is rather different from common passalora-like species (Fig. 15), in having sparsely septate, flexuous conidiophores, and predominantly smooth, olivaceous, 1–2-septate conidia constricted at the basal septum, with somewhat to distinctly thickened, darkened, and refractive loci. The placement of the hundreds of passalora-like species that are not known from their DNA is not yet possible, and these would for the interim have to be retained in *Passalora s. lat.* as a wide, morphologically circumscribed genus, pending cultures and re sults of DNA sequence analyses.

Clade 35: *Zymoseptoria*

Zymoseptoria Quaedvlieg & Crous, Persoonia 26: 64. 2011.

Description (from Quaedvlieg *et al.* 2011): *Conidiomata* pycnidial, semi-immersed to erumpent, dark brown to black, subglobose, with central ostiole; wall of 3–4 layers of brown *textura angularis*. *Conidiophores* hyaline, smooth, 1–2-septate, or reduced to conidiogenous cells, lining the inner cavity. *Conidiogenous cells* tightly aggregated, ampulliform to doliiform or subcylindrical, phialidic with periclinal thickening, or with 2–3 inconspicuous, percurrent proliferations at apex. *Type I conidia* solitary, hyaline, smooth, guttulate, narrowly cylindrical to subulate, tapering towards acutely rounded apex, with bluntly rounded to truncate base, transversely euseptate, with unthickened and colourless hila. On OA and PDA aerial hyphae disarticulate into phragmospores (*Type II conidia*), that again give rise to Type I conidia via

microcyclic conidiation; yeast-like growth and microcyclic conidiation (*Type III conidia*) common on agar media.

Type species: *Zymoseptoria tritici* (Desm.) Quaedvlieg & Crous (≡ *Septoria tritici* Desm.).

Zymoseptoria tritici (Desm.) Quaedvlieg & Crous, Persoonia 26: 67. 2011.

Basionym: *Septoria tritici* Desm., Ann. Sci. Nat., Bot., Ser. 2, 17: 107. 1842.

Description and illustration: Quaedvlieg *et al.* (2011).

Materials examined: **France**, on *Triticum* sp. (**holotype** of *Septoria tritici*; PC). **Germany**, Oestrich, on *Triticum repens*, Fuckel, Fungi Rhen. Exs. no. 1578 (isotype of *Mycosphaerella graminicola*, L). **Netherlands**, Brabant West, on *Triticum aestivum*, coll. R. Daamen, 6 May 1981, isol. as single conidium, W. Veenbaas, 810507/1, 7 May 1981 (**epitype** designated by Quaedvlieg *et al.* 2011, CBS H-20545, including sexual morph material on *Triticum* leaf of heterothallic mating IPO 323 (MAT 1-1) × IPO 94269 (MAT 1-2), culture ex-epitype IPO 323 = CBS 115943).

Notes: *Zymoseptoria* was introduced to include septoria-like species from graminaceous hosts that did not cluster with the type of *Septoria s. str*. in the phylogenetic analysis (Quaedvlieg *et al.* 2011). In addition, *Zymoseptoria* is morphologically distinct from *Septoria* by its yeast-like growth in culture, and by producing up to three different conidial types (Type I—pycnidial conidia; Type II—phragmospores on aerial hyphae; Type III— yeast-like growth proliferating via microcyclic conidiation). In the phylogenetic analyses in the present study, *Zymoseptoria* species cluster within the *Mycosphaerellaceae* (Fig. 1, clade 35; Fig. 2, clade 36) and close to *Ramularia*, as observed in previous studies (Quaedvlieg *et al.* 2013, Stukenbrock *et al.* 2012, Videira *et al.* 2016). *Zymoseptoria* currently comprises seven species including *Zymoseptoria tritici*, the causal agent of septoria tritici blotch on wheat, and *Zymoseptoria passerinii*, the causal agent of septoria speckled leaf blotch of barley, which are important crop pathogens responsible for severe yield losses (Stukenbrock *et al.* 2012).

Clade 36: *Xenoramularia*

Xenoramularia Videira *et al.*, Stud. Mycol. 83: 96. 2016.

Description (from Videira *et al.* 2016): Phytopathogenic, causing leaf spots. *Mycelium* composed of hyaline, septate, branched hyphae. *Conidiophores* hyaline to pigmented, solitary, simple, straight or slightly curved, often reduced to conidiogenous cells, thin-walled, smooth. *Conidiogenous cells* hyaline, integrated in the mycelium or terminal in the conidiophores, subcylindrical to geniculate-sinuous, with one or multiple thickened but not darkened conidiogenous loci. *Conidia* hyaline, thin-walled, smooth, formed singly or catenate, aseptate or 1-septate, subcylindrical, apex obtuse to subacute, base truncate; hila thickened but not darkened.

Type species: *Xenoramularia polygonicola* Videira *et al.*

Xenoramularia polygonicola Videira *et al.*, Stud. Mycol. 83: 98. 2016.

Description and illustration: Videira *et al.* (2016).

Materials examined: **Republic of Korea**, Pyeongchang, on *Polygonum* sp., 20 Sep. 2003, H.D. Shin (**holotype** KUS F19688, isotype CBS H-22541, culture ex-type CBS 141102 = CPC 10852); *idem*., cultures CPC 10853, CPC 10854.

Notes: The genus *Xenoramularia* was recently introduced in the *Mycosphaerellaceae* to accommodate a group of species that was phylogenetically closely related to *Zymoseptoria* and *Ramularia* (Videira *et al.* 2016) but morphologically distinct. The phylogeny in the present work agrees with the previous results (Fig. 1, clade 36; Fig. 2, clade 37). *Xenoramularia* can be morphologically distinguished from *Ramularia* by having conidiogenous loci that are thickened, but not darkened and refractive and differs from *Zymoseptoria* by not forming acervular conidiomata and producing only one type of conidia.

Clade 37: *Ramularia*

Ramularia Unger, Exanth. Pflanzen (Wien): 169. 1833. emend. U. Braun (nom. cons.).
Synonyms: Didymaria Corda, Icon. fung. (Prague) 5: 9. 1842.
Phacellium Bonord., in Rabenh., Fungi Eur. Exs., Edn. 2, Ser. 2: no. 288. 1860.
Acrotheca Fuckel, Jahrb. Vereins Naturk. Herzogth. Nassau 15: 43. 1860.
Septocylindrium Bonord. ex Sacc., Michelia 2: 15. 1880.
Ovularia Sacc., Michelia 2: 17. 1880.
Mycosphaerella Johanson, Öfvers. Kongl Vetensk-Akad. Förh,. 41(9): 163. 1884, *s. str.*
Ophiocladium Cav., Z. Pflanzenkrankh. 3: 26. 1893.
Pseudovularia Speg., Anales Mus. Nac. Buenos Aires, Ser. 3, 20: 418. 1910.
For additional synonyms see Braun (1998) or Videira *et al.* (2016).

Description (from Videira *et al.* 2016): Mostly phytopathogenic (leaf spots, chlorosis or necrosis), sometimes saprobic or mycophilic. *Conidiophores* individual or synnematous, sometimes forming small to sporodochial caespituli, emerging through stomata or through the cuticle, straight, subcylindrical to geniculate-sinuous, continuous or septate, hyaline or in some species with a faintly reddish tinge, occasionally branched, thin-walled, usually smooth but rarely rough. *Conidiogenous cells* integrated, terminal, polyblastic, sympodially elongating, straight to geniculate-sinuous, conidiogenous loci conspicuously thickened, darkened and refractive, coronate (cladosporoid). *Conidia* consistently solitary or in simple or branched chains, solitary conidia 0–1-septate, catenate conidia aseptate to multiseptate (mostly 1–4 eusepta), hyaline, in a few species with a faintly reddish tinge, usually ellipsoid-ovoid, cylindrical-fusiform, rarely filiform, occasionally constricted at the septa, thin-walled, smooth to verruculose-echinulate, hila distinct, slightly to conspicuously thickened, darkened, refractive; conidial secession schizolytic.

Type species: *Ramularia pusilla* Unger.

Ramularia pusilla Unger, Exanth. Pflanzen: 169. 1833.
Synonyms: *Caeoma pusilla* (Unger) Bonord., Handb. Mykol.: 41. 1851.

Ovularia pusilla (Unger) Sacc., Syll. Fung. 4: 140. 1886.
Ramularia pulchella Ces., Bot. Zeitung (Berlin) 11: 238. 1853.
For additional synonyms see Braun (1998), Braun *et al.* (2015a) or MycoBank.

Descriptions and illustrations: Braun (1998), Kirschner (2009), Braun *et al.* (2015a), Videira *et al.* (2016).

Materials examined: **Austria**, on *Poa nemoralis*, Unger, Exanth. Pfl., Pl. II, fig. 12, (**lectotype** [iconotype] see Braun 1998). **Germany**, Frankfurt am Main, Botanical Garden, on leaves of *Poa annua*, 25 Feb. 2008, R. Kirschner (**epitype** designated by Videira *et al.* 2016, CBS H-22527, culture ex-epitype CBS 124973 = RoKi 3143).

Notes: Species of *Ramularia* are phytopathogenic and mostly cause leaf spots but they can also be endophytic, saprobic and mycophilic. There are about 325 species accepted in this genus (Braun 1998) of which only six have thus far been experimentally linked to a *Mycosphaerella* sexual morph (Videira *et al.* 2015b). Currently *Ramularia* is accepted as being a host-specific genus of phytopathogenic fungi (Braun 1998), although some exceptions are known (e.g. *Ramularia vizellae*, Videira *et al.* 2015b). *Ramularia pusilla* is the type species of the genus *Ramularia* and has a broad host range within the family *Poaceae* and a worldwide distribution (Braun 1998). Phylogenetically, species of *Ramularia s. str.* cluster in a well-supported clade (Fig. 1, clade 37; Fig. 2, clade 35) as observed in a previous study (Videira *et al.* 2016).

Clade 38: *Paracercosporidium*

Paracercosporidium Videira & Crous, **gen. nov.** MycoBank MB822601.

Etymology: Morphologically similar to *Cercosporidium*.

Description: Phytopatogenic. *Mycelium* internal, hyaline, smooth. *Stromata* small, composed of few dark brown cells, or medium in size, mainly hypophyllous, substomatal, dark brown. *Conidiophores* loosely fasciculate, emerging from stromata, pale to dark brown, paler towards the apex, thin- to thick-walled, cylindrical, mildly to strongly geniculate, simple or branched. *Conidiogenous cells* integrated, terminal or intercalary, polyblastic, proliferating sympodially, with rim-like conidiogenous loci, thickened and darkened, located at the shoulders and apex. *Conidia* solitary, hyaline to pale olivaceous brown, thick-walled, cylindrical to obclavate, rounded at the apex, usually tapering towards the base, sometimes swollen at the base or truncate, hila rim-like, darkened and refractive.

Type species: *Paracercosporidium microsorum* (Sacc.) U. Braun *et al.* (≡ *Cercospora microsora* Sacc.).

Paracercosporidium microsorum (Sacc.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822819. Fig. 16.
Basionym: *Cercospora microsora* Sacc., Michelia 2(6): 128. 1880.
Synonyms: *Passalora microsora* (Sacc.) U. Braun, Mycotaxon 55: 233. 1995.
Cercospora microsora var. *tiliae-platyphyllae* Roum., Rev. Mycol. 16: 109. 1894.
Cercospora exitiosa Syd. & P. Syd., Ann. Mycol. 4(6): 485. 1907.

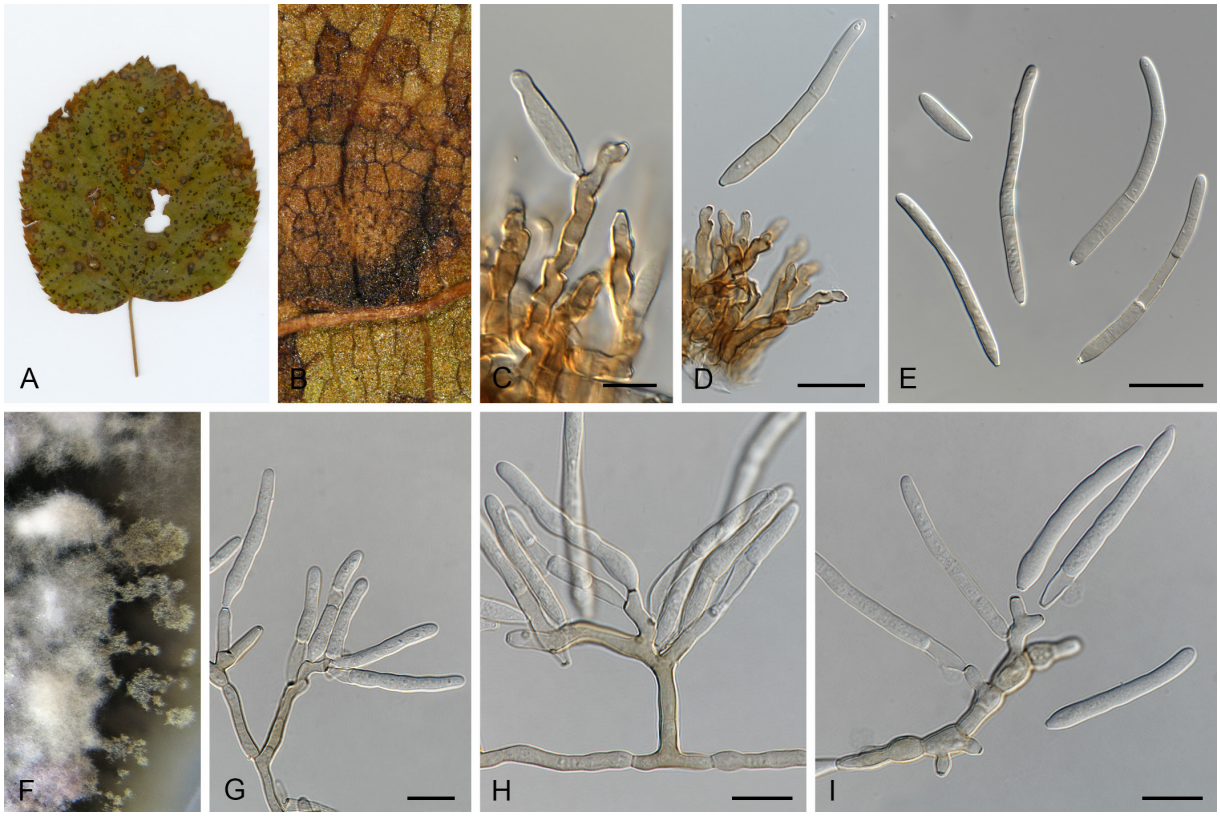


Fig. 16. *Paracercosporidium microsorum* (CPC 15550). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C, D. Conidiophores, conidiogenous cells and conidia. E. Conidia. F–I. Observations *in vitro*. F. Culture on OA. G, H. Conidiophore, conidiogenous cells and conidia. I. Conidiogenous cells and conidia. Scale bars = 10 µm.

Cercospora zahariadii Svavul. & Sandu, Hedwigia 75: 226. 1935.
Mycosphaerella microsora Syd. & P. Syd., Ann. Mycol. 38: 465. 1940.
Sphaerella microsora (Syd. & P. Syd.) Sandu, Ciuperci Pyrenomycetes-Sphaeriales din România: 135. 1971.

Description in vivo: *Leaf spots* scattered, amphigenous, dark brown, later bown with dark brown border, irregular to angular, vein-limited, 1–3 mm in size. *Caespituli* amphigenous, pale brown, effuse. *Mycelium* internal, hyphae hyaline, smooth. *Stromata* small, composed of few dark brown cells, or medium in size and up to 40 µm diam, amphigenous, mainly hypophyllous, substomatal, dark brown. *Conidiophores* loosely fasciculate, emerging from upper part of stromata, dark brown to pale, paler towards the apex, thick-walled, cylindrical, well-geniculate due to sympodial proliferation, 20–98 × 5–6.5 µm. *Conidiogenous cells* integrated, terminal or intercalary, polyblastic, proliferating sympodially, with conidiogenous loci rim-like, darkened and thickened, located at the shoulders and apex, 1.5–2.5 µm diam. *Conidia* solitary, hyaline to pale olivaceous brown, thick-walled, cylindrical to obclavate, obconicaly truncate and thickened at the base, rounded at the apex, 24–66 × 5–7.5 µm, 1–5-septate, hila thickened and darkened, 1.5–2.5 µm diam.

Description in vitro (on SNA; CPC 15550): *Mycelium* composed of hyaline to pale brown hyphae, uniform in width, smooth, 1.5–2 µm. *Conidiophores* macronematous, pale to pale brown,

smooth, straight to well-geniculate due to sympodial proliferation, simple or branched, 25–90 × 3–5 µm. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, mono- or polyblastic, with rim-like conidiogenous loci, thickened, darkened and refractive, located on the shoulders and the apex, 2–2.5 µm diam. *Conidia* solitary, hyaline to pale brown, cylindrical to obclavate, obconically truncate at the base, rounded at the apex, 1–53 × 3–5 µm, indistinctly 1–6-euseptate, hilum slightly thickened, darkened and refractive, 2–2.5 µm diam.

Materials examined: **Czech Republic**, Moravia, Veltice, Forest of Rendez Vous, leaf spot on *Tilia* sp., 16 Sep. 2008, G. Verkley, culture CBS 123735. **Netherlands**, Z. Flevoland, Zeewolde, Hulkesteynse bos, old leaves of *Tilia cordata* (after hibernation), 1 Apr. 1998, H.A. van der Aa No. 12451, culture CBS 101017; same location, leaf spot of *Tilia cordata*, 19 Oct. 1997, H.A. van der Aa No. 12409, culture CBS 100352. **Romania**, Bucuresti, on *Tilia tomentosa*, isol. O. Constantinescu, 16 Jun. 1965, culture CBS 254.67; Bucuresti, Mogosoaia, on *Tilia platyphyllos*, 8 Oct. 1969, O. Constantinescu, CBS H-9853, culture CBS 552.71 = BUCM 2014. **Ukraine**, Donetsk, Svjatie Gory, vicinities of Svjatogorsk, National Nature Park, flood-plain forest on the left bank of Seversky Donets river, on *Tilia cordata*, 18 Jul. 2008, A. Akulov (**epitype** designated here CBS H-22942, MBT378695, ex-epitype culture CBS 142176 = CPC 15550); [**lectotype** designated here, MycoBank, MBT378694, PAD, Letendre sin. num.; see notes below].

Notes: The genus *Paracercosporidium* is hereby introduced to accommodate two species from the host *Tilia* that, due to the obclavate-like morphology of their conidia, were previously placed in *Passalora* but cluster apart from the type species *Passalora bacilligera* in a well-supported clade (Fig. 1, clade 38; Fig. 3, clade 3). In literature, only two species of passalora-like fungi have been described from the host *Tilia*, namely *Passalora microsora* and *Passalora tiliae* (Y.L. Guo & X.J. Liu) U. Braun & Crous (≡ *Tandonella tiliae* Y.L. Guo & X.J. Liu). While the latteris only known from China, the first has a worldwide distribution (Crous & Braun 2003). In the description of *Passalora microsora*, the size of the conidiophores, 10–40 × 2–3.5(–5) µm, and conidia (20–60 × 2.5–4 µm, rarely 80 × 5 µm, as large as 100 × 6 µm) of observed specimens can vary significantly (Chupp 1954). Based on the phylogenetic analyses, two clades representing two species can be observed, one including strains from Europe and the other with strains from Canada, for which the name *Cercospora tiliae*, based on type material on *Tilia americana* collected in Vermont, USA, is available. Morphologically, these two species are quite similar, but differ *in vivo* as in *Paracercosporidium microsorum* (Fig. 16) conidiophores are shorter and once abruptly geniculate, while *Paracercosporidium tiliae* (Fig. 17) has longer conidiophores which are strongly geniculate. The DNA sequences representative of each species clade differ one base pair on LSU, three base pairs on ITS and 21 base pairs on *rpb2*. According to Klebahn (1918), *Passalora microsora* is the asexual morph of *Mycosphaerella millegrana*. However, Sydow (1940) stated that this species is not the asexual morph of *Mycosphaerella millegrana* and described the true sexual morph as *Mycosphaerella microsora* (Tomilin 1979). The epitypification requires the citation of the type. However, the typification needs a detailed discussion and clarification. Chupp (1954: 565) mentioned: "No definite type given. Saccardo states it is common on *Tilia europaea* and *Tilia americana* in Europe and America." This is not correct and, although not mentioned by Chupp (l.c.), undoubtedly refers to Saccardo (1886). Saccardo (1880b) described this species in a paper dealing with specimens collected by P. Brunaud, Abb. Letendre, A. Malbranche, and J. Therry in Roumeguère's under no. 1041, so that specimens collected in France by the persons concerned represent potential syntypes. However,

the number cited in Saccardo (1880b) does not refer to "Roum., Fungi Sel. Gall. Exs. 1041" which is a collection of *Torula herbarum* f. *solani-pseudocapsici*. A collection of *Cercospora microsora* was issued as "Roum., Fungi Sel. Gall. Exs. 2062" [France, Parc du Grand-Quévilly (Seine-Inf.), on *Tilia* × *europaea*, Automne 1881, Rev. Abb. Letendre (e.g. BPI, FH, PC, PAD)] containing a copy of Saccardo's original description, but this gathering cannot be considered original material since it had been collected in 1881, i.e. one year after Saccardo's original publication. However, there is a sample in Saccardo's herbarium collected by Letendre that can be designated as lectotype.

Paracercosporidium tiliae (Peck) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822772. Fig. 17.
Basionym: *Cercospora tiliae* Peck, Bot. Gaz. 6(10): 277. 1881.

Description in vivo: *Leaf spots* scattered, amphigenous, dark brown, irregular to angular, vein-limited, 1–3 mm in size. *Caespituli* amphigenous, pale brown, effuse. *Mycelium* internal, hyaline, smooth. *Stromata* composed of a few dark brown cells, up to 30 µm diam, amphigenous, mainly hypophyllous, substomatal. *Conidiophores* emerging from upper part of stromata in dense fascicles, pale brown, thick-walled, cylindrical, straight or slightly curved, 35–85 × 3–4 µm. *Conidiogenous cells* integrated, polyblastic, terminal, proliferating sympodially, with rim-like conidiogenous loci, thickened and darkened, located at the shoulders and apex, 1.5–2.6 µm diam. *Conidia* single, hyaline to pale olivaceous, cylindrical to obclavate, obconicaly truncate at the base, rounded at the apex, thick-walled, 15.5–54 × 2–4 µm, 1–5-septate, 1.5–2 µm diam.

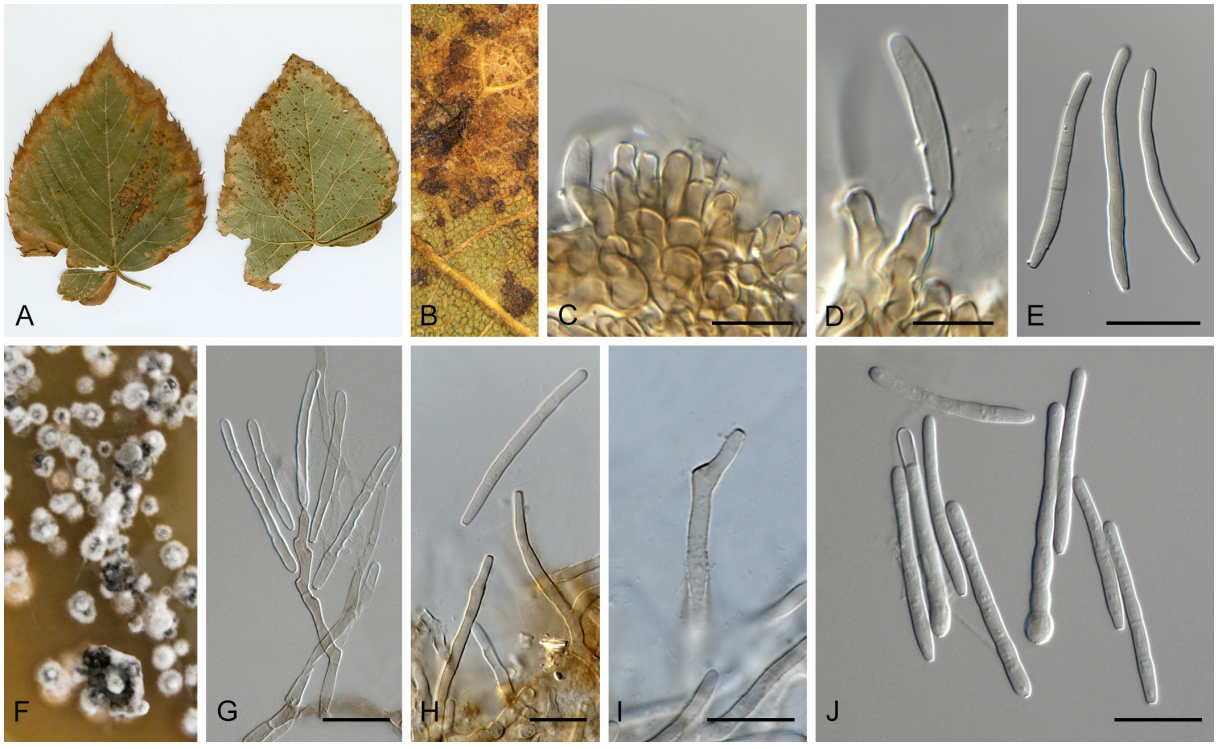


Fig. 17. *Paracercosporidium tiliae* (CBS 112734). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Conidiophores. D. Conidiophores, conidiogenous cells and conidia. E. Conidia. F–J. Observations *in vitro*. F. Culture on V8. G, H. Conidiophore, conidiogenous cell and conidia. I. Conidiophore. J. Conidia. Scale bars = 10 µm.

Description in vitro (on SNA; CPC 112734): *Mycelium* hyaline, hyphae uniform in width, smooth, 1.5–2 µm. *Conidiophores* macronematous, pale to pale brown, smooth, straight to well-geniculate due to sympodial proliferation, 35–87 × 2.5–3.5 µm. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, mono- or polyblastic, with rim-like conidiogenous loci, thickened, darkened and refractive, located on the shoulders and the apex, 2–2.5 µm diam. *Conidia* solitary, hyaline to pale, cylindrical to obclavate, 15–40 × 2–3 µm, indistinctly 1–6-euseptate, obconically truncate at the base, with slightly thickened and refractive hilum, 1.5–2 µm diam.

Materials examined: **Canada**, Ottawa, on *Tilia americana*, 30 Aug. 2000, K.A. Seifert (**epitype** designated here CBS H-22943, MBT378600, ex-epitype culture CBS 112734 = CPC 3952); *idem*. culture CBS 115526 = CPC 3953. **USA**, Vermont, Charlotte, on *Tilia americana*, June 1881, C.G. Pringle (**holotype** NYS-F-3187).

Note: See notes under *Paracercosporidium microsora*.

Clade 39: *"Sirosporium"*

Sirosporium celtidis (Biv.) M.B. Ellis, Mycol. Pap. 87: 4. 1963.
Basionym: *Monilia celtidis* Biv., Stirp. Rar. Sicilia 3: 18. 1815.
Synonyms: *Gyrocerus celtis* (Biv.) Mont. & Ces., Syll. Gen. Sp. Crypt.: 308. 1856.
Helicoceras celtidis (Biv.) Linder, Ann. Missouri Bot. Gard. 18: 3. 1931.
For additional synonyms see MycoBank.

Descriptions and illustrations: Chupp (1954), Ellis (1971).

Materials examined: **Algeria**, on *Celtis australis*, Nov. 1923, C. Killian, dep. 1925, culture CBS 158.25. **Italy**, Rome, on *C. australis*, Aug. 1949, V. Mezzetti, dep. 1950, culture CBS 289.50. **Portugal**, unknown host, date and collector, dep. Estação Agronómica Nacional (Sacavém), 1948, culture CBS 238.48.

Notes: The species *Sirosporium celtidis* is based on *Monilia celtidis*, which was described from the host *Celtis australis*, probably from Sicily (Italy), although it is not clearly stated in the original publication, and the herbarium specimen could not be located. The species has previously been reported from Algeria, India, Israel, Italy, Japan, Morocco, Portugal, Taiwan and Turkey (Crous & Braun 2003). The cultures observed in this study are presently sterile, but at the time they were collected, the strains CBS 158.25 and CBS 289.50, were subjected to a thorough morphological characterisation (Killian 1925, Mezzetti 1950). The morphological description agrees with more recent treatments of the genus *Sirosporium* (Chupp 1954, Ellis 1971). *Sirosporium celtidis* differs from the type of *Sirosporium*, *Sirosporium antenniforme*, by producing conidiophores with thin walls and producing longer and narrower conidia that only rarely show 1–2 longitudinal septa (Ellis 1971). Since there are no cultures available of *Sirosporium antenniforme*, the precise phylogenetic position of the genus remains unresolved. The present strains cluster in a well supported clade in the pylogenetic analyses (Fig. 1, clade 39; Fig. 3, clade 4).

Clade 40: *Cercosporidium*

Cercosporidium Earle, Muhlenbergia 1: 16. 1901, emend.

Description: *Foliicolous*. *Mycelium* internal, hyaline to pale olivaceous brown, or dark brown. *Stromata* small to developed, olivaceous brown to brown. *Conidiophores* solitary or in fascicles, micro- to macronematous, sometimes irregular in width, very pale to olivaceous brown, smooth to rough, simple or branched, straight to geniculate-sinuous, sometimes reduced to conidiogenous cells. *Conidiogenous cells* terminal, proliferation sympodial or percurrent, mono- or polyblastic, with conidiogenous loci slightly to distinctly thickened and darkened. *Conidia* solitary *in vivo*, rarely catenate *in vitro*, hyaline to pale olivaceous, smooth to verruculose, thick-walled, cylindrical, ovoid, obovoid or obclavate, straight or slightly curved, slightly thickened, truncate or short obconical truncate at the base, broadly rounded or beak-like at the apex, euseptate, hilum thickened, darkened and refractive.

Type species: *Scolicotrichum euphorbiae* Tracy & Earle (= *Cercosporidium chaetomium* (Cooke) Deighton; ≡ *Cladosporium chaetomium* Cooke).

Cercosporidium californicum (S.T. Koike & Crous) Videira & Crous, **comb. nov.** MycoBank MB822747. Fig. 18.
Basionym: *Passalora californica* S.T. Koike & Crous, IMA Fungus 2: 8. 2011.

Description (adapted from Koike *et al.* 2011): Phytopathogenic, causing black and irregular leaf spots. *Stroma* amphigenous, globose, brown, 10–30 µm long and 30–100 µm wide. *Conidiophores* arising from stroma in dense sporodochia, brown, verruculose, subcylindrical, mostly straight, at times geniculate-sinuous, 15–25 × 3–8 µm, occasionally up to 100 µm long and 4–5 µm wide, frequently reduced to conidiogenous cells. *Conidiogenous cells* terminal, integrated, brown, verruculose, subcylindrical, straight or geniculate-sinuous, usually 10–15 × 4–6 µm, occasionally 15–35 × 4–5 µm, conidiogenous loci apical and lateral, thickened, darkened and refractive, 1–1.5 µm diam. *Conidia* solitary, brown, verruculose, guttulate, obclavate to subcylindrical, apex obtusely rounded, base obconically truncate, (32–)55–95(–180) × (4–)5–6 µm, (1–)3–5(–9)-septate, hilum darkened, thickened and refractive, 2 µm diam.

Materials examined: **USA**, California, Santa Clara County, on leaves of *Asclepias fascicularis*, 19 Jul. 2010, S.T. Koike (**holotype** CBS H-20512, ex-type cultures CBS 128857 = CPC 18389); *idem*. cultures CPC 18390, CPC 18391.

Notes: Including *Cercosporidium californicum* (Fig. 18), several passalora-like species are known from the host genus *Asclepias*, namely *Passalora clavata* var. *clavata*, *Passalora clavata* var. *hansenii*, *Passalora venturioides* and *Passalora elaeochroma* (Braun & Mel'nik 1997, Koike *et al.* 2011). Unfortunately, no cultures of the previous species were available for this study and their phylogenetic position will remain unknown until they are recollected and their DNA analysed. In a phylogenetic analysis based on LSU data, *Cercosporidium californicum* was described (as *Passalora californica*) as closely related to *Passalora arachidis* (as *Mycosphaerella arachidis*) (Koike *et al.* 2011). In this study, the phylogenetic analyses place *Cercosporidium californicum* strains in a well-supported clade closely related to *Cercosporidium miurae* (Fig. 1, clade 40; Fig. 3, clade 5).

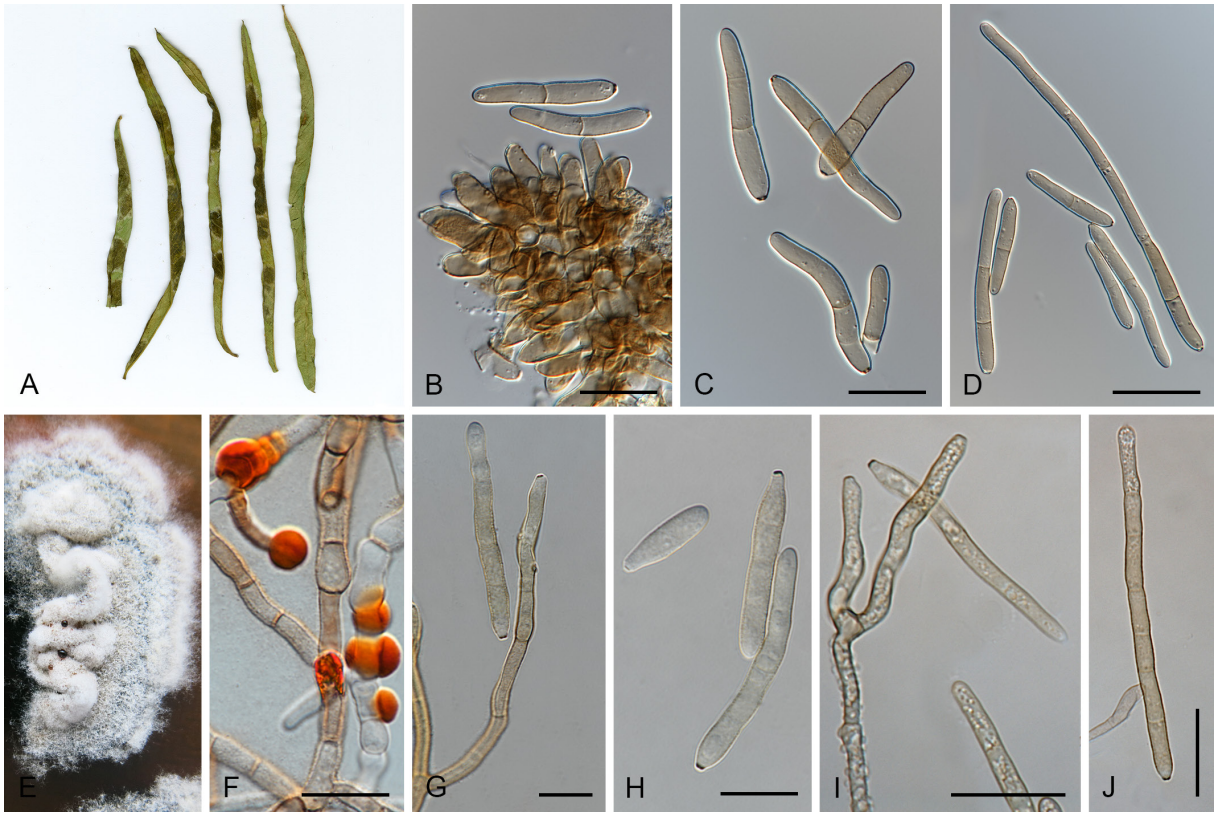


Fig. 18. *Cercosporidium californicum* (CBS 128857). A–D. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores, conidiogenous cells and conidia. C. Conidiophores and conidiogenous cells. D. Conidia. E–J. Observations *in vitro*. E. Culture on V8. F. Mycelium producing red pigment inside the cells and outside. G, I. Conidiophore, conidiogenous cell and conidia. H, J. Conidia. Scale bars = 10 µm.

Cercosporidium chaetomium (Cooke) Deighton, Mycol. Pap. 112: 27. 1967. Fig. 19.
Basionym: *Cladosporium chaetomium* Cooke, Grevillea 17(83): 66. 1889.
Synonyms: *Scolicotrichum euphorbiae* Tracy & Earle, Bull. Torrey Bot. Club 23(5): 209. 1896. *Pyricularia euphorbiae* (Tracy & Earle) G.F. Atk., Bull. Cornell Univ. (Science) 3(1): 40. 1897. *Passalora chaetomium* (Cooke) Arx, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 86(1): 44. 1983.
For additional synonyms see MycoBank.

Description in vivo (CBS H-22944): Phytopathogenic, causing small leaf spots, brown to reddish brown with purplish brown border, circular to subcircular, 2–3 mm diam. *Caespituli* amphigenous, olivaceous, effuse. *Mycelium* internal, hyaline, pale to pale olivaceous brown, or dark brown. *Stromata* amphigenous, substomatal, epidermal, olivaceous brown to brown, small to well developed, 15–90 µm diam. *Conidiophores* erumpent through the cuticle, or emerging from stomata, solitary or in dense fascicles, smooth, thick-walled, very pale to olivaceous brown, paler towards the apex, simple, cylindrical, straight, sinuous to geniculate, irregular in width, 17–45 × 3.5–8 µm, sometimes reduced to conidiogenous cells. *Conidiogenous cells* terminal, proliferating sympodially or percurrently, polyblastic, with rim-like conidiogenous loci, slightly thickened and darkened, located on the shoulders and apex, 2–3 µm diam. *Conidia* solitary, hyaline to pale olivaceous, smooth to verruculose, thick-walled, ovoid, cylindrical,

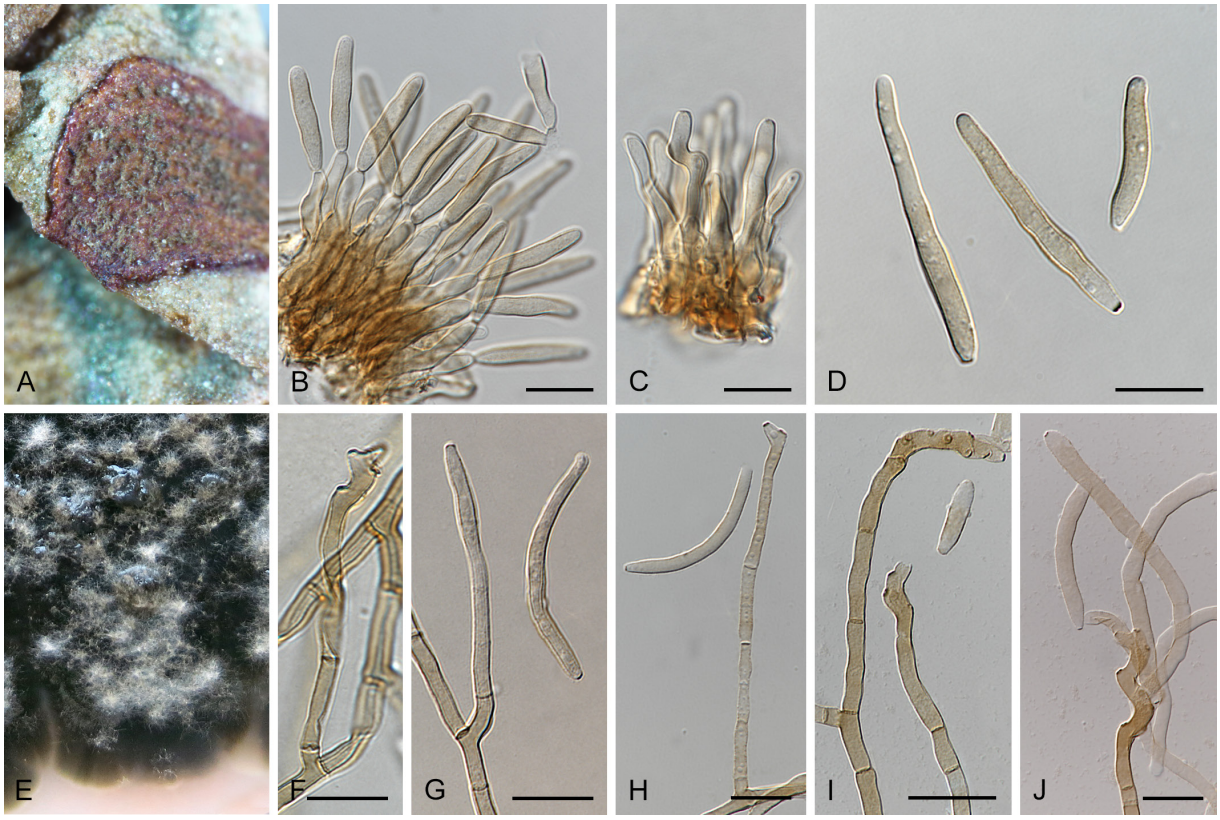


Fig. 19. *Cercosporidium chaetomium* (CBS 142177). A–D. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores, conidiogenous cells and conidia. C. Conidiophores and conidiogenous cells. D. Single conidia. E–J. Observations *in vitro*. E. Culture on OA. F. Conidiophore and conidiogenous cell. G–J. Conidiophore, conidiogenous cell and conidia. Scale bars = 10 µm.

straight or slightly curved, base obconically truncate, apex broadly rounded or beak-shaped, 26–48 × 3.5–5 µm, 0–3-euseptate, hila slightly thickened and darkened, 2–3 µm diam.

Description in vitro (on V8; CPC 18624): *Mycelium* hyaline to pale olivaceous brown, smooth to rough, uniform to variable in width, 2–3 µm, sometimes constricted at septa. *Conidiophores* micro- or macronematous, straight or mildly sinuous, simple or branched, pale to pale olivaceous brown, 2.5–250 × 2.5–5 µm. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, mono- or polyblastic, with conidiogenous loci slightly thickened and darkened, 2–2.5 µm diam. *Conidia* solitary or catenate, hyaline to pale olivaceous brown, smooth to rough, cylindrical to obclavate, long-obconically truncate at the base, rounded or beak-like at the apex, 10–75 × 2.5–5 µm, indistinctly 0–5-euseptate, slightly constricted at septa, hila slightly thickened and darkened, 2–2.5 µm diam.

Materials examined: **Canada**, Ontario, Guelph, on *Euphorbia* sp., 28 Sep. 2010, P.W. Crous & K.A. Seifert (**epitype** designated here CBS H-22944, MBT378571, ex-epitype culture CBS 142177 = CPC 18624). **USA**, New Jersey, Newfield, on leaves of *Euphorbia* sp., J.B. Ellis No. 2289 (**holotype** K; isotype IMI 118400).

Notes: Several researchers have discussed the taxonomic position of the genus *Cercosporidium* to date (Deighton 1967, Ellis 1971, Arx 1983, Braun 1995, Baker *et al.* 2000, Crous & Braun

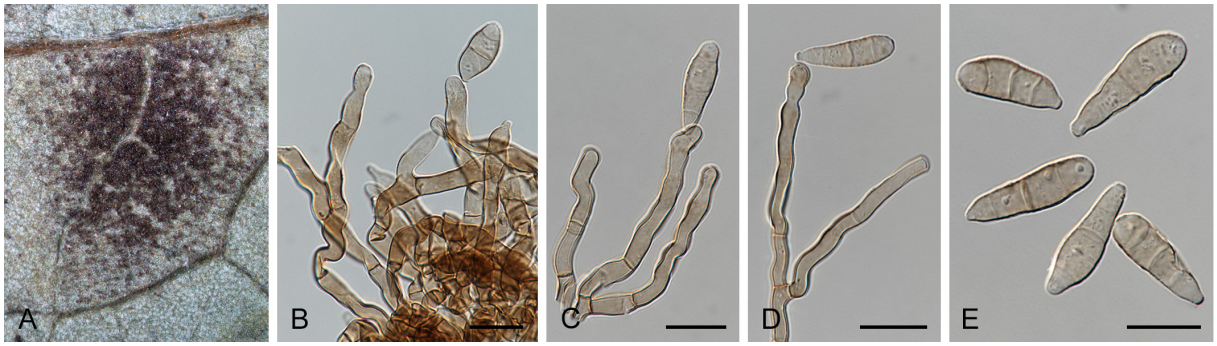


Fig. 20. *Cercosporidium helleri* (NY00945740). A–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B, D. Conidiophores, conidiogenous cells and conidia. C. Partial conidiophore, conidiogenous cell and conidia. E. Conidia. Scale bars = 10 µm.

2003, Braun *et al.* 2013). The genus was described by Earle (1901: 16) who designated *Scoletotrichum euphorbiae* as type of the genus ["As the type of this genus I take the species published as *Scoletotrichum* (?) *euphorbiae* Tracy & Earle, Bull. Torr. Bot. Club, 23: 209, also as *Piricularia euphorbiae* (T. & E.) Atkinson, Bull. Cornell univ. 3: 40"]). Deighton (1967) stated that although Earle (1901) designated *Scoletotrichum euphorbiae* as the type species of *Cercosporidium*, he did not validly publish the combination in the genus. Deighton (1967) published a revised description of the genus and introduced a combination of the older name *Cladosporium chaetomium* into *Cercosporidium*. Subsequent authors followed this treatment (Baker *et al.* 2000, Crous & Braun 2003). However, Braun *et al.* (2013) cited *Cercosporidium helleri* Earle (Fig. 20), described on *Sphenoclea zeylanica* from Puerto Rico [**lectotype** (designated here), MBT378572, Puerto Rico, near Añasco, 6 Feb. 1900, A.A. Heller, Plants of Porto Rico 4537 (NY00945749); isolectotypes e.g. in BPI, CHRB, CUP, F, FH, MSC, NEB, NY, UC], as type species of *Cercosporidium*. *Cercosporidium helleri* was described as a new species on the same page as the genus was introduced (Earle 1901) and represents the only species in the original publication with description and with a name affiliated with *Cercosporidium*, which was the source of the error in the type citation in Braun *et al.* (2013). The status of the genus *Cercosporidium* was extensively debated over the years with some authors defending *Cercosporidium* as a synonym of *Passalora* (Arx 1983, Castañeda & Braun 1989, Braun 1995), while other authors (Pons & Sutton 1996, Baker *et al.* 2000) defended *Cercosporidium* as a recognisably distinct genus (for extensive arguments see Baker *et al.* 2000). From the results of exhaustive phylogenetic analyses and morphological observations of passalora-like fungi in this study, the genus *Cercosporidium* is resurrected here (Fig 1, clade 40; Fig. 3, clade 5), typified by *Scolicotrichum euphorbiae* (= *Cercosporidium chaetomium*), with a well-developed stroma, and geniculate-sinuous conidiophores with rim-like conidial loci, conidia solitary, subcylindrical to obclavate, pale coloured, relatively thick-walled, smooth to verruculose surface, and darkened hila (Fig. 19).

Cercosporidium miurae (Syd. & P. Syd.) X.J. Liu & Y.L. Guo, Acta Mycol. Sinica 1(2): 98. 1982. Fig. 21.
Basionym: *Cercospora miurae* Syd. & P. Syd., Ann. Mycol. 11: 117. 1913.
Synonyms: *Cercosporiopsis miurae* (Syd. & P. Syd.) Miura, Flora of Manchuria and East Mongolia. Part III. Cryptogams, fungi 3: 533. 1928.
Passalora miurae (Syd. & P. Syd.) U. Braun & H.D. Shin, Mycotaxon 49: 354. 1993.

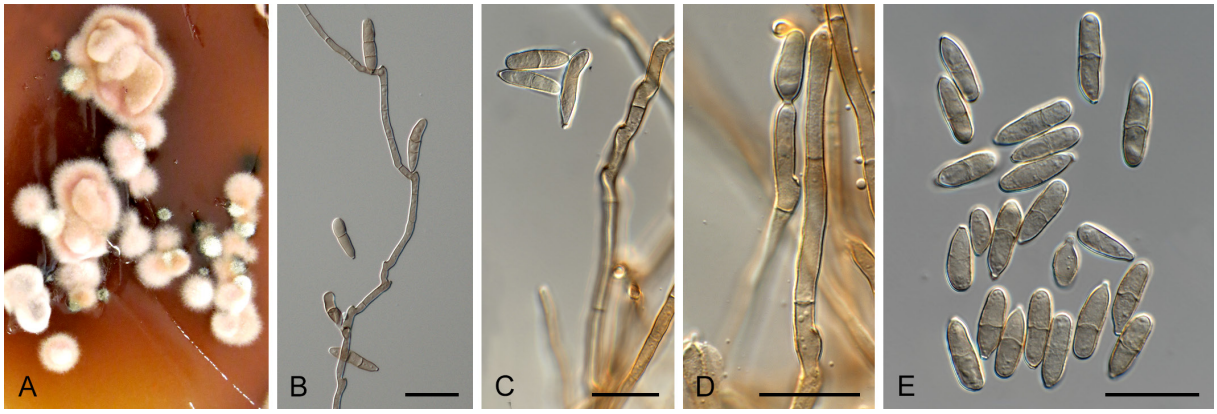


Fig. 21. *Cercosporidium miurae* (CPC 14628). A–E. Observations *in vitro*. A. Culture on V8. B–D. Conidiophore, conidiogenous cell and conidia. E. Single conidia. Scale bars = 10 µm.

Passalora miurae (Syd. & P. Syd.) Poonam Srivast., J. Living World 1(2): 117. 1994.

Description in vivo: *Leaf spots* indistinct, yellowish brown, 1–5 mm. *Mycelium* internal, hyaline to pale brown, smooth. *Caespituli* hypophyllous, effuse. *Stromata* lacking or small, composed of few brown cells, stomatal. *Conidiophores* emerging through the stroma, brown, thick-walled, smooth to rough, often rugged by the forming of numerous loci, straight, flexuous or geniculate, branched, 15–250 × 5 µm. *Conidiogenous cells* intercalary and terminal, proliferating sympodially, polyblastic, with rim-like conidiogenous loci, thickened and darkened, located on the apex or shoulders, 2–2.5 µm diam. *Conidia* solitary, pale brown, thick-walled, smooth to rough, obovoid, obclavate, cylindrical, straight to sharply curved, base obconicaly truncate, apex rounded or beak-like, 15–60 × 5–10 µm, 1–3-septate, hilum slightly thickened and darkened, 2–2.5 µm diam.

Description in vivo (on OA; CPC 14628): *Mycelium* hyaline to brown, uniform in width, 2.5 µm diam. *Conidiophores* micro- or macronematous, pale brown to pale olivaceous brown, smooth to rough, septate, straight, geniculate-sinuous, 25–180 × 2.5–3.8 µm. *Conidiogenous cells* integrated, apical and intercalary, mono- or polyblastic, proliferating sympodially, with conidiogenous loci slightly thickened and darkened, 1–2.5 µm diam. *Conidia* solitary, pale brown to pale olivaceous brown, finely verruculose, ovoid, cylindrical, apex broadly rounded, base obconically truncate, 20–28 × 3.8–10 µm, 1–3-euseptate, occasionally constricted at septa, hilum slightly thickened loci and darkened, 1–2.5 µm diam.

Materials examined: **Japan**, Hokkaido, Sapporo, Yamahana, on *Cynanchum caudatum*, 15 Sep. 1907, M. Miura (**holotype** S F37417; isotype NIAES C-268); Iwate, on *Cynanchum caudatum*, 25 Sep. 1926, K. Togashi, CNS 426. **Republic of Korea**, on *Metaplexis japonica*, 1 Oct. 2007, H.D. Shin, CBS H-22945, culture CBS 142235 = CPC 14628; on *Metaplexis japonica*, 22 Sep. 2007, H.D. Shin, culture CPC 14643.

Notes: The type species of *Cercosporidium miurae* was described from *Cynanchum caudatum* collected in Japan. The morphology of observed specimens and cultures (Fig. 21), originating from *Metaplexis japonica*, are in agreement with the description available in literature (Chupp 1954), and in line with the *Cercosporidium* generic description. Both host genera belong to the

family *Asclepiadaceae*. In the phylogenetic analyses, the two available strains cluster in a clade well-supported by all three phylogenetic methods employed (Fig. 1, clade 40; Fig. 3, clade 5).

Clade 41: *Collarispora*

Collarispora Videira & Crous, **gen. nov.** MycoBank MB822584.

Etymology: Producing conidia with marginal frill.

Description: Phytopathogenic, causing leaf spots. *Ascostromata* amphigenous, black, erumpent through epidermis, thick-walled, composed of several layers of *textura angularis*, ostiole central, periphysate. *Asci* fasciculate, ellipsoid, straight to incurved, bitunicate, 8-spored, with apical chamber. *Ascospores* hyaline, smooth, fusoid-ellipsoidal, medianly 1-septate, guttulate, slightly incurved, widest just above septum, tapering towards both acutely rounded ends, thick-walled; ascospores germinate from both ends, germ tubes parallel to the long axis of the spore, lateral branches also developing, becoming constricted at median septum, but remaining hyaline. *Mycelium* consisting of hyaline, smooth, septate and branched hyphae. *Conidiogenous* cells terminal on hyphae, hyaline, subcylindrical, smooth, conidiogenous loci not thickened nor darkened. *Conidia* solitary, subcylindrical to narrowly obclavate, straight to flexuous, apex obtuse, base truncate, multiseptate, hila not thickened nor darkened, with visible marginal frill; with age conidia tend to become pale olivaceous and finely verruculose.

Type species: *Collarispora valgourgensis* (Crous) Videira & Crous (≡ *Mycosphaerella valgourgensis* Crous).

Collarispora valgourgensis (Crous) Videira & Crous, **comb. nov.** MycoBank MB822752.
Basionym: *Mycosphaerella valgourgensis* Crous, Persoonia 26: 151. 2011.

Description and illustration: Crous *et al.* (2011a).

Materials examined: **France**, Ardeche, Valgourge, Domaine Le Fraysse, N44°35.4690 E004°07.7100, on leaves of *Yucca* sp., 15 Jul. 2010, P.W. Crous (**holotype** CBS H-20593, culture ex-type CBS 129531 = CPC 18385). **USA**, Ohio, Columbus, on *Malus* sp., 29 Sep. 2005, M. Ellis, culture CBS 125311.

Notes: *Collarispora valgourgensis* was described based on both the sexual morph, which is mycosphaerella-like, and the asexual morph, which is pseudocercospora-like (Crous *et al.* 2011a, as *Mycosphaerella valgourgensis*). However, the asexual morph differed from *Pseudocercospora* by producing subcylindrical to narrowly obclavate conidia that are initially hyaline but later become pale brown and verruculose, with a basal marginal frill. The phylogenetic analyses place this strain in a well-supported clade (Fig. 1, clade 41; Fig. 3, clade 6) that is closely related to *Cercosporidium* as presently defined. According to Deighton (1967) and the morphological review presented in this study, the conidia in *Cercosporidium* can be narrowly obclavate and verruculose, but a basal marginal frill has not been observed. In a supplementary phylogenetic analysis performed using a smaller dataset (sequences in dataset 3 corresponding to Fig. 3, clades 1–15), this clade separates from the *Cercospordium* clade. Based on a BLAST comparison against the alignment, *Collarispora valgourgensis* CBS 129531 is 100 % (473/473)

identical to *Amycosphaerella* sp. CBS 111001 based on ITS and 92 % (718/ 780) identical to *Cercosporidium chaetomium* CPC 18624 based on *rpb2*. The morphological differences and the instability of the phylogenetic position of these strains indicate that it is rather better to introduce this species into a new genus than combine it into *Cercosporidium*.

Clade 42: *Neocercosporidium*

Neocercosporidium Videira & Crous, **gen. nov.** MycoBank MB822596.

Description: Phytopathogenic. *Caespituli* amphigenous, punctiform, scattered to dense, dark brown to blackish. *Mycelium* both internal and external, hyphae branched, septate, subhyaline to medium olivaceous brown, thin-walled, smooth. *Stromata* well-developed, substomatal to intraepidermal, immersed, brown to dark brown. *Conidiophores* arising from stromata, occasionally from superficial hyphae, in small to large and loose to dense fascicles, when dense almost coremioid, rarely solitary, smooth, olivaceous to dark olivaceous brown throughout or paler at the tips, thin-walled, erect, straight, subcylindrical to strongly geniculate-sinuous, simple or occasionally branched, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, proliferating sympodially, occasionally percurrently, conidiogenous loci minute but slightly thickened, darkened and refractive, front view resembling minute circles. *Conidia* solitary, subhyaline to pale olivaceous or brownish, smooth, thin-walled, multi-septate, obclavate-cylindrical, apex obtuse to subobtuse, base rounded to short obconically truncate, hila slightly thickened, darkened and refractive.

Type species: *Neocercosporidium smilacis* (Thüm.) U. Braun *et al.*

Neocercosporidium smilacis (Thüm.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822765. Fig. 22.
Basionym: *Cercospora smilacis* Thüm., Contrib. Fl. Mycol. Lusit. 2: 14. 1879.
Synonyms: *Passalora smilacis* (Thüm.) U. Braun, Arnoldia 14: 30. 1997.
Cercospora smilacina Sacc., Michelia 2(7): 364. 1881.
Cercospora smilacis var. *asperae* Gonz. Frag., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 9: 66. 1916.

Descriptions and illustrations: Ellis (1976), Braun *et al.* (2014).

Description in vitro (on SNA; CPC 19342): *Mycelium* hyaline to pale brown, 2.5–3 µm diam. *Conidiophores* emerging from hyphae or bunching large brown cells, micro- or macronematous, pale to pale olivaceous brown, multiseptate, cylindrical, straight to slightly curved, geniculate-sinuous at the apex, often bearing microcyclic conidia, 7.5–125 × 3.5–5 µm. *Conidiogenous cells* integrated, terminal, intercalary, mono- or polyblastic, proliferating sympodially, apex conically truncate, with conidiogenous loci thickened, darkened and protruding, 1.5–2.5 µm diam. *Conidia* solitary, subhyaline to pale olivaceous brown, often undergoing microcyclic sporulation, obclavate to long cylindrical, base obconically truncate, apex rounded and long-beak shaped, 32–120 × 3.5–5 µm, 7–10-euseptate, hilum thickened, darkened and refractive, 1.5–2.5 µm diam.

Materials examined: **Italy**, Sardinia, Monte Ferru, on *Smilax aspera*, 18 May 1971, W. Gams, CBS H-9864, culture CBS 556.71; Lazio, Viterbo, Selva del Lamone, Il sentiero dei Briganti,

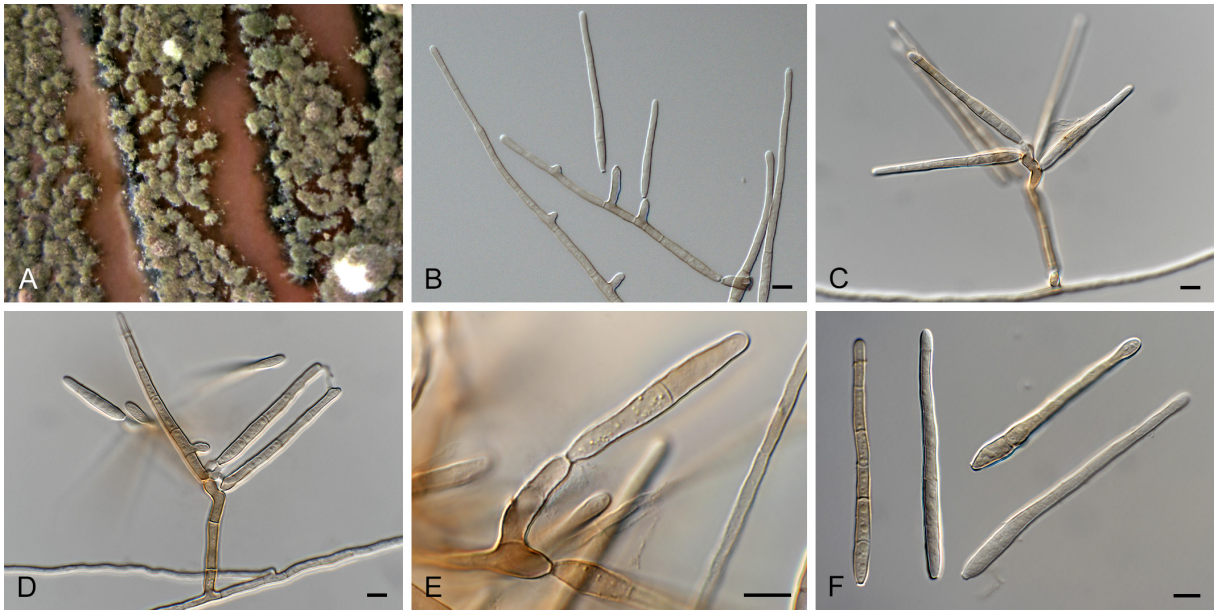


Fig. 22. *Neocercosporidium smilacis* (CPC 19342). A–F. Observations *in vitro*. A. Culture on V8. B–D. Conidiophore, conidiogenous cell and conidia. E. Conidiogenous cell and conidia. F. Single conidia. Scale bars = 10 µm.

on *Smilax* sp., 30 Apr. 2011, W. Gams, culture CPC 19342. **Portugal**, Algarve, Carvoeiro, leaf spot on *Smilax aspera*, 23 Jan. 2008, G. Verkley (**epitype** designated here MBT378573, CBS 122888, preserved as metabolically inactive); *idem*. cultures CBS 122889, CBS 122890, CBS 123352, CBS 123353); Coimbra, on *Smilax aspera* [mauritanica], May 1879, F. Moller, (**lectotype** designated by Braun *et al.* 2014, BPI 441368; **topotypes** [Thüm., Mycoth. Univ. 1670] BPI 441367, 441368, CUP 41239, HAL, LEP).

Notes: Braun *et al.* (2014) enumerated the cercosporoid species on *Smilaceae* hosts and provided an identification key for those genera. *Cercospora smilacis* was allocated to *Passalora s. lat.* due to its cylindrical-obclavate pigmented conidia and conspicuous conidiogenous loci that look like minute circles in front view (Fig. 22). *Passalora s. str.* has more prominently obclavate conidia that are single and 1-septate (Fig. 15). The strains used in this study cluster apart from the *Passalora* type species in a clade well-supported by all the phylogenetic analyses (Fig. 1, clade 42; Fig. 3, clade 1). Based on a BLAST comparison against the alignment, *Neocercosporidium smilacis* CPC 19342 shares 96 % (455/476) similarity with *Paramycovellosiella passaloroides* CPC 14694 based on ITS and 91 % (706/780) similarity with *Paracercosporidium tiliae* CBS 115526 based on *rpb2*.

Clade 43: *Sultanimyces*

Sultanimyces Videira & Crous, **gen. nov.** MycoBank MB822704.

Etymology: Based on "Sultana" (a race of white wine grape) and -myces (fungus).

Description: Phytopathogenic. *Caespituli* hypophyllous, punctiform, dark brown. *Mycelium* internal, hyphae almost hyaline. *Stroma* substomatal, composed of densely packed pale

olivaceous hyphae. *Conidiophores* in fascicles, emerging from stromata, pale to deep olivaceous, straight, smooth. *Conidiogenous cells* polyblastic, integrated, terminal, more or less clavate, usually continuous above basal septum but sometimes septate and swollen at the base, conidiogenous loci conspicuous and slightly protruding. *Conidia* solitary, pale to moderate olivaceous, ellipsoid, fusiform, subcylindrical or obclavate, straight, smooth to verruculose, aseptate but usually septate, median septum usually thicker, sometimes slightly constricted at median septum, with conspicuous and slightly protruding hila.

Type species: *Sultanimyces vitiphyllus* (Speschnew) Videira & Crous (≡ *Coryneum vitiphyllum* Speschnew).

Sultanimyces vitiphyllus (Speschnew) Videira & Crous, **comb. nov.** MycoBank MB822802.
Basionym: *Coryneum vitiphyllum* Speschnew, Trudy Tiflissk. Bot. Sada 5: 177. 1901.
Synonyms: *Cercospora roesleri* f. *vitiphylla* (Speschnew) Elenkin, Bolez. Rast.: 68. 1909.
Scolicotrichum vitiphyllum (Speschnew) Karak. & Vassiljevsky, Fungi imperfecti Parasitici. I. Hyphomycetes: 215. 1937.
Cercospora vitiphylla (Speschnew) Barbarin, Ezeg. Sved o Boleznj. Povrezden. Kul't. Dikorast. Polezn. Rast. VII–VIII: 351. 1911–1912.
Asperisporium vitiphyllum (Speschnew) Deighton, Mycol. Pap. 138: 184. 1975.
Exosporium sultanae du Plessis, Ann. Univ. Stellenbosch, Reeks A, 24: 19. 1946.
Stigmina esfandiarii Petr., Sydowia 4(1-6): 35. 1950.

Description in vivo (adapted from Sutton 1975 and Ellis 1976): *Caespituli* hypophyllous, punctiform, dark brown, spread over light brown lesion. *Mycelium* internal, hyphae almost hyaline, 2.5–3.5 µm. *Stroma* substomatal, 40–50 µm high, composed of densely packed, pale olivaceous hyphae about 4 µm wide. *Conidiophores* in dense fascicles, emerging from stromata, pale to deep olivaceous, straight, smooth, up to 30 × 5–7 µm. *Conidiogenous cells* polyblastic, integrated, terminal, more or less clavate, usually continuous above basal septum but sometimes 1–3-septate and swollen at the base (up to 9 µm), conidiogenous loci conspicuous and slightly protruding, about 2 µm. *Conidia* pale to moderate olivaceous, ellipsoid, fusiform, subcylindrical or obclavate, straight, smooth to verruculose, 13–34 × 5.5–8 µm (Sutton 1975) or 15–28 × 7–10 µm (Ellis 1976), mostly 1–3-septate, rarely 5-septate, median septum usually thicker, sometimes slightly constricted at median septum, with hila conspicuous and slightly protruding.

Materials examined: **Uzbekistan**, Samarkand (Buaki, Fusayne), on living leaves of *Vitis vinifera*, unknown collector and date (**lectotype** [iconotype] designated here MBT378577, tab. 2, Figs. 20–26 in Speschnew 1901). **South Africa**, Northern Cape Province, Kenhardt district, on *Vitis* sp. (Sultana vines), 1948, isol. and dep. S.J. du Plessis, culture CBS 206.48.

Notes: *Coryneum vitiphyllum* was transferred to the genus *Asperisporium* based on the polyblastic conidiogenous cells with conspicuous scars and euseptate, verrucose conidia with conspicuous hila. A culture of *Exosporium sultanae* isolated by du Plessis, who described the species (Plessis 1946), was analysed and found to be sterile. The strain CBS 206.48 (Fig. 1, clade 43; Fig. 3, clade 2) is not congeneric with the type species of the genus *Asperisporium*, *Asperisporium caricae* (Fig. 1, clade 43; Fig. 3, clade 13). Conidiophores of *Asperisporium caricae* also emerge from dark stromata, are densely arranged and have polyblastic conidiogenous

cells, but conidia are shorter and wider (14–22 × 8–13 µm), mostly ellipsoid and typically 1-septate (Minnis *et al.* 2011a). The phylogenetic position of *Asperisporium vitiphyllum*, among cercosporidium-like species with which it shares few characters (e.g. multiseptate conidia), and apart from *Asperisporium caricae*, is suggestive that this type of morphology emerged more than once within the *Mycosphaerellaceae*. Based on a BLAST comparison against the alignment, *Sultanimyces vitiphyllus* CBS 206.48 shares 95 % (448/474) similarity based on ITS and 91 % (711/780) similarity based on *rpb2* with with *Paracercosporidium tiliae* CBS 115526. Therefore, based on phylogenetic differences and distinctive morphological characters, the new monotypic genus *Sultanimyces* is hereby introduced to accommodate this species.

Clade 44: *Paramycovellosiella*

Paramycovellosiella Videira, H.D. Shin & Crous, **gen. nov.** MycoBank MB822603.

Etymology: Derived from "Para" (similar to) + resembling the genus *Mycovellosiella*.

Description: Phytopathogenic. *Caespituli* hypophyllous, occasionally epiphyllous. *Mycelium* internal and external, olivaceous brown to olivaceous, septate, branched. *Stromata* lacking or rudimentary, composed only of a few brown swollen hyphal cells. *Conidiophores* in loose fascicles, emerging through stomata or as lateral branches of external hyphae, pale olivaceous brown throughout or paler at the apex, continuous or septate, straight to geniculate. *Conidiogenous cells* integrated, terminal or intercalary, pale olivaceous brown, smooth, mono- or polyblastic, determinated or proliferating sympodially, conidiogenous loci small, thickened and darkened, located on apex or shoulders. *Conidia* solitary or catenate, cylindrical, clavate, obclavate, straight to mildly curved, subhyaline to pale olivaceous brown, aseptate to multiseptate, non-constricted at the septa, hila small, thickened, darkened and slightly protuberant, basal (terminal conidia) or at both ends (intercalary conidia and ramoconidia).

Type species: *Paramycovellosiella passaloroides* (G. Winter) Videira, H.D. Shin & Crous (≡ *Cercospora passaloroides* G. Winter).

Paramycovellosiella passaloroides (G. Winter) Videira, H.D. Shin & Crous, **comb. nov.** MycoBank MB822820. Fig. 23.
Basionym: *Cercospora passaloroides* G. Winter, Hedwigia 22: 71. 1883.
Synonyms: *Cylindrosporium passaloroides* (G. Winter) J.C. Gilman & W.A. Archer, Iowa St. Coll. J. Sci. 3: 334. 1929.
Mycovellosiella passaloroides (G. Winter) J.K. Bai & M.Y. Cheng, Acta Mycol. Sin. 11: 120. 1992.
Passalora passaloroides (G. Winter) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser.: 309. 2003.

Descriptions and illustrations: Chupp (1954), Shin & Kim (2001).

Description in vitro (on V8; CPC 14694): *Mycelium* hyaline to pale, hyphae smooth, uniform in width, (1–)2(–3) µm diam. *Conidiophores* micronematous, erect, simple, straight, pale olivaceous, (30–)79–110(–230) × (2.5–)3–4(–5) µm. *Conidiogenous cells* integrated, terminal or intercalary, pale olivaceous, smooth, determinate or proliferating sympodially, mono- or

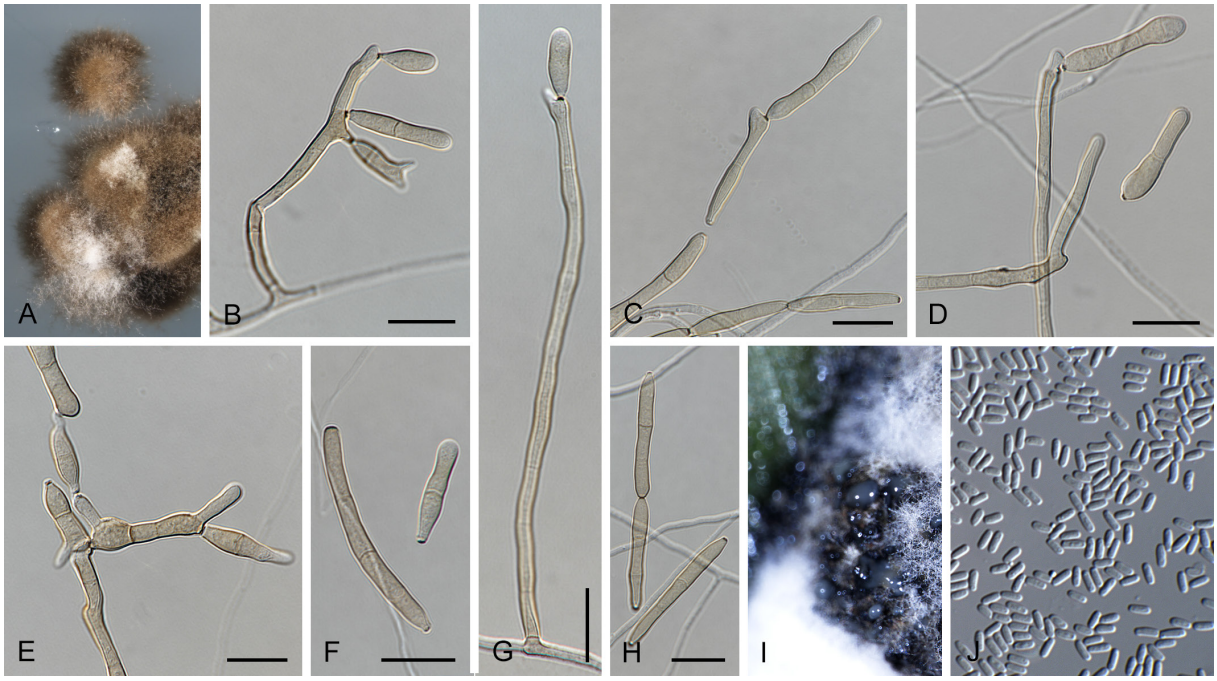


Fig. 23. *Paramycovellosiella passaloroides* (CPC 14694). A–J. Observations *in vitro*. A. Culture on SNA. B, G. Conidiophore, conidiogenous cell and conidia. C, D, E. Conidiogenous cell and conidia. F, H. Single and catenate conidia. I. Culture on V8 supplemented with banana leaf promoted the development of black spermogonia and spermatia whitish in mass. J. Hyaline spermatia. Scale bars = 10 µm.

polyblastic, with conidiogenous loci small, thickened, darkened and protruding, 1–1.5 µm diam. *Conidia* catenate (*in vivo* usually solitary), in single or double chains, pale olivaceous, smooth to verruculose, cylindrical to obclavate, straight to slightly curved, base rounded or obconically truncate, sometimes swollen, apex rounded, sometimes beak-like or swollen, variable in width, (11.5–)20–27(–43.5) × (3.5–)4.5–5(–6) µm, 1–2(–4)-septate, with hila small, thickened, darkened and refractive. *Spermogonia* formed on the surface of sterilized banana leaf placed on the medium surface, pycnidial, globose, apical ostiole, black. *Spermatia* hyaline, whitish in mass, smooth-walled, ellipsoid to subcylindrical, with rounded ends, aseptate, 2–4 × 2 µm.

Materials examined: **Republic of Korea**, Pyeongchang, on *Amorpha fructicosa*, 29 Sep. 2003, H.D. Shin, culture CPC 10770; on *Amorpha fructicosa*, 30 Oct. 2007, H.D. Shin, culture CPC 14694.

Notes: The genus *Paramycovellosiella* is established to accommodate a mycovellosiella-like species that is not congeneric (Fig. 1, clade 44; Fig. 3, clade 7) with the type of *Mycovellosiella*, *Mycovellosiella cajani*, as it is circumscribed in this study (Fig. 1, clade 7; Fig. 2, clade 10). Morphologically it is almost indistinguishable from *Mycovellosiella*. It can be distinguished from the most closely related genera, *Cercosporidium*, *Paracercosporidium* and *Neocercosporidium*, by forming catenate conidia (Fig. 23). The type specimen of *Cercospora passaloroides* (USA, Illinois, on *Amorpha canescens*, A.B. Seymour) could not be located and is likely not preserved (Chupp 1954).

Clade 45: *Amycosphaerella*

Amycosphaerella Quaedvlieg & Crous, Persoonia 33: 22. 2014.

Description (from Quaedvlieg *et al.* 2014): Foliicolous, plant pathogenic. *Ascomata* pseudothecial, amphigenous, solitary, black, subepidermal, globose, with central apical ostioles, becoming papillate; walls of 2–3 layers of medium brown *textura angularis*, subhymenium of 1–2 layers of hyaline cells. *Asci* obovoid to broadly ellipsoidal, straight or incurved, 8-spored. *Ascospores* bi- to triseriate, overlapping, hyaline, guttulate, straight, fusoid-ellipsoidal with obtuse ends, widest in middle of apical cells, medianly 1-septate, tapering toward both ends, but more prominently toward base.

Type species: *Amycosphaerella africana* (Crous & M.J. Wingf.) Quaedvlieg & Crous (≡ *Mycosphaerella africana* Crous & M.J. Wingf.).

Amycosphaerella africana (Crous & M.J. Wingf.) Quaedvlieg & Crous, Persoonia 33: 23. 2014.
Basionym: *Mycosphaerella africana* Crous & M.J. Wingf., Mycologia 88: 450. 1996.
Synonyms: *Teratosphaeria africana* (Crous & M.J. Wingf.) Crous & U. Braun, Stud. Mycol. 58: 8. 2007.
Mycosphaerella aurantia A. Maxwell, Mycol. Res. 107: 353. 2003.
Mycosphaerella ellipsoidea Crous & M.J. Wingf., Mycologia 88: 452. 1996.
Mycosphaerella aggregata Carnegie & Keane, Mycol. Res. 98: 415. 1994, nom. illegit (Art. 53.1), non *Mycosphaerella aggregata* (Schwein.) J.A. Stev. 1918.
Mycosphaerella gregaria Carnegie & Keane, Mycol. Res. 101: 843. 1997, nom. inval. (Art. 41.5).
Phaeophleospora gregaria (Carnegie & Keane) Quaedvlieg & Crous, Persoonia 33: 23. 2014, nom. inval. (Art. 41.4).
Mycosphaerella buckinghamiae Crous & Summerell, Australas. Pl. Pathol. 29(4): 272. 2000.

Description and illustration: Crous (1998).

Materials examined: **Australia**, New South Wales, Mangrove Mountain, on leaves of *Buckinghamia* sp., Aug. 1999, P.W. Crous & B. Summerell (JT 902, DAR 74865, **holotype** of *Mycosphaerella buckinghamiae*, cultures ex-type CBS 111996 = CPC 3006, CPC 3007); Victoria, Nowa Nowa, on leaves of *Eucalyptus grandis*, 11 Nov. 1990, A.J. Carnegie (**holotype** of *Mycosphaerella gregaria* IMI 353729b, isotype VPRI 20739a, cultures ex-type CBS 134927 = DAR 72368); Western Australia, Bunbury, Summerlea plantation of Western Australian Chip and Pulp (WACAP), E115°370, S33°400, on *Eucalyptus globulus*,1 May 2000, A. Maxwell (**holotype** of *M. aurantia*, PERTH 05849543, isotype MURU0001, culture ex-type CBS 110500 = CMW 14460). **Colombia**, Sinai, on leaves of *Eucalyptus grandis*, 1995, M.J. Wingfield, PREM 54978. **New Zealand**, on *Dracaena draco*, 1 Mar. 2004, M. Braithwaite, culture CPC 12678. Portugal, on leaves of *Eucalyptus globulus*, Jun. 1995, S. McRae, PREM 54974, cultures CPC 1196–1198. **South Africa**, Western Cape Province, Stellenbosch, Stellenbosch Mountain, leaves of *Eucalyptus viminalis*, Oct. 1994, P.W. Crous (**holotype** of *M. africana*, PREM 51917, cultures ex-type CPC 794–796 = CBS 116154, 116155, 680.95); on leaves of *Eucalyptus deanei*, Oct. 1994, P.W. Crous, PREM 51918, culture CPC 816; Rust and Vrede Farm, leaves

of *Eucalyptus radiata*, Nov. 1994, P.W. Crous, cultures CPC 896–898; Darling, Pampoenvlei, leaves of *E. globulus*, Nov. 1994, P.W. Crous, PREM 51919, cultures CPC 838–840; leaves of *E. grandis*, Nov. 1994, P.W. Crous, PREM 51920, cultures CPC 833–837; Darling, Pampoenvlei, on leaves of *Eucalyptus cladocalyx*, 7 Nov. 1994, P.W. Crous (**holotype** of *M. ellipsoidea*, PREM 51924, cultures ex-type CPC 849–851, 850 = CBS 110843); Kwazula-Natal Province, Richmond, leaves of *Eucalyptus smithii*, Nov. 1994, G. Kemp, PREM 51921, cultures CPC 819–821. **Zambia**, on leaves of *E. globulus*, Aug. 1995, T. Coutinho, PREM 54973, cultures CPC 1229–1231.

Notes: Only the mycosphaerella-like sexual morph is known for this genus that until now included only one species (Quaedvlieg *et al.* 2014). Morphologically, *Amycosphaerella africana* ascospores germinate from both cells and become distorted (though this character was found to vary among different collections, e.g. see *Mycosphaerella gregaria*). Phylogenetically, *Amycosphaerella* clusters close to *Asperisporium* in a clade well-supported by all three phylogenetic analyses (Fig. 1, clade 45; Fig. 3, clade 8). Based on the phylogenetic analyses, the ex-type strain of *Mycosphaerella buckinghamiae* is identical to *Amycosphaerella africana* and is therefore considered as a synonym.

Amycosphaerella keniensis (Crous & T.A. Cout.) Videira & Crous, **comb. nov.** MycoBank MB822738.
Basionym: *Mycosphaerella keniensis* Crous & T.A. Cout., Mycol. Mem. 21: 74. 1998.

Description and illustration: Crous (1998).

Materials examined: **Australia**, on *Musa* sp., unkown collector and date, culture CBS 121391. Kenya, on leaf litter of *Eucalyptus grandis*, May 1995, M.J. Wingfield (**holotype** PREM 54402, cultures ex-type CBS 111001 = CPC 1084 = CMW 5147) *idem*., cultures CPC 1085, CPC 1086.

Notes: The morphological characteristics and phylogenetic position of *Mycosphaerella keniensis* agree with those of the genus *Amycosphaerella*, and a new combination is hereby proposed as *Amycosphaerella keniensis*. Phylogenetically, this species is represented by two strains that cluster in a clade well-supported by all three phylogenetic methods (Fig. 1, clade 45; Fig. 3, clade 8). The strain CBS 121391 was previously classified as *Mycosphaerella mozambica* based on phylogenetic similarity to the ex-type strain CBS 122464, since it was sterile in culture (Arzanlou *et al.* 2008). When comparing the type culture of *Mycosphaerella mozambica* CBS 122464 and strain CBS 121391 using BLAST, they are nearly identical on ITS, but significantly different on *actA* and *his3*: on ITS 99 % (496/497) similarity between GenBank EU514257 and GenBank EU514258; on *actA* 86 % (154/179) similarity and 2 % (5/179) gaps between GenBank EU514318 and GenBank EU514319; on *his3* 95 % (378/396) similarity and 2 % (8/396) gaps between GenBank EU514371 and GenBank EU514372. The partial *rpb2* sequences generated in this study for the same strains showed only 85 % (659/779) similarity. In addition, when comparing the partial *rpb2*, between the type of *Mycosphaerella keniensis* CBS 111001 and strain CBS 121391, they are 100 % identical, and the strain is therefore renamed as *Amycosphaerella keniensis*.

***Amycosphaerella* sp.**

Materials examined: **Brazil**, Par a, Tom e Acu, on *Theobroma cacao*, unknown date, H.C. Evans, dep. in 1980, culture CBS 441.80.

Notes: This strain was initially identified as *Crinipellis perniciosa*, an agaric responsible for the destructive Witches Broom disease on Cocoa (*Theobroma cacao*). The present strain clusters in the *Amycosphaerella* clade (Fig. 3, clade 8), therefore it is not a basidiomycete, and is sterile in culture. There is only a single *Mycosphaerella* species known to infect *Theobroma cacao*, namely *Mycosphaerella theobromae*, but it was described from Africa and the whereabouts of the specimen is unkown (Aptroot 2006). Cacao tree pathogens and endophytes have been studied recently (Mejía *et al.* 2008), but no mycosphaerella-like fungi have been detected so far. Another mycosphaerella-like pathogen known from cacao is *Ceratosperma theobromae*, but little is known about this pathogen (see section Genera of *Mycosphaerellaceae* below).

Clade 46: *Pseudocercosporella*

Pseudocercosporella Deighton, Mycol. Pap. 133: 38. 1973.

Description (from Frank *et al.* 2010): Colonies *in vivo*. *Mycelium* consisting of primary internal and secondary external hyphae, hyaline to pale brown, septate, branched, smooth; stromata lacking or weakly to well-developed, substomatal to intraepidermal. *Conidiophores* solitary to fasciculate, emerging through stomata or erumpent through the cuticle, arising from inner hyphae or from stromata, sometimes formed as lateral branches of superficial hyphae, or forming crustose to subglobose sporodochia; conidiophores rarely branched, straight and subcylindrical to geniculate-sinuous, hyaline, occasionally faintly pigmented, reduced to conidiogenous cells, or septate. *Conidiogenous cells* integrated, terminal, mono- to polyblastic, sympodial; conidiogenous loci inconspicuous, unthickened, hyaline. *Conidia* formed singly, rarely in simple or branched chains, subcylindrical, filiform, somewhat obclavate, euseptate, 1–multi-septate, hyaline, thin-walled, apex obtuse to subacute, subtruncate in catenate conidia, base truncate or subtruncate, hilum unthickened, not darkened, nor refractive.

Type species: *Pseudocercosporella bakeri* (Syd. & P. Syd.) Deighton (≡ *Cylindrosporium bakeri* Syd. & P. Syd.).

Pseudocercosporella bakeri (Syd. & P. Syd.) Deighton, Mycol. Pap. 133: 41. 1973.
Basionym: *Cylindrosporium bakeri* Syd. & P. Syd., Ann. Mycol. 14(5): 372. 1916.
Synonyms: *Ramularia ipomoeae* F. Stevens, Bull. Bern. Bishop Mus. 19: 150. 1925.
Cercosporella ipomoeae Sawada, Rep. Gov. Agric. Res. Inst. Formosa 86: 161. 1943.
Cercosporella ipomoeicola Sawada, Special Publ. Coll. Agric. Natl. Taiwan Univ. 8: 192. 1959.
Pseudocercosporella ipomoeae Deighton, Mycol. Pap. 133: 38. 1973.

Descriptions and illustrations: Braun (1995), Frank *et al.* (2010).

Materials examined: **Laos**, Vientiane Capital, Xaythany District, Xay Villiage, on *Ipomoea* sp., 8 Sep. 2009, P. Phengsintham (**epitype** designated by Frank *et al.* 2010, CBS H-20409, ex-epitype culture CBS 125685 = CPC 17570). **New Zealand**, Auckland, St. Johns, Morrin Road,

Univ. Campus, on leaf spots on *Ipomoea indica*, unknown date, C.F. Hill, culture CBS 119488 = Lynfield 1252. **Philippines**, Los Banos, on *Ipomoea* sp., Dec. 1915, Baker 4029 (**lectotype** of *Cylindrosporium bakeri*, S F40429; isolectotype S F42032, see Braun 1995). Taiwan, Taipei, on *Ipomoea indica*, 14 Feb. 1913, Y. Fujikuro (**isotype** of *P. ipomoeae* TNS-F-220454).

Notes: Based on examination of type materials and additional collections of *Pseudocercosporella bakeri* and *Pseudocercosporella ipomoeae*, Braun (1995) concluded that they represented a single taxon. Frank *et al.* (2010) supported the conclusion of Braun (1995) and designated an epitype for *Pseudocercosporella bakeri*. *Pseudocercosporella*, based on *Pseudocercosporella bakeri*, clusters in a well-supported clade (Fig. 1, clade 46; Fig. 3, clade 10) close to *Asperisporium* and *Amycosphaerella*. Based on the single-gene trees of dataset 3 (not shown, in TreeBASE), *Pseudocercosporella* is reliably distinguished from other genera based on *rpb2* sequences while it is less distinct based on LSU and ITS data. Several species that were pseudocercosporella-like in morphology but are phylogenetically not congeneric with the genus type species have been recently assigned to new genera (Videira *et al.* 2016). As in other cercosporoid genera, morphology alone is insufficient for allocations of new species to the phylogenetically delineated genera.

Clade 47: *Distomycovellosiella*

Distomycovellosiella U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822588.

Etymology: Derived from "Disto-" (referring to distoseptation) + resembling the genus *Mycovellosiella*.

Description: Phytopathogenic. *Caespituli* hypophyllous, pale brown or olivaceous, floccose. *Mycelium* internal composed of hyaline hyphae, external mycelium composed of pale brown to brown hyphae that arise from internal hyphae. *Stromata* lacking or small, composed of few brown cells. *Conidiophores* emerging through stomata in loose to dense coremioid fascicles, or arising solitary from external hyphae, brown, straight to geniculate, simple, sometimes branched. *Conidiogenous cells* integrated, terminal or intercalary, polyblastic, proliferating sympodially, with conidiogenous loci thickened and darkened, flat or protruding. *Conidia* catenate in unbranched or branched chains, pale brown to pale olivaceous, smooth to verruculose, ovoid, obovoid, obclavate, clavate, cylindrical, fusiform, straight or slightly curved, aseptate, euseptate or distoseptate, hila thickened, darkened and refractive. Differs from the genus *Mycovellosiella* by forming distoseptate conidia with slightly thickened and refractive loci.

Type species: *Distomycovellosiella brachycarpa* (Syd.) U. Braun *et al.* (≡ *Cercospora brachycarpa* Syd.).

Distomycovellosiella brachycarpa (Syd.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MB822756. Fig. 24.
Basionym: *Cercospora brachycarpa* Syd., Ann. Mycol. 28: 207. 1930.
Synonyms: *Mycovellosiella solanicola* (Viégas) Munt.-Cvetk., Lilloa 30: 178. 1960.
Mycovellosiella brachycarpa (Syd.) Deighton, Mycol. Pap. 137: 8. 1974.
Passalora brachycarpa (Syd.) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser.: 87. 2003.

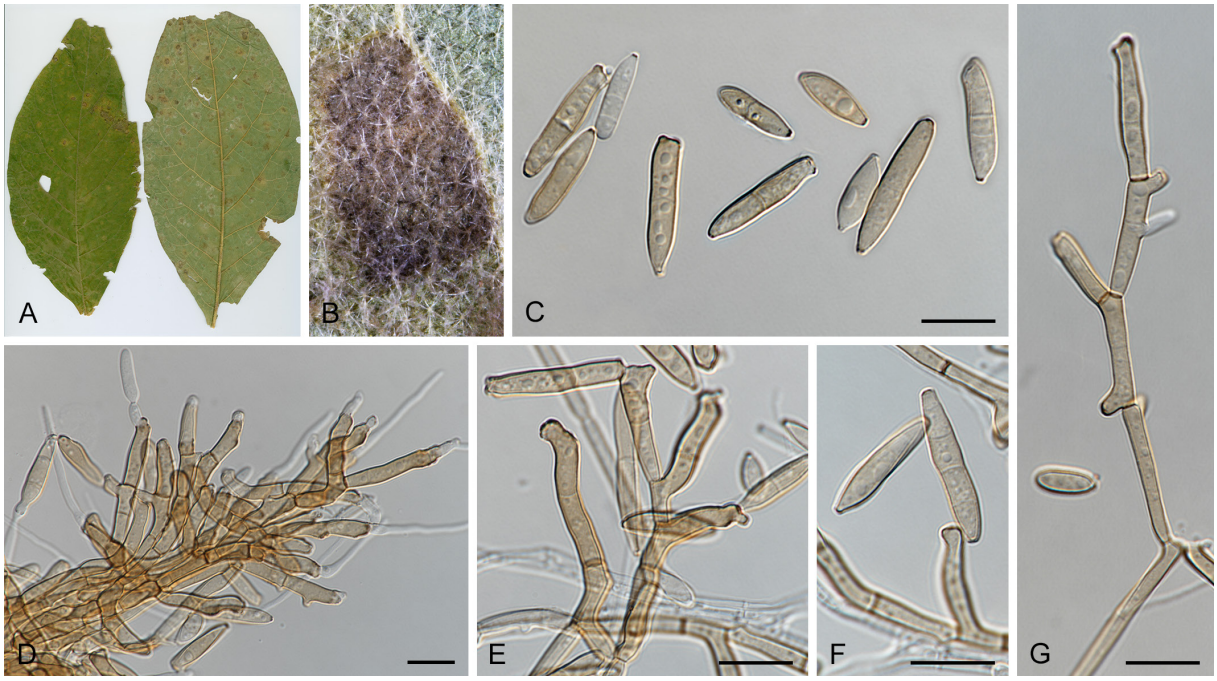


Fig. 24. *Distomycovellosiella brachycarpa* (CPC 18381). A–D. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Catenate and single conidia. D. Conidiophores synnematous-like, conidiogenous cells and conidia. E–G. Observations *in vitro*. E–G. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

For additional synonyms see MycoBank.

Description in vivo (CBS H-22948): *Leaf spots* circular to subcircular, yellow to pale brown on the upper surface, brown on the lower surface, with indistinct margin, 3–7 mm diam. *Caespituli* hypophyllous, pale brown or olivaceous, floccose. *Mycelium* internal composed of hyaline hyphae, external mycelium composed of pale brown to brown hyphae that arise from internal hyphae creeping on the lower leaf surface. *Stromata* lacking or small, composed of few brown cells. *Conidiophores* emerging from internal hyphae, bearing through the stomata in loose to dense coremioid fascicles of 4–10 conidiophores, or solitary arising from external hyphae, brown, smooth, branched, straight to geniculate, 11–38 × 2.5–5 µm. *Conidiogenous cells* integrated, terminal and intercalary, polyblastic, proliferating sympodially, with conidiogenous loci thickened, darkened and somewhat protruding, 1.5–2 µm diam. *Conidia* catenate in single or branched chains, pale brown to pale olivaceous brown, smooth to verruculose, variable in shape, ovoid, obovoid, obclavate, cylindrical, fusiform, 10–40 × 3–7 µm, 0–3-eu- or distoseptate, hila thickened and darkened, 1.5–2 µm diam.

Description in vitro (on V8; CPC 18381): *Mycelium* hyaline to pale olivaceous, smooth, uniform in width, 2–2.5 µm. *Conidiophores* arising from hyphae, macronematous, hyaline to pale brown, smooth, straight, simple or branched, 7.5–215 × 2.5–3 µm. *Conidiogenous cells* integrated, terminal and intercalary, hyaline to pale brown, smooth, mono- or polyblastic, determinated or proliferating sympodially, conidiogenous loci darkened and thickened, 1–2.5 µm diam. *Conidia* catenate, in single or branched chains, hyaline to pale olivaceous, smooth to verruculose, guttulate, obovoid, clavate, cylindrical to obclavate, 12.5–55 × 2.5–5 µm, 0–3 indistinctly eu- or distoseptate, hila slightly thickened and darkened.

Materials examined: **New Zealand**, Coromandel, Thames, on *Solanum mauritianum*, unknown collector and date, isol. C.F. Hill, Feb. 2004, 1001, MAF, Auckland, culture CBS 115124; same country, unkown host, collector and date, isol. E. McKenzie, 29 Mar. 2003, dep. B.F. Brandwagt, culture CBS 114855. **South Africa**, KuwaZulu Natal, on *Solanum mauritianum*, 6 Jul. 2010, A.R. Wood (**epitype** designated here CBS H-22948, MBT378601, ex-epitype culture CBS 142178 = CPC 18381). **Venezuela**, D.F., Puerto La Cruz, on *Solanum hirtum* (= *S. obtusifrons*), 24 Dec. 1927, H. Sydow 90 (**holotype** S F23388; **isotype** IMI 8500).

Notes: *Distomycovellosiella* is a monotypic genus that is morphologically similar to *Mycovellosiella* but is not congeneric with its type, *Mycovellosiella cajani*. Morphologically, *Distomycovellosiella* differs from *Mycovellosiella* by forming distoseptate conidia with slightly thickened and refractive loci (Fig. 24). *Distomycovellosiella* forms a clade well-supported by all three phylogenetic methods (Fig. 1, clade 47; Fig. 3, clade 9) and that is closely related to *Pseudocercosporella* as defined by its type, *Pseudocercosporella bakeri*. Based on a BLAST comparison against the alignment, *Distomycovellosiella brachycarpa* CPC 18381 shares 99 % (470/474) similarity based on ITS with *Clarohilum henningsi* CPC 17314 and 93 % (723/778) similarity based on *rpb2* with *Amycosphaerella keniensis* CBS 111001. Cultures of collections from South America in general and Venezuela in particular are not yet available, but the collections from New Zealand and South Africa agree with type material of this species and descriptions in literature so that we have decided to fix the application of this species by epitypification.

Clade 48: *Asperisporium*

Asperisporium Maubl., Bull. Trimestriel Soc. Mycol. France 29: 357. 1913.

Description (from Braun *et al.* 2014): Usually foliicolous, leaf-spotting hyphomycetes. *Mycelium in vivo* internal; hyphae branched, septate, hyaline to pigmented, thin-walled, smooth or almost so. *Stromata* usually well-developed, substomatal to intraepidermal, often somewhat erumpent, pigmented. *Conidiophores* macronematous, usually densely fasciculate, forming sporodochial conidiomata, continuous to septate, pigmented, wall thin to slightly thickened, smooth or almost so. *Conidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, usually polyblastic, sympodial, but mostly not strongly geniculate, conidiogenous loci conspicuous, thickened and darkened. *Conidia* solitary, amero- to phragmosporous (non-scolecosporous), mostly ellipsoid-ovoid, obovoid, fusiform to short cylindrical or obclavate, mostly with 0–3-eusepta, sometimes with a single or several oblique or longitudinal septa, pigmented, distinctly verruculose to coarsely verrucose, basal hilum thickened and darkened, conidial secession schizolytic.

Type species: *Asperisporium caricae* (Speg.) Maubl (≡ *Cercospora caricae* Speg.).

Asperisporium caricae (Speg.) Maubl., Bull. Trimestriel Soc. Mycol. France 29: 358. 1913.
Basionym: *Cercospora caricae* Speg., Anales Soc. Ci. Argent. 22 (4): 215. 1886.
Synonyms: *Fusicladium caricae* (Speg.) Sacc., Atti Congr. Bot. Palermo: 58. 1902.
Pucciniopsis caricae (Speg.) Höhn., Centralbl. Bakteriol., Abt. II, 60: 5. 1926, nom. illeg (Art. 53.1), non Earle 1902.

Description and illustrations: Minnis *et al.* (2011a).

Materials examined: **Brazil**, intercepted at USA, Washington, Seattle, entering from Brazil, on fruit of *Carica papaya*, 16 Apr. 2010, coll. C. Weight, isol. by J.F. Bischoff from BPI 880773 (**epitype** designated by Minnis *et al.* 2011a, is a dried culture on SDA (BPI 881135), ex-epitype culture CBS 130298); on fruit of *Carica papaya*, Mar. 2013, A.C. Alfenas, culture CPC 22691. **Paraguay**, Guarapi, on leaves of *Carica papaya*, Feb. 1881, B. Balansa, no. 2739 (**lectotype** designated by Chupp 1954, LPS).

Notes: Morphologically, *Asperisporium* is passalora-like but with verrucose conidia (Crous & Braun 2003). The phylogenetic position of *Asperisporium* within the *Mycosphaerellaceae* has been resolved by Minnis *et al.* (2011a), based on the ITS and LSU of the type species *Asperisporium caricae*. *Asperisporium* clusters in a well-supported clade (Fig. 1, clade 48; Fig. 3, clade 13) and is closely related to *Amycosphaerella* and *Paramycovellosiella*. Other species assigned to *Asperisporum* must be individually reassessed.

Asperisporium caricicola Crous & C. Nakash., Sydowia 67: 87. 2015.

Description and illustration: Crous *et al.* (2015c).

Materials examined: **Republic of Fiji**, Viti Levu, Navua, on leaves of *Carica papaya*, 10 Sep. 2013, leg. C. Nakashima (**holotype** CBS H-22252, **isotype** TSU: MUMH 11477, cultures ex-holotype CPC 24348 = CBS 139998); *idem*., culture CPC 24349.

Notes: *Asperisporium caricicola* is represented by a single strain in the phylogenetic analyses (Fig. 1, clade 48; Fig. 3, clade 13). At the time it was described, *Asperisporium caricicola* was found to be morphologically very similar to *Asperisporium caricae*, but phylogenetically distinct based on the partial sequences of LSU and ITS (Crous *et al.* 2015c). The ITS sequence of *Asperisporium caricicola* is 97 % (463/477) similar to *Asperisporium caricae* (GenBank JN190955). The partial sequence of *rpb2*, however, shares 99 % (778/780) similarity with *Asperisporium caricae* (GenBank JN190955). More isolates of both species should be analysed in order to determine whether these represent two distinct species or whether they are conspecific with some intraspecific variation.

Clade 49: *Pantospora*

Pantospora Cif., Ann. Mycol. 36: 242. 1938.
Unconfirmed synonym: *Dictyocephala* A.G. Medeiros (Medeiros 1962).

Description (from Braun *et al.* 2013): Foliicolous hyphomycetes, associated with leaf spots. *Mycelium* internal; hyphae hyaline or almost so. *Stromata* developed, pigmented. *Conidiophores* macronematous, in dense coremioid fascicles or synnemata, septate, pigmented, thin-walled, smooth. *Conidiogenous cells* integrated, terminal, proliferation sympodial and percurrent, with planate to slightly convex, neither thickened nor darkened loci (pseudocercospora-like). *Conidia* formed singly, shape variable, ellipsoid-ovoid, fusiform, clavate to obclavate, didymo- to scolecosporous, with 1–11 transverse eusepta and often a single or few oblique to longitudinal septa, hila neither thickened nor darkened.

Type species: *Pantospora guazumae* Cif.

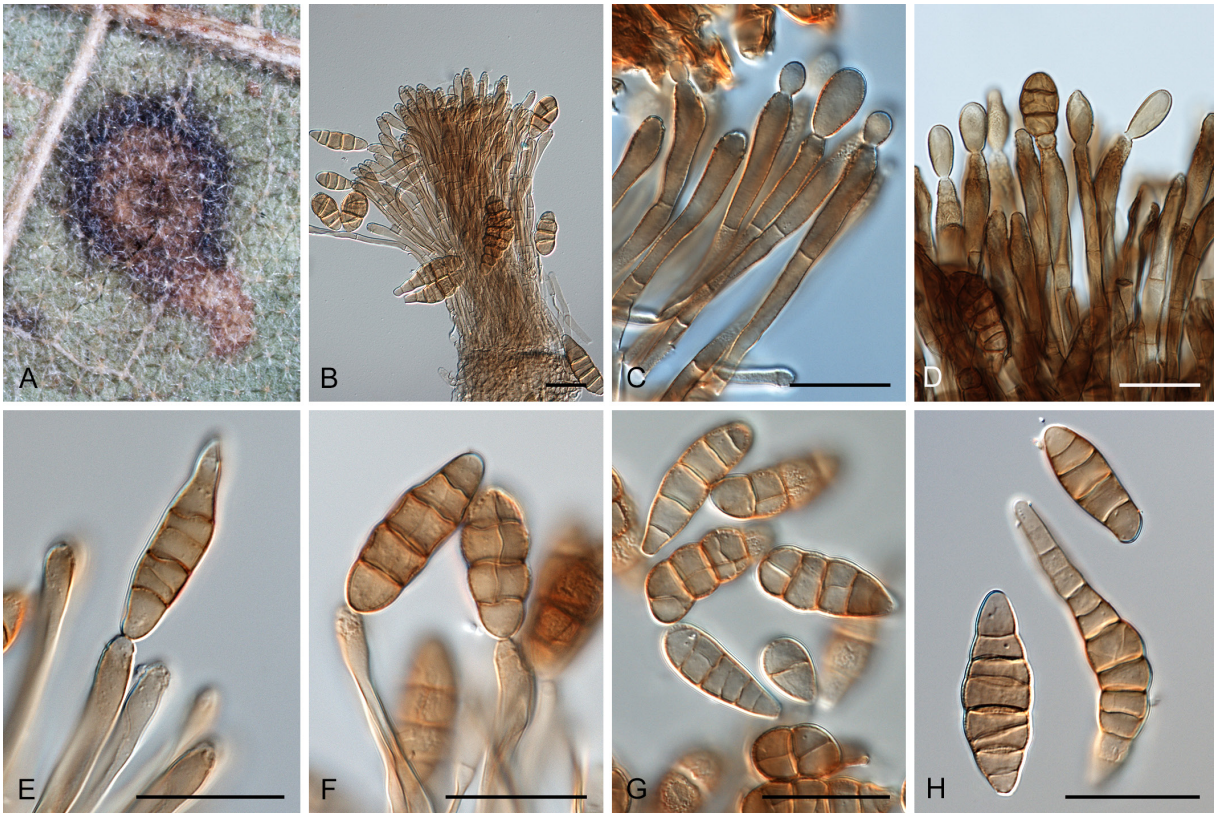


Fig. 25. *Pantospora guazumae* (IMI 59269). A–H. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores and conidia. C–F. Partial conidiophore, conidiogenous cells and conidia. G–H. Conidia. Scale bars = 10 µm.

Pantospora guazumae Cif., Ann. Mycol. 36: 242. 1938. Fig. 25.
Synonyms: *Cercospora ulmifoliae* Obreg.-Bot., Caldasia 1: 51. 1941.
Dictyocephala ulmifoliae (Obreg.-Bot.) A.G. Medeiros, Publ. Inst. Micol. Recife 372: 15. 1962.
Pseudocercospora ulmifoliae (Obreg.-Bot.) U. Braun & Crous, inCrous & Braun, CBS Biodiversity Ser.: 415. 2003.

Description and illustration: Minnis *et al.* (2011a), present study (Fig. 25).

Materials examined: **Cuba**, Bayamo, on *Guazuma ulmifolia* (= *G. tomentosa*), 16 Feb. 1966, R. Urtiaga-Martinez, IMI 117605. **Dominican Republic**, Valle del Cibao, prov. Santiago, Hato del Yaque, on leaves of *Guazuma ulmifolia*, 20 Apr. 1930, coll. R. Ciferri & A.M. Borgna Ciferri, Batey no. 1, Mycoflora Domingensis Exsiccata 210 (lectotypus of *Pantospora guazumae* designated by Deighton 1976a: (IMI 59269). **Mexico**, intercepted at USA, Arizona, Nogales, entering from Mexico, on leaf of *Guazuma ulmifolia*, 12 Feb. 2009, coll. J. Moore (**epitype** designated by Minnis *et al.* 2011a: BPI 880778, culture ex-epitype CBS 130299).

Notes: *Pantospora* is a monotypic genus with no known sexual morph that is reminiscent of *Pseudocercospora* but with synnematous conidiomata, percurrent and sympodial conidiogenous cells and frequently dictyosporous conidia (Crous & Braun 2003). Since the formation of dictyosporous conidia also occurred in the type of *Pseudocercospora* (*Pseudocercospora vitis*), Crous & Braun (2003) reduced *Pantospora* to synonymy with *Pseudocercospora*. The

phylogenetic position of *Pantospora* within the *Mycosphaerellaceae* has been established by Minnis *et al.* (2011a), based on the ITS and LSU sequences of the epitype culture of the type species *Pantospora guazumae*. In the present study *Pantospora* is represented by a single strain lineage (Fig. 1, clade 49; Fig. 3, clade 12) closely related to *Paracercospora*.

Clade 50: *Paracercospora*

Paracercospora Deighton, Mycol. Pap. 144: 47. 1979.

Description (from Braun *et al.* 2013): *Mycelium in vivo* internal. *Conidiophores* macronematous, fasciculate, pigmented. C*onidiogenous cells* integrated, terminal or conidiophores reduced to conidiogenous cells, conidiogenous loci subconspicous by being circular with very slightly thickened and darkened-refractive rim. *Conidia* solitary, scolecosporous, subhyaline to very pale olivaceous, hila very slightly thickened and darkened-refractive along the rim.

Type species: *Paracercospora egenula* (Syd.) Deighton (≡ *Cercoseptoria egenula* Syd.).

Paracercospora egenula (Syd.) Deighton, Mycol. Pap. 144: 48. 1979.
Basionym: *Cercoseptoria egenula* Syd., Ann. Mycol. 33(3–4): 235. 1935.
Synonyms: *Cercospora egenula* (Syd.) Chupp & Doidge, Bothalia 4: 885. 1948.
Pseudocercospora egenula (Syd.) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser.: 171. 2003.
Cercospora solani-melongenae Chupp, Bothalia 4: 892. 1948.

Descriptions and illustrations: Chupp (1954), Deighton (1979), Crous *et al.* (2013a).

Materials examined: **India**, on *Solanum melongena*, N. Ponnapa, No. 109/1981, culture CBS 485.81. **Japan**, Shimane, on leaves of *Solanum melongena*, 5 Aug. 1998, T. Mikami, CNS-415, cultures MUCC 883 = MAFF 237766. **Republic of Korea**, Hongcheon, on leaves of *S. melongena*, 26 Oct. 2005, H.D. Shin, CBS H-20836, culture CBS 132030 = CPC 12537. **South Africa**, Gauteng Province, Barberton, on *Solanum panduriforme*, May 1931, L. Liebenberg No. 25999 (**holotype** PREM 25999, **isotype** IMI 89597).

Notes: *Paracercospora* was introduced by Deighton (1979) in order to accommodate *Paracercospora egenula*, a pseudocercospora-like species with distinct circular conidiogenous loci (scars) with a slightly thickened dark rim. This type of scar, however, is also present is some species of *Pseudocercospora* and with further support from earlier phylogenetic works (Stewart *et al.* 1999, Crous *et al.* 2000, 2001b), *Paracercospora* was synonymised with *Pseudocercospora* (Crous & Braun 2003). When representatives of the type species, *Paracercospora egenula*, were recollected, their partial LSU DNA sequences placed them apart from *Pseudocercospora* (Crous *et al.* 2013a, Vaghefi *et al.* 2016). *Paracercospora* is maintained as a separate genus based on the combination of its phylogenetic position (Fig. 1, clade 50, Fig. 3; clade 11), minimal marginal thickening of the conidiogenous loci and subhyaline conidia. Closely related species to *Paracercospora egenula* include *Passalora brachycarpa* (pale olivaceous, catenate conidia, prominent, thickened, darkened scars), and *Pseudocercospora tibouchinigena* (subhyaline conidia, unthickened hila and scars) (Crous *et al.* 2013a). In the present study, with the addition of the ITS and partial *rpb2* sequences to

the phylogenetic analysis, the strains of *Passalora brachycarpa* (now *Distomycovellosiella brachycarpa*) cluster in a separate clade from *Paracercospora egenula*. Unfortunately, the phylogenetic position of *Pseudocercospora tibouchinigena* was not reassessed in this study and it may eventually be shown to represent a distinct genus since phylogenetically, it clusters apart from *Pseudocercospora* and, morphologically it is neither a species of *Pseudocercospora s. str.* (subhyaline conidia), nor *Paracercospora* (lacking any scar thickening). In a recently published paper (Ou *et al.* 2015), with the description of a new species of *Paracercospora*, *Paracercospora dictamnicola*, all three species '*Pseudocercospora tibouchinigena*', *Paracercospora egenula* and *Paracercospora dictamnicola* cluster together in a phylogeny based on LSU and ITS. However, *Paracercospora dictamnicola* is described as having conidiogenous loci unthickened and not darkened (pseudocercospora-like) and conidia solitary, subhyaline to pale olivaceous (paracercospora-like). Thus, the case of *Paracercospora dictamnicola* adds to the morphological vs. phylogenetic placement of cercosporoid species dilemma.

Clade 51: *Nothopassalora* [and *Clarohilum*]

Nothopassalora U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822696.

Etymology: From the greek notho-, meaning false, and resembling the genus *Passalora*.

Description: Hyphomycetous, phytopathogenic. *Mycelium* internal, hyaline to pale brown, branched, septate hyphae. *Stromata* dark, epidermal, substomatal, subglobose. *Conidiophores* emerging in fascicles from stromata, through stomata, pale to medium brown, smooth to verruculose, simple, straight to flexuous, geniculate-sinuous at the apex, multiseptate, but sometimes with a single basal septum or reduced to conidiogenous cell. *Conidiogenous cells* integrated, terminal, proliferating sympodially, mono- or polyblastic, conidiogenous loci rim-like, darkened, thickened and refractive. *Conidia* solitary, pale brown to olivaceous, smooth, thin-walled, cylindrical to long-obclavate, straight or gently curved, apex rounded and sometimes narrowing into a beak, base rounded or obconically truncate, multiseptate, hila thickened, darkened and refractive, sometimes protruding.

Type species: *Nothopassalora personata* (Berk. & M.A. Curtis) U. Braun *et al.* (≡ *Cladosporium personatum* Berk. & M.A. Curtis).

Nothopassalora personata (Berk. & M.A. Curtis) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822766. Fig. 26.
Basionym: *Cladosporium personatum* Berk. & M.A. Curtis, Grevillea 3(27): 106. 1875.
Synonyms: *Cercospora personata* (Berk. & M.A. Curtis) Ellis & Everh., J. Mycol. 1: 63. 1885.
Cercosporiopsis personata (Berk. & M.A. Curtis) Miura, Flora of Manchuria and East Mongolia. Part III. Cryptogams, fungi 3: 529. 1928.
Passalora personata (Berk. & M.A. Curtis) S.A. Khan & M. Kamal, Pakistan J. Sci. Res. 13: 188. 1961.
Cercosporidium personatum (Berk. & M.A. Curtis) Deighton, Mycol. Pap. 112: 71. 1967.
Mycosphaerella berkeleyi Jenkins, J. Agr. Res. 56: 325. 1938.
For additional synonyms see Crous & Braun (2003) or MycoBank.

Description in vivo (CBS H-22946): *Leaf spots* amphigenous, blackish brown, circular to subcircular, with yellow halo, 5–12 mm diam. *Mycelium* internal, composed of hyaline to pale

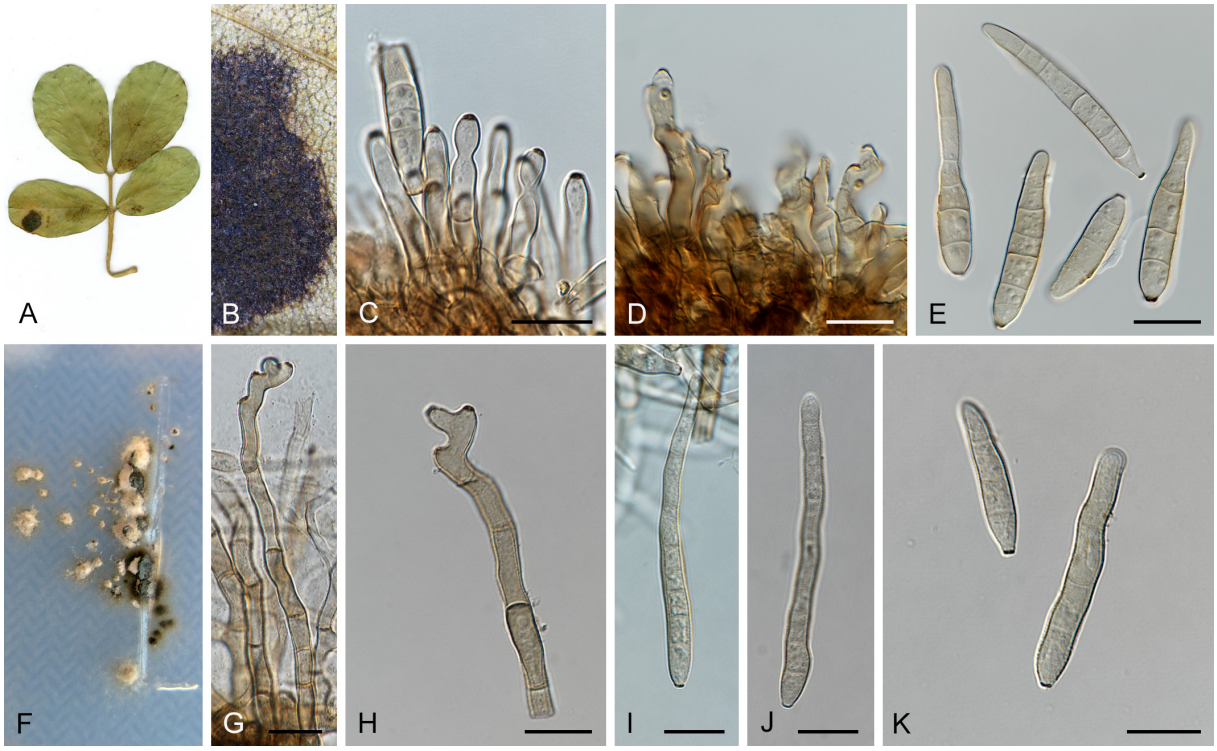


Fig. 26. *Nothopassalora personata* (CPC 19466). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C, D. Conidiophores and conidiogenous cells. E. Single conidia. F–K. Observations *in vitro*. F. Culture on SNA. G. Conidiophore and conidiogenous cell. H. Partial conidiophore and conidiogenous cell. I–K. Single conidia. Scale bars = 10 µm.

brown hyphae, smooth, septate, branching. *Stromata* amphigenous, mainly hypophyllous, well-developed, 42–165 µm diam, brown to dark brown, epidermal, substomatal, subglobose and composed of *textura angularis*. *Conidiophores* emerging from upper part of stromata, densely fasciculate, pale brown to brown olivaceous, smooth to verruculose, erect, simple, straight to sinuous, geniculate-sinuous or conically truncate at the apex, irregular in width, 28–63 × 5–7.3 µm, sometimes only 1-septate. *Conidiogenous cells* integrated, terminal, mono- or polyblastic, proliferating sympodially, with rim-like conidiogenous loci distinctly thickened, darkened and refractive, located on the shoulders and the apex, 3–4 µm diam. *Conidia* solitary, pale to pale olivaceous brown, thick-walled, cylindrical to long-obclavate, straight or gently curved, apex rounded and sometimes narrowing into a beak, base rounded or obconicaly truncate, 38–85 × 5–8 µm, 2–7-euseptate, hila thickened, darkened and refractive, 3–4 µm diam.

Description in vitro (on V8; CPC 19466): *Mycelium* composed of hyaline to olivaceous hyphae, smooth to finely verruculose, septate, branching, uniform in width, 2.5 µm. *Conidiophores* pale brown to brown, micro- to macronematous, darker at the middle part, and paler towards apex, smooth to rough, cylindrical, geniculate-sinuous at the apex, simple, 50–100 × 3–5 µm. *Conidiogenous cells* integrated, terminal, mono- or polyblastic, proliferating sympodially, with conidiogenous loci rim-like, thickened, darkened and refractive, located at the shoulders and apex, 2.5 µm diam. *Conidia* solitary, pale to pale brown, cylindrical to long-obclavate, rounded at the apex and obconicaly truncate at the base, 45–110 × 5–7 µm, 2–10-euseptate, hila thickened, darkened and refractive, 2.5 µm diam.

Materials examined: **Australia**, Northern Territory, Darwin, on *Arachis hypogaea*, 30 Apr. 2011, P.W. Crous (**epitype** designated here, CBS H-22946, MBT378602, ex-epitype culture CBS 142236 = CPC 19466). **USA**, Georgia, Spalding Co., Georgia Experiment Station, on *Arachis hypogaea*, 23 Jun. 1937, W.A. Jenkins (CUP-027308, **isotype** of *Mycosphaerella berkeleyii*, ex-isotype culture CBS 222.38); South Carolina, Santee River, on *Arachis hypogaea*, Ravenel 1612 (**holotype** K, **isotype** IMI 104552).

Notes: The two major foliar diseases occurring on peanut, Early leaf spot and Late leaf spot, are respectively caused by *Cercospora arachidicola* (= *Mycosphaerella arachidis*) and *Passalora personata* (= *Mycosphaerella berkeleyi*) (Jenkins 1938, Kokalis-Burelle *et al.* 1997). Both diseases occur wherever peanut is grown but is usually manageable with timely fungicide applications (Kokalis-Burelle *et al.* 1997). The strains used in this study are identical based on their DNA sequences (Fig. 1, clade 51; Fig. 3, clade 14) and closely related with *Asperisporium*, despite their morphological differences (Fig. 26).

Clarohilum Videira & Crous, **gen. nov.** MycoBank MB822583.

Etymology: from the latin clarus- that means visible + hilum.

Description (adapted from Little 1987): Phytopathogenic, causing leaf spots. *Ascomata* globose, subepidermal, mostly epiphyllous, brown or dark brown, ostiolate, thin wall composed of pseudo-parenchymatous cells. *Asci* cylindrical, tapering towards the base, bitunicate, thick-walled, 8-spored. *Ascospores* hyaline, tapering at both ends, two-celled with the upper cell slightly broader than the lower. *Conidiophores* mononematous, pale olivaceous brown, not branched, with slight geniculations, septate. *Conidiogenous cells* terminal, elongating sympodially, polyblastic, with conidiogenous loci thickened and darkened, located both apical and laterally. *Conidia* single, pale olivaceous, smooth, obovoid, obclavate, cylindrical to long-obclavate, slightly curved, apex obtuse, base rounded or short obconicaly truncate, septate, hila thickened, darkened and usually protruding.

Type species: *Clarohilum henningsii* (Allesch.) Videira & Crous Crous (≡ *Cercospora henningsii* Allesch.).

Clarohilum henningsii (Allesch.) Videira & Crous, **comb. nov.** MycoBank MB822748. Fig. 27.
Basionym: *Cercospora henningsii* Allesch., Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete. Teil C: 35. 1895.
Synonyms: *Cercosporidium henningsii* (Allesch.) Deighton, More dematiaceous Hyphomycetes: 295. 1976.
Passalora henningsii (Allesch.) Poonam Srivast., J. Living World 1(2): 116. 1994, nom. inval. (Art. 41.1).
Passalora henningsii (Allesch.) R. F. Castañeda & U. Braun, Cryptog. Bot. 1: 46. 1989.
Cercospora cassavae Ellis & Everh., Bull. Torrey Bot. Club 22: 438. 1895.
Cercospora manihotis Henn., Hedwigia 41: 18. 1902.
Mycosphaerella henningsii Sivan., Trans. Brit. Mycol. Soc. 84: 552. 1985.
For additional synonyms see MycoBank.

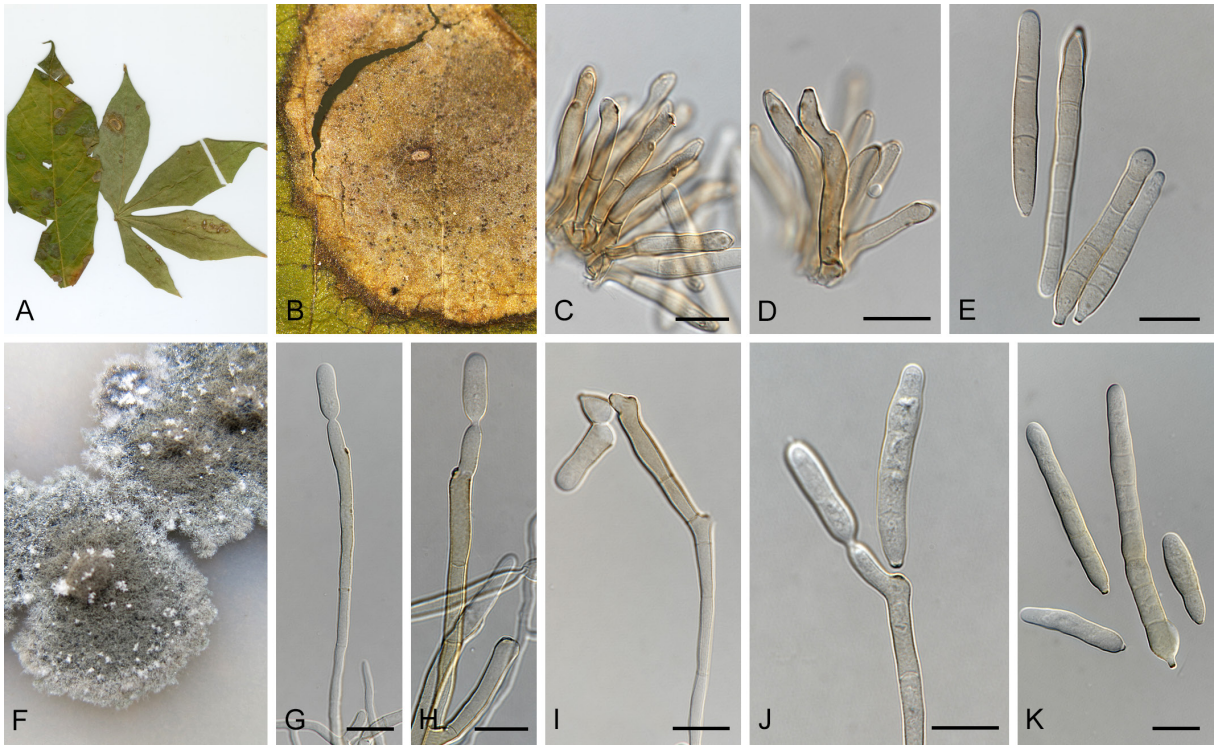


Fig. 27. *Clarohilum henningsii* (CPC 17314). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C, D. Conidiophores and conidiogenous cells. E. Single conidia. F–K. Observations *in vitro*. F. Culture on OA. G–J. Partial conidiophore, conidiogenous cell and conidia. K. Single conidia. Scale bars = 10 µm.

Descriptions and illustrations: Ellis (1976), Little (1987).

Description in vitro (on V8; CPC 17314): *Mycelium* hyaline to olivaceous brown, smooth to rough, septate, branching, uniform in width, 2.5–7.5 µm. *Conidiophores* micro- and macronematous, pale brown to olivaceous brown, paler at the apex, smooth, straight, simple or occasionally branched, cylindrical, geniculate sinuous at the apex, 75–170 × 5–7.5 µm. *Conidiogenous cells* integrated, terminal, proliferating sympodially, mono- or polyblastic, with conidiogenous loci thickened, darkened and protruding, 2.5 µm diam. *Conidia* solitary, hyaline to pale brown, smooth, obovoid, cylindrical, obclavate, base rounded or obconically truncate, sometimes sligltly swollen, apex rounded, 30–75 × 5–7 µm, 0–8-euseptate, sometimes slightly constricted at the septa, hila rim-like, thickened, darkened and refractive, sometimes protruding, 2.5 µm diam.

Material examined: **Laos**, on *Manihot esculenta*, 5 May 2006, P. Pheng, NOUL 26, culture CPC 17314. **Tanzania**, Usambara (Amboni), on *Manihot esculenta* (= *M. utilissima*), Holst No. 2899 (**lectotype** of *C. henningsii* designated here, MBT378578, S F37294; **isolectotype** S F37295).

Notes: *Passalora henningsii* is widely distributed in tropical to subtropical regions along with its host plant, *Manihot esculenta*. Morphologically, the description of the observed strain is similar to that available in literature (Chupp 1954, Castañeda & Braun 1989). In this study, caespituli of this species are paler than that of the other species of *Passalora s. lat*. and has

conidia with distinctly protruding hila (Fig. 27). The phylogenetic analyses place this strain in a single-strain lineage (Fig. 3, clade 15) that is closely related to *Nothopassalora* (Fig. 1, clade 51; Fig. 3, clade 14). Morphologically, a few conidia of *Passalora henningsii* showed less protruding hila that tapered towards the base like some of the conidia of *Nothopassalora personata* (Fig. 26). In a supplementary phylogenetic analysis performed using a smaller dataset (sequences in dataset 3 corresponding to Fig. 3, clades 1–16), this single-strain lineage remains apart from the *Nothopassalora* clade. Based on a BLAST comparison against the alignment, the present strain shares only 95 % (447/473) similarity on ITS and 91 % (686/750) similarity on *rpb2* with *Nothopassalora personata.* The morphological differences and the instability of the phylogenetic position of these strains indicate that it is better to introduce this species into a new genus than combine it into *Nothopassalora*. Type material of *Cercospora manihotis* Henn. 1902 (Brazil, Pará, on *Manihot esculenta*, May 1901, J. Huber 42) is not preserved at B and could not be traced in other herbaria. Syntype material of the illegitimate name *Cercospora manihotis* Henn., in de Wildemann, Ann. Mus Congo, 5 Sér., Vol. II, Fasc. II: 104. 1907 [non *Cercospora manihotis* Henn. 1902] is presenved in B and S (Congo, Kwango, Kisantu, May 1906, H. Vanderyst 179). Syntypes of *Cercospora cassava* are housed in several herbaria, including BPI 434310, 437138, FH 01012118, and S F278433 (USA, Florida, Lake County, Eustis, on Cassava leaves (*Manihot* sp.), 28 May 1895, Geo. V. Nash).

Clade 52: *Pluripassalora*

Pluripassalora Videira & Crous, **gen. nov.** MycoBank MB822611.

Etymology: The name is a combination of pluri- (many) which refers to the multiseptate conidia + passalora, due to the similarity to the *Passalora* genus.

Description: Phytopathogenic, forming leaf spots. *Mycelium* internal, septate, smooth, hyaline to pale brown. *Stromata* amphigenous, mainly hypophyllous, well-developed, epidermal, substomatal, subglobose. *Conidiophores* emerging from upper part of stromata in dense fascicles, or emerging singly from internal hyphae, pale brown to brown, simple, sinuous, sometimes geniculate, irregular in width, smooth to verruculose, aseptate or septate. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, mono- or polyblastic, conidiogenous loci rim-like, thickened, darkened and refractive. *Conidia* solitary, pale to pale olivaceous brown, paler towards the apex, smooth, thick-walled, mostly obclavate (in host), cylindrical-obclavate (in culture), euseptate, multiseptate, sometimes constricted at the septa (in culture), rounded at the base, beak-like and rounded at the apex, hila thickened, darkened and refractive.

Type species: *Pluripassalora bougainvilleae* (Munt.-Cvetk.) U. Braun *et al.* (≡ *Cercospora bougainvilleae* Munt.-Cvetk.).

Pluripassalora bougainvilleae (Munt.-Cvetk.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822822. Fig. 28.
Basionym: *Cercospora bougainvilleae* Munt.-Cvetk., Revista Argent. Agron. 24: 84. 1957.
Synonyms: *Cercosporidium bougainvilleae* (Munt.-Cvetk.) Sobers & C.P. Seym., Proc. Florida State Hort. Soc.: 398. 1969.
Passalora bougainvilleae (Munt.-Cvetk.) R.F. Castañeda & U. Braun, Cryptog. Bot. 2: 291. 1991.

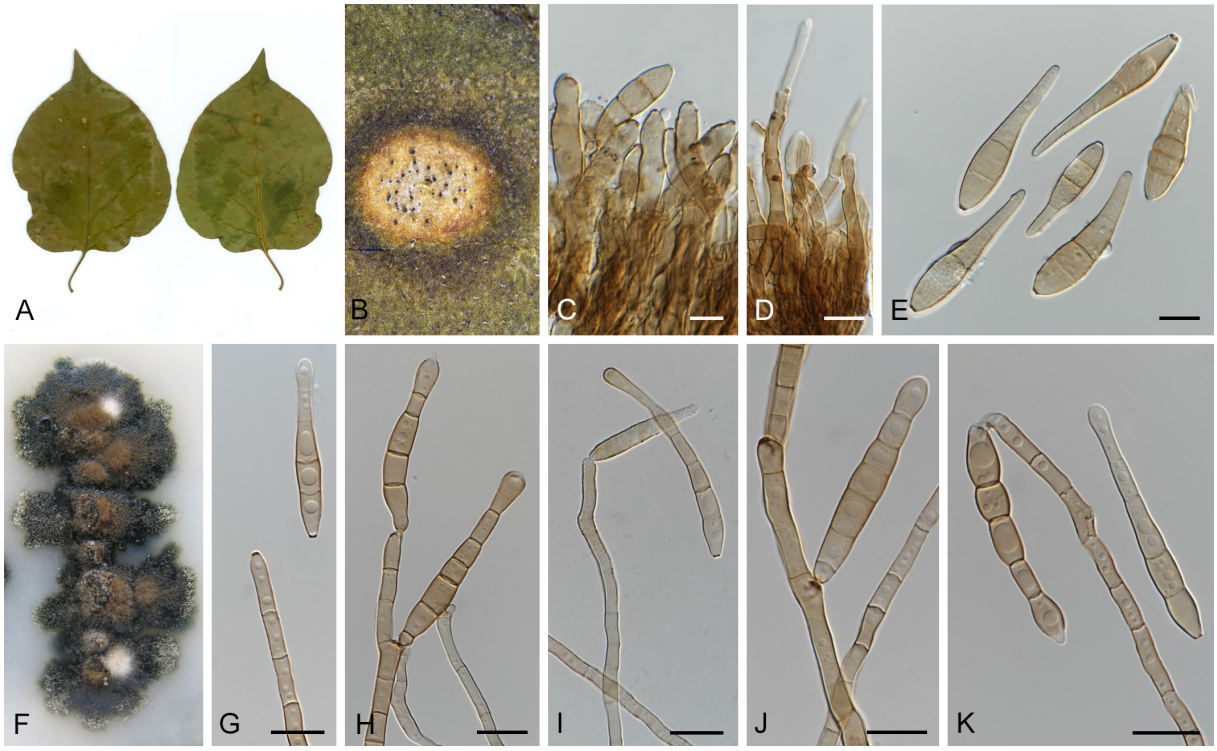


Fig. 28. *Pluripassalora bougainvilleae* (CPC 19327). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C, D. Conidiophores, conidiogenous cells and conidia. E. Single conidia. F–K. Observations *in vitro*. F. Culture on OA. G–K. Partial conidiophore, conidiogenous cell and conidia. Scale bars = 10 µm.

Description and illustration: Ellis (1976), present study (Fig. 28).

Description in vivo (CBS H-22947): *Leaf spots* amphigenous, brown to whitish brown, circular to subcircular, with a dark brown concentric ring, 2–5 mm diam. *Mycelium* internal, hyaline to pale brown. *Stromata* amphigenous, mainly hypophyllous, well-developed, 25–50 µm diam, brown, epidermal, substomatal, subglobose. *Conidiophores* emerging from upper part of stromata in dense fascicles, or emerging singly from internal hyphae, pale brown to brown, smooth, simple, straight to geniculate-sinuous, irregular in width, 24–62 × 5–6 µm, septate. *Conidiogenous cells* integrated, terminal and intercalary, mono-or polyblastic, proliferating sympodially, with rim-like conidiogenous loci thickened, darkened and refractive, located on on the shoulders and apex, 2–3 µm diam. *Conidia* solitary, smooth, pale to pale olivaceous brown, paler towards the apex, thick-walled, mostly obclavate or long-obclavate, base rounded, apex rounded and beak-like, 40–116 × 7–10 µm, 3–10-euseptate, sometimes constricted at the septa, hila distinctly thickened, darkened and refractive, 2–3 µm diam.

Description in vitro (on MEA; CPC 19327): *Mycelium* composed of hyphae uniform in width, hyaline and 1–2 µm diam when young, pale brown and 3.8–5 µm diam when mature, septate and branching. *Conidiophores* emerging from large brown aggregated cells 7.5–12.5 µm diam, micro- or macronematous, pale brown, septate, straight to curved in segments, occasionally geniculate-sinuous, uniform in width, 100–150 × 5 µm. *Conidiogenous cells* integrated, terminal and intercalary, pale brown, straight to mildly geniculate, mono- or polyblastic, conidiogenous

loci thickened, darkened and refractive, 2–2.5 µm diam. *Conidia* solitary, pale brown, smooth, cylindrical-obclavate, long-obclavate, base obconically truncate, apex rounded, beak-like, sometimes swollen, 45–75 × 5–7.5 µm, 3–7-euseptate, slightly to strongly constricted at the septa, hila thickened, darkened and refractive, 2–2.5 µm diam.

Material examined: **Australia**, Northern Territory, Darwin, on *Bougainvillea* sp., 30 Apr. 2011, P.W. Crous, CBS H-22947, culture CBS 142237 = CPC 19327.

Notes: The present species was initially described as *Cercospora bougainvilleae* and was described on the host *Bougainvillea stipitata* from Argentina (Muntañola-Cvetkovic 1957) but no original material could be traced. The designation of a neotype is necessary, but the present strain is from a different geographical location. In the phylogenetic analyses, this species is represented by a single-strain lineage (Fig. 1, clade 52; Fig. 3, clade 16) closely related to *Nothopassalora*. Based on a BLAST comparison, *Pluripassalora* shares 90 % (418/463) similarity on ITS and 87 % (679/780) similarity on *rpb2*, with *Nothopassalora personata* CPC 19466. Morphologically, *Pluripassalora* can be distinguished from *Nothopassalora* by its obclavate and multiseptate conidia and also differs from *Passalora s. str.* by its multiseptate conidia.

Clade 53: *Micronematomyces*

Micronematomyces U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822595.

Etymology: Derived from the micronematous conidiophores (micronemato-) and fungus (-myces).

Differs from *Passalora* in forming short and micronematous to submicronematous conidiophores, and solitary and cylindrical, long-obclavate to filiform conidia.

Type species: *Micronematomyces caribensis* (Crous & Den Breeÿen) U. Braun, C. Nakash., Videira & Crous (≡ *Passalora caribensis* Crous & Den Breeÿen).

Micronematomyces caribensis (Crous & Den Breeÿen) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822763.
Basionym: *Passalora caribensis* Crous & Den Breeÿen, Fungal Diversity 23: 98. 2006.

Description and illustration: Breeÿen *et al.* (2006).

Materials examined: **Cuba**, near Havana, *Chromolaena. odorata*, 28 Oct. 1997, S. Neser, culture CBS 113376 = MJM 1539 = C487. **Jamaica**, Central Jamaica, between Guinea corm and John's Hall, on *C. odorata*, 31 Oct. 1997, M.J. Morris (**holotype** CBS H-19754, culture ex-type CBS 113380 = MJM 1550 = C498); Kingston, road to Strawberry Hill off Blue Mountain road, on *C. odorata*, M.J. Morris, 30 Oct. 1997, cultures CBS 113374 = MJM 1545 = C481, CBS 113375 = MJM 1543 = C482; between Maypen and Chapleton, on *C. odorata*, 30 Oct. 1997, M.J. Morris, culture CBS 113381 = MJM 1549 = C500; on highway to Kingston, between Moneague and Edwarton, on *Chromolaena odorata*, 1 Nov. 1997, M.J. Morris, culture CBS 113378 = MJM 1552 = C494; Strawberry Hill, on *C. odorata*, 30 Oct. 1997, M.J. Morris, culture CBS 113379 = MJM 1544 = C495.

Notes: The genus *Micronematomyces* is phylogenetically and morphologically distinct from *Passalora* as circumscribed in this study. It encompasses two species, *Micronematomyces caribensis* and *Micronematomyces chromolaenae*, that cluster together in a well-supported clade in the phylogenetic analyses performed in this study (Fig. 1, clade 53; Fig. 3, clade 17). Morphologically, species in the genus *Micronematomyces* differ from *Passalora s.str.* in forming short conidiophores, and multiseptate conidia that are cylindrical, long-obclavate to filiform. *Micronematomyces caribensis* can be distinguished from *Micronematomyces chromolaenae* by its shorter and slightly wider conidia. The strains CBS 113378 and CBS 113379 were identified as *Passalora perfoliati* based on morphological characters (Breeÿen *et al.* 2006) using the descriptions available in literature (Ellis 1971, Braun 1998). Unfortunately, when the cultures were observed in this study they did not sporulate and the fungarium material was depauperate. Based on a BLAST against the entire alignments, these two strains share 99 % (779/ 780) similarity on *rpb2* and 98 % (465/474) similarity on ITS with *Micronematomyces caribensis*. The type of *Passalora perfoliati* was isolated from *Eupatorium perfoliatum* from Wisconsin, USA (Ellis & Everhart 1889; **syntypes** NY, WIS-F-0003831) while the aforementioned two strains were obtained from a different host (*Chromolaena odorata*) and from a different location (Jamaica). Therefore, these two strains will henceforth be treated as *Micronematomyces caribensis*.

Micronematomyces chromolaenae (Crous & Den Breeÿen) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822764.
Basionym: *Passalora chromolaenae* Crous & Den Breeÿen, Fungal Diversity 23: 98. 2006.

Description and illustration: Breeÿen *et al.* (2006).

Materials examined: **Mexico**, Veracruz Province, Catemaco Lake, on *Chromolaena odorata*, 12 Oct. 1997, M.J. Morris (**holotype** CBS H-19753, culture ex-type CBS 113611 = MJM 1498 = C452); Entrada Corretera, on *C. odorata*, 12 Oct. 1997, M.J. Morris, culture CBS 113371 = MJM 1490 = C450.

Notes: The host *Chromolaena odorata* (≡ *Eupatorium odoratum*) is considered to be the one of the most problematic invasive species within protected rainforests in Africa (Struhsaker *et al.* 2005). Among plant pathogens those considered to be host-specific are considered to be potentially good as biological control agents (Barreto & Evans 1994). *Micronematomyces chromolaenae* is distinguished from other species occurring on this host by its conidial dimensions (up to 200 µm long and 4 µm wide) and shape that is never curled (Breeÿen *et al.* 2006). The representative strains of this species cluster in a clade well-supported by all three phylogenetic methods employed in this study (Fig. 3, clade 17). They were, unfortunately, sterile in culture at the time this study was performed and the herbarium specimens were depauperate.

Clade 54: *Rhachisphaerella*

Rhachisphaerella U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822702.

Etymology: Derived from the conidiogenous cells forming a rachis and the mycosphaerella-like sexual morph.

Description (adapted from Arzanlou *et al.* 2008): Phytopathogenic. *Ascomata* amphigenous, dark brown, subepidermal, becoming erumpent, globose; wall composed of layers of medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid to broadly ellipsoid, straight to slightly curved, 8-spored. *Ascospores* bi- to tri-seriate, overlapping, hyaline, thin-walled, straight to curved, fusoid-ellipsoidal with obtuse ends, widest in middle of apical cell, medianly 1-septate, not to slightly constricted at the septum, tapering towards both ends but more prominently towards the lower end; ascospores becoming distorted upon germination, becoming constricted at the septum, with irregular, wavy germ tubes, growing 90° to the long axis, and not arising from the polar ends of the spore. (*In vitro*) *Mycelium* submerged and superficial; submerged hyphae hyaline to subhyaline, thin-walled, smooth or slightly rough; aerial hyphae pale olivaceous, smooth or finely verruculose. *Conidiophores* arising from hyphae, occasionally reduced to conidiogenous cells, hyaline, subcylindrical. *Conidiogenous cells* integrated, terminal, proliferating sympodially, polyblastic, conidiogenous loci aggregated, flat, not protuberant (not denticle-like), unthickened, but somewhat darkened. *Conidia* solitary, hyaline, thin-walled, smooth, obovoid, ellipsoidal, obclavate, aseptate or multiseptate, hilum truncate, flat, broad, unthickened, slightly darkened.

Type species: *Rhachisphaerella mozambica* (Arzanlou & Crous) Videira & Crous (≡ *Mycosphaerella mozambica* Arzanlou & Crous).

Rhachisphaerella mozambica (Arzanlou & Crous) Videira & Crous, **comb. nov.** MycoBank MB822798.
Basionym: *Mycosphaerella mozambica* Arzanlou & Crous, Persoonia 20: 26. 2008.

Description and illustration: Arzanlou *et al.* (2008).

Materials examined: **Mozambique**, Chimoio, Bairro, on leaf of *Musa* cv., 2003, A. Viljoen (**holotype** CBS H-20039, culture ex-type CBS 122464); *idem*. CBS H-20040, CBS H-20041, CBS H-20042.

Notes: *Mycosphaerella mozambica* is a common pathogen occurring on banana in Mozambique (Arzanlou *et al.* 2008). The sympodially proliferating conidiogenous cells are reminiscent of *Ramichloridium*, but the type species of that genus, *Ramichloridium apiculatum*, has been found to cluster within *Dissoconiaceae* (Arzanlou *et al.* 2007). As other ramichloridium-like species within *Mycosphaerellaceae*, *M. mozambica* needed to be reassigned into a new genus. Phylogenetically, the representative strain of this species forms a single species lineage closely related to *Micronematomyces* (Fig. 1, clade 54; Fig. 3, clade 18). Morphologically, *Rhachisphaerella mozambica* is quite distinct from species of *Micronematomyces*, since its conidiogenous cells form a rachis with unthickened conidiogenous loci and the conidia are generally obovoid, 0–1-septate with unthickened hila.

Clade 55: *Neophloeospora*

Neophloeospora U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822598.

Etymology: Derived from the similarity to the genus *Phloeospora* (neo- = new).

Description (adapted from Punithalingam 1990): Phytopathogenic, causing leaf spots. *Pseudothecia* on overwintered, fallen leaves, initially immersed, later erumpent, epiphyllous, dark brown, spherical, with short necks and circular ostioles, wall composed of several cell layers of *textura angularis*, the outer cells dark brown, the inner cells hyaline. *Asci* fasciculate, cylindrical to clavate, hyaline, 8-spored, bitunicate. *Ascospores* biseriate or irregularly biseriate, ellipsoid, medianly or slightly unequally 1-septate, upper cell slightly wider than the lower cell, guttulate. *Conidiomata* epiphyllous, acervular, subepidermal, separate or confluent, composed of *textura angularis*; dehiscence irregular. *Conidiogenous cells* terminal, hyaline, cylindrical, proliferating percurrently with inconspicuous annellations or sympodially. *Conidia* hyaline or subhyaline, smooth, cylindrical to obclavate, straight or curved, septate, guttulate, with age becoming darker, constricted at the septa and slightly verruculose.

Type species: *Neophloeospora maculans* (Bérenger) Videira & Crous (≡ *Fusarium maculans* Bérenger).

Neophloeospora maculans (Bérenger) Videira & Crous, **comb. nov.** MycoBank MB822823. Fig. 29.
Basionym: *Fusarium maculans* Bérenger, Atti Riunione Sci. Ital. (Milano) 6: 474. 1845 (1844).
Synonyms: *Phloeospora maculans* (Bérenger) Allesch., in Rabenh., Krypt.-Fl., Edn 2, 1(6): 935. 1900 (1899).
Phloeosporella maculans (Bérenger) Höhn., Mitt. Bot. Lab. T. H. Wien 4(2): 77. 1927.
Cercosporella maculans (Bérenger) F.A. Wolf, J. Elisha Mitchell Sci. Soc. 51: 165.1935.
Septoria mori Lév., Ann. Sci. Nat., Bot., Sér. 3, 5: 279. 1846.
Cheilaria mori (Lév.) Desm., Ann. Sci. Nat., Bot., Sér. 3, 8: 27. 1847.
Phloeospora mori (Lév.) Sacc., Michelia 1(2): 175. 1878.
Septogloeum mori (Lév.) Briosi & Cavara, Fung. Paras. Piante Colt. Util., Fasc. 1: no. 21. 1888.
Cylindrosporium mori (Lév.) Berl., Riv. Patol. Veg., Pavia 5: 205. 1896.
Sphaerella mori Fuckel, Jahrb. Nassauischen Vereins Naturk. 23-24: 106. 1870 (1869–1870).
Mycosphaerella mori (Fuckel) F.A. Wolf, J. Elisha Mitchell Sci. Soc. 51: 165. 1935.
Sphaerella morifolia Pass., Erb. Critt. Ital., Ser. 2, Fasc. 30: no. 1464. 1885.
Mycosphaerella morifolia (Pass.) Cruchet, Bull. Soc. Vaud. Sci. Nat. 55: 43. 1923.
Sphaeria mori Nitschke, Fungi Rhen. Exs.: no. 1784. 1866.
Cercospora pulvinulata f. *angulosa* Savul. & Sandu, Herb. Mycol. Rom.: no. 188. 1931.

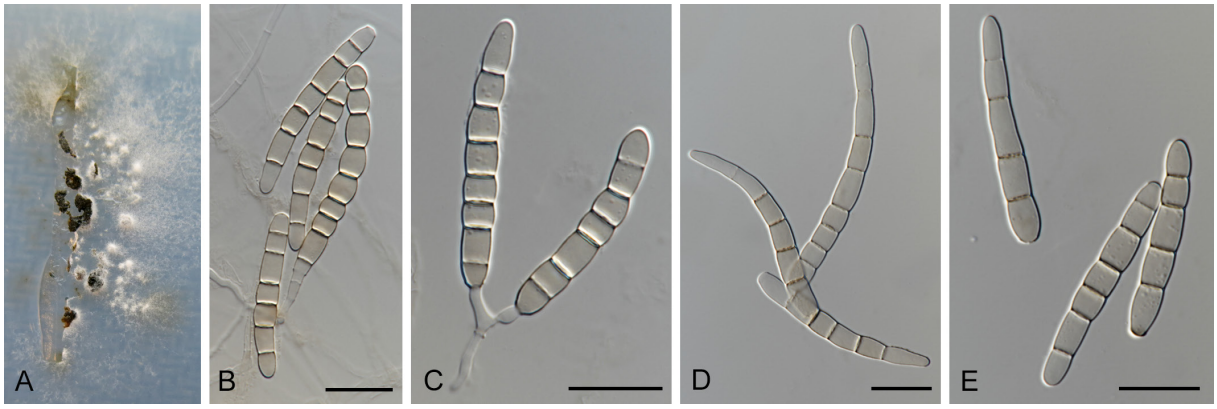


Fig. 29. *Neophloeospora maculans* (CBS 115123). A–E. Observations *in vitro*. F. Culture on SNA. B, C. Conidiophore and conidia. D, E. Conidia. Scale bars = 10 µm.

Description and illustration: Punithalingam (1990).

Description in vitro (on OA; CBS 115123): *Mycelium* hyaline to subhyaline, uniform in width, 2.5–3 µm diam. *Conidiophores* micronematous, hyaline, smooth, 5–10 × 1–2 µm. *Conidiogenous cells* terminal, indistinct. *Conidia* solitary, smooth, hyaline to pale brown, cylindrical to obclavate, subtruncate to truncate at the base, rounded to beak-like at the apex, straight to mildly sinuous, 38–70 × 3–5 µm, 3–10-euseptate, not or only slightly constricted at the septa, with age becoming darker, slightly verruculose, strongly constricted at the septa and wider (5–10 µm).

Material examined: **New Zealand**, Auckland, Mt. Albert, on *Morus alba*, isol. CF Hill (996), MAF, Mar. 2004, herbarium material U. Braun, Fungi Sel. Exs. 101, e.g. HAL, PDD 93510, culture CBS 115123.

Notes: This genus is introduced to accommodate the species *Phloeospora maculans* that is not congeneric with the type of *Phloeospora*, *Phloeospora ulmi*, and clusters in a single strain lineage in the phylogenetic analyses performed in this study (Fig. 1, clade 55; Fig. 2, clade 19). Morphologically, *Neophloeospora* can be distinguished from *Phloeospora* by the subhyaline to pale brown conidia constricted at the septum (Fig. 29). *Neophloeospora maculans* is a pathogen causing leaf spot on mulberry (*Morus alba*), a native tree to China that is commonly used to feed silkworms and is now cultivated worldwide for its berries (Punithalingam 1990, Hong *et al.* 2011). The ITS sequence generated here matches those of Hong *et al.* (2011).

Clade 56: *Dothistroma*

Dothistroma Hulbary, Bull. Illinois Nat. Hist. Surv. 21: 235. 1941.

Description (from Sutton 1980): *Mycelium* immersed, branched, septate, pale brown to hyaline. *Conidiomata* sometimes acervular, initially subepidermal later erumpent, composed of pale brown, thin-walled *textura angularis*, sometimes eustromatic, multilocular and of darker brown, thick-walled tissue. Dehiscence irregular, stromata strongly erumpent and finally pulvinate. *Conidiophores* absent. *Conidiogenous cells* holoblastic, discrete, determinate, ampulliform, hyaline, smooth, non-proliferating, formed from the upper cells of stroma or from inner cells of the locular walls. *Conidia* acrogenous, solitary, hyaline, straight or curved, filiform, 1–5-euseptate, continuous, thin-walled, smooth.

Type species: *Dothistroma pini* Hulbary.

Dothistroma pini Hulbary, Bull. Illinois Nat. Hist. Surv. 21: 235. 1941.

Descriptions and illustrations: Barnes *et al.* (2004, 2016).

Materials examined: **Russia**, Rostov oblast, Kamensky district, Kamensky timber enterprise, Kamenskoye forestry, 3 km to the east of Staraya Stanitsa village, pine planting, on *Pinus pallasiana*, 8 Oct. 2006, T.S. Bulgakov, culture CBS 121005 = CMW 24852. **USA**, Illinois, De Kalb County, on *P. nigra* subsp. *austriaca*, 29 Nov. 1938, J. Cedric Carter (**holotype** ILLS 27093, **isotype** CBS H-12211); Michigan, Massaukee County, McBain, Riverside Township,

on *Pinus nigra*, Aug. 2001, G. Adams, CBS H-12203, culture CBS 116483 = CMW 14905; Michigan, Montcalm County, Stanton, Evergreen Township, on *P. nigra*, 2001, G. Adams (**epitype** designated by Barnes *et al.* 2016, CBS H-12211, culture ex-epitype CBS 116487 = CMW 10951); *idem*., culture CBS 116486.

Notes: Dothistroma needle blight is one of the most important diseases of *Pinus* spp., both in natural forest ecosystems and particularly in plantations of non-native pines. The causal agent of the disease has been narrowed down to two species, *Dothistroma septosporum* (worldwide) and *Dothistroma pini* (USA) (Barnes *et al.* 2004, Groenewald *et al.* 2007). The type of *Dothistroma pini* was originaly isolated from *Pinus nigra* in the USA and an epitype has recently been designated (Barnes *et al.* 2016). *Dothistroma* clusters in a clade well-supported by all three phylogenetic methods employed in this study (Fig. 1, clade 56; Fig. 3, clade 20) and is closely related to *Stromatoseptoria*.

Dothistroma septosporum (Dorog.) M. Morelet, Bull. Soc. Sci. Nat. Archéol. Toulon & Var 177: 9. 1968.
Basionym: *Cytosporina septospora* Dorog., Bull. Bull. Trimestriel Soc. Mycol. France 27: 106. 1911.
Synonyms: *Septoriella septospora* (Dorog.) Sacc., Syll. Fung. 25: 480. 1931.
For additional synonyms see MycoBank.

Description and illustrations: Barnes *et al.* (2004, 2016).

Materials examined: **Brazil**, São Paulo, Santo Antonio do Pinhal, on needles of *Pinus pinaster*, 1974, T. Namekata, culture CBS 543.74. Ecuador, on needles of *Pinus radiata*, culture CBS 112498 = CPC 3779. **France**, Meurthe et Moselle, Arboretum d'Amance, on needles of *Pinus coulteri*, 27 Feb. 1970, culture CBS 383.74. **Netherlands**, Lunteren, Pinetum Dennenhorst, on needles of *Pinus mugo* 'Rostrata', 1 June 2009, W. Quaedvlieg, cultures CBS 128782 = CPC 16798, CBS 128783 = CPC 16799. **Russia**, St. Petersburg, Park Sosnovka, from *Pinus sylvestris*, 14 Nov. 2013, R. Drenkhan & D.L. Musolin (**neotype** designated by Barnes *et al.* 2016, CBS H-22299, culture ex-neotype CMW 44656 = CBS 140339 = TAAM 168554A). **Poland**, Miechów Forest District, Goszcza Forest Unit, on *Pinus nigra*, Jun. 2003, T. Kowalski, CBS H-12209, cultures CBS 116488 = CMW 13004, CMW 13010. **South Africa**, Tzaneen, on *P. radiata*, 2002, M.J. Wingfield, CBS H-12210, culture CBS 116489 = CMW 11372.

Notes: *Dothistroma septosporum* is one of the causal agents of Dothistroma needle blight (Red band disease of pine) and used to be listed as a species of quarantine importance to Europe (Quaedvlieg *et al.* 2012, EPPO 2012). This disease occurs wherever *Pinus* and *Larix* species are grown (Groenewald *et al.* 2007) and can cause varying degrees of damage depending on humidity and temperature (Evans 1984, Barnes *et al.* 2004). In the phylogenetic analyses, the strains clustered in a well supported clade (Fig. 1, clade 56; Fig. 3, clade 20). The herbarium material of the holotype was lost and a neotype was recently designated (Barnes *et al.* 2016).

Clade 57: *Hyalocercosporidium*

Hyalocercosporidium Videira & Crous, **gen. nov.** MycoBank MB822592.

Etymology: Similar to *Cercosporidium* but with hyaline conidia.

Description: Phytopathogenic. *Mycelium* internal, composed of hyaline to pale brown hyphae. *Conidiophores* solitary, simple, pale to brown, straight or mildly sinuous, geniculate. *Conidiogenous cells* terminal and intercalary, geniculate-sinuous, determinate or proliferating sympodially, monoblastic, with conidiogenous loci slightly thickened, darkened and refractive, located on the shoulders and apex. *Conidia* solitary, hyaline, smooth, obovoid, long-obclavate, straight or slightly curved, base obconical truncate or short obconical truncate, apex rounded, aseptate or euseptate, hila slightly thickened, darkened and refractive.

Type species: *Hyalocercosporidium desmodii* Videira & Crous.

Hyalocercosporidium desmodii Videira & Crous, **sp. nov.** MycoBank MB822712. Fig. 30.

Etymology: Named after the genus of the host it was isolated from, *Desmodium.*

Description in vitro (on MEA; CPC 19483): *Mycelium* composed of hyaline to pale brown hyphae, smooth to verruculose, septate, branching, 2–3.5 µm diam. *Conidiophores* pale brown, smooth to lightly verruculose, simple, straight or mildly sinuous, up to 3-geniculate, (52.5–)98–126(–167) × (2.5–)3(–4) µm. *Conidiogenous cells* integrated, terminal and intercalary, monoblastic, determinate or proliferating sympodially, monoblastic, with conidiogenous loci slightly thickened, darkened and refractive, 1.5 µm diam. *Conidia* solitary, hyaline, smooth, obovoid, cylindrical to long obclavate, truncate to long-obconically truncate at the base, rounded at the apex, (14.5–)24–30(–40) × (3–)4(–6) µm, aseptate to 3-septate, septa indistinct, hila slightly thickened, darkened and refractive, 1.5 µm diam.

Material examined: **Brazil**, Minas Gerais, Vale da Lua, Alto Paraiso de Goias, on *Desmodium tortuosum*, 2 Aug. 2009, R.W. Barreto (**holotype** CBS H-22949, ex-type culture CBS 142179 = CPC 19483).

Notes: Two *Passalora* species (*s. lat.*) are known from *Desmodium* in literature, namely *Passalora desmodii* and *Passalora atropunctata*. From these two species, only the last one has been previously reported from the host *Desmodium tortuosum* in Brazil (Crous & Braun 2003). *Passalora atropunctata* produces very pale brown and wider conidia (25–50 × 7–8 µm; Ellis 1976) compared with *Hyalocercosporidium desmodii*, and *Passalora desmodii* has multilocal conidiogenous cells with 1–5 minute apical to lateral conidiogenous loci which are unthickened or almost so, only somewhat darkened or refractive and in front view visible as a minute circle [based on comparision with North American material of *Passalora desmodii*, including Petr., Mycoth. Gen.1220, GZU (**lectotype** of *Cercospora desmodii* Ellis & Kellerm., designated here, MBT378579: **USA**, Kansas, Manhattan, on *Desmodium acuminatum*, 30 Jul. 1884, W.A. Kellerman 585, BPI 435642; **isolectotypes**, MU 10493, NY 270695); **syntypes**: CUP 39659 (only July), NY 838298 (1 July, Kellerman s.n., marked as "type"); **topotype** collections distributed as Ellis & Everh., N. Amer. Fungi 1501] (Chupp 1954). The original specimen of *Hyalocercosporidium desmodii* was, unfortunately, not available for morphological examination and a dried culture specimen was prepared. The representative ex-type strain of *Hyalocercosporidium desmodii* formed a single-strain lineage in the phylogenetic analyses (Fig. 1, clade 57; Fig. 3, clade 21) and is closely related to *Dothistroma* and *Stromatoseptoria*.

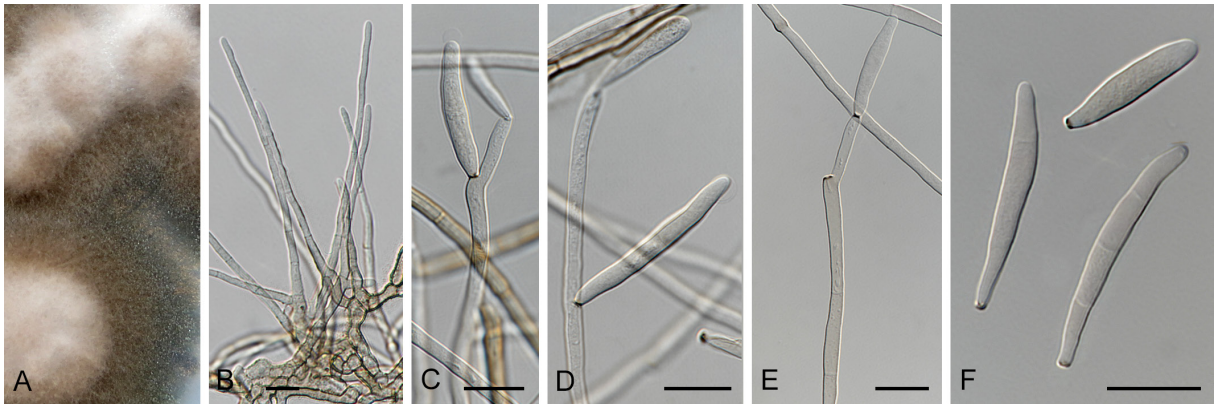


Fig. 30. *Hyalocercosporidium desmodii* (CPC 19483). A–F. Observations *in vitro*. A. Culture on OA. B. Mycelium. C–E. Partial conidiophore, conidiogenous cell and conidia. F. Conidia. Scale bars = 10 µm.

Morphologically, *Hyalocercosporidium desmodii* cannot be accommodated in *Dothistroma* or in *Stromatoseptoria*, since these genera have conidiogenous cells that proliferate percurrently and produce pigmented conidia (Quaedvlieg *et al.* 2013, Barnes *et al.* 2004).

Clade 58: *Stromatoseptoria*

Stromatoseptoria Quaedvlieg *et al.*, Stud. Mycol. 75: 353. 2013.

Description (from Quaedvlieg *et al.* 2013): Foliicolous, plant pathogenic. *Conidiomata* pycnidial, hypophyllous, subglobose to lenticular, very pale brown to dark brown, immersed to erumpent, exuding conidia in white cirrhus; ostiolum central, circular, surrounding cells concolorous; conidiomatal wall composed of a homogenous tissue of hyaline to very pale brown, angular to irregular cells. *Conidiophores* subcylindrical, branched, hyaline, septate. *Conidiogenous cells* hyaline, discrete or integrated, cylindrical or narrowly ampulliform, holoblastic, often also proliferating percurrently. *Conidia* solitary, cylindrical, slightly to distinctly curved, broadly rounded apex, attenuated towards a truncate base, transversely euseptate, mostly constricted at septa.

Type species: *Stromatoseptoria castaneicola* (Desm.) Quaedvlieg *et al.* (≡ *Septoria castaneicola* Desm.).

Stromatoseptoria castaneicola (Desm.) Quaedvlieg, Verkley & Crous, Stud. Mycol. 75: 353. 2013.
Basionym: *Septoria castaneicola* Desm., Ann. Sci. Nat., Bot., Sér. 3, 8: 26. 1847.

Description and illustration: Quaedvlieg *et al.* (2013).

Material examined: **France**, on leaves of *Castanea sativa*, Aug. and Sep. 1843, M. Roberge, 'Coll. Desmazières 1863, no. 8' (**holotype** PC 0084574). **Netherlands**, Utrecht, Baarn, near Lage Vuursche, on *Castanea sativa*, 29 Aug. 1999, G. Verkley, CBS H-21200, culture CBS 102322; Mook en Middelaar, St. Jansberg, on on *Castanea sativa*, 9 Sep. 1999, G. Verkley, No. 932, culture CBS 102377.

Notes: *Stromatoseptoria* is a monotypic genus that differs from *Septoria s. str.* by forming a stroma that gives rise to the conidiophores, by producing conidia that are olivaceous in mass and, although hyaline and smooth at first, become olivaceous and verruculose with age (Quaedvlieg *et al.* 2013). Phylogenetically, *Stromatoseptoria* clusters within the *Mycosphaerellaceae* in a clade well-supported by all three phylogenetic methods employed (Fig. 1, clade 58; Fig. 3, clade 22) and is closely related to *Dothistroma*.

Clade 59: *Fulvia*

Fulvia Cif., Atti Ist. Bot. Univ. Lab. Crittog. Pavia 10: 246. 1954.

Description (from Ellis 1971): *Colonies* effuse, velvety, buff to brown or purplish. *Stroma* present, pale, substomatal. *Conidiophores* macronematous, mononematous, caespitose, emerging through stomata, unbranched or occasionally branched, straight or flexuous, narrow at the base, thickening towards the apex, with unilateral nodose swellings which may proliferate as short lateral branchlets, very pale to mid pale brown or olivaceous brown, smooth. *Conidiogenous cells* mono- or polyblastic, integrated, terminal becoming intercalary, sympodial, clavate or cylindrical, cicatrized. *Conidia* catenate, chains frequently branched, acropleurogenous, simple, cylindrical with rounded ends or ellipsoidal, very pale to mid pale brown or olivaceous brown, smooth, 0–3-septate, hilum sometimes slightly protuberant.

Type species: *Fulvia fulva* (Cooke) Cif. (≡ *Cladosporium fulvum* Cooke).

Fulvia fulva (Cooke) Cif., Atti Ist. Bot. Univ. Lab. Crittog. Pavia 10: 245. 1954. Fig. 31.
Basionym: *Cladosporium fulvum* Cooke, Grevillea 12(61): 32. 1883.
Synonyms: *Mycovellosiella fulva* (Cooke) Arx, Proc. Kon. Ned. Akad. Wetensch., C86(1): 48. 1983.
Passalora fulva (Cooke) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. 1: 453. 2003.

Description and illustrations: Ellis (1971).

Description in vitro (on SNA; CPC 13652): *Mycelium* composed of hyaline to pale brown hyphae, uniform in width, 2 µm diam. *Conidiophores* arising from hyphae, pale brown, smooth to rough, micro- or macronematous, multi-septate, simple or short branched, straight or sinuous, often strongly curved at the tip, 20–160 µm × 2.5–10 µm, variable in width, sometimes reduced to conidiogenous cell. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, polyblastic, with rim-like conidiogenous loci that are darkened and thickened, 1–2.5 µm. *Conidia* catenate, often forming branched chains, ovoid, obovoid, ellipsoidal, sphaerical, cylindrical, straight or strongly curved, 10–30 × 5–10 µm, 1–4-septate, hila thickened and darkened, 1–2.5 µm diam.

Materials examined: **Cuba**, on leaves of *Solanum lycopersicum*, 2006, B. Summerell (**epitype** designated here: CBS H-22950, MBT378581, culture ex-epitype CBS 142314 = CPC 13652). **Netherlands**, unknown host, and collector, 1946, isol. CBS Practicum, culture CBS 119.46. **Switzerland**, fruit of *S. lycopersicum*, unknown collector, dep. L. Zobrist, 1946, culture CBS 120.46 = VKM F-3053. **USA**, South Carolina, Aiken, on *S. lycopersicum*, H.W. Ravenel, Fungi

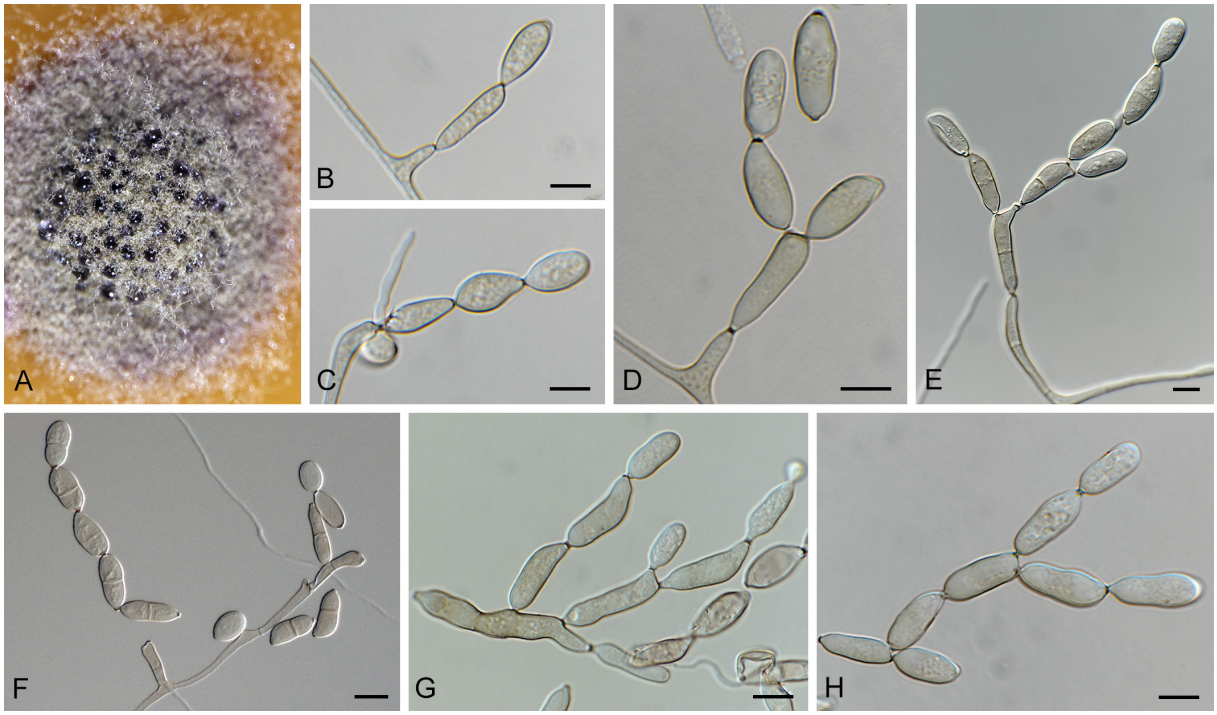


Fig. 31. *Fulvia fulva* (CPC 13652). A–H. Observations *in vitro*. A. Culture on V8. B, D. Conidiophore reduced to conidiogenous cell and catenate conidia. C. Conidiogenous cell and catenate conidia. E, F. Conidiophore and catenate conidia. G, H. Catenate conidia. Scale bars = 10 µm.

Amer. Exs. 599 (**lectotype**, designated here: BPI 426698, MBT378580; isolectotypes, Ravenel, Fungi Amer. Exs. 599, e.g. B, CUP, K, NEB).

Notes: The genus *Fulvia* is no longer considered a synonym of *Passalora* as a result of analysis of the type species, *Fulvia fulva* (≡ *Cladosporium fulvum* ≡ *Passalora fulva*), which was recollected and epitypified in this study. *Fulvia fulva* clusters close to *Stromatoseptoria* in the phylogenetic analyses (Fig. 1, clade 59; Fig. 3, clade 23). The single-gene trees indicate that both LSU and ITS are able to distinguish this species but *rpb2* is more reliable. *Fulvia fulva* is the causal agent of tomato leaf mould, a disease that affects mostly the leaves of tomato but occasionally also stems, blossoms, petioles and fruit (Butler & Jones 1949, de Wit 1977, 1992, Jones *et al.* 1997). The interaction between *Fulvia fulva* and tomato is governed by a gene-for-gene relationship, a characteristic that made this organism an interesting model to study plant-pathogen interactions (Wit 1981, 1992). The resistance of tomato against *Fulvia fulva* was genetically determined by the presence of *Cf* (*Cladosporium fulvum*) resistance genes of which now five have been cloned. Cf proteins mediate the recognition of effector proteins secreted by *Fulvia fulva* of which all encoding genes have been cloned (Wit 2016). *Fulvia fulva* was once a devastating pathogen of tomato that required treatment with agrochemicals, but since various *Cf* genes from different wild *Solanum* species were introduced in commercial tomato cultivars by breeders the pathogen is now under control. Commercially grown tomato cultivars contain up to five different *Cf* genes (*Cf-2*, *Cf-4*, *Cf-4E*, *Cf-5* or *Cf-9*) (Thomma *et al.* 2005).

Clade 60: *Ragnhildiana*

Ragnhildiana Solheim, Mycologia 23: 402. 1931.

Description: Hyphomycetous, phytopathogenic. *Mycelium* internal and external, composed of hyaline to pigmented hyphae, branched, septate. *Stromata* lacking or developed, composed of brown pseudoparenchymatal cells. *Conidiophores* formed in fascicles, sometimes coremioid, emerging through stomata, through the epidermis, or single and arising from external hyphae, olivaceous to brown, septate, simple or branched, straight or geniculate-flexuous, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, mono- or polyblastic, with conidiogenous loci somewhat thickened and darkened. *Conidia* solitary or catenate, chains simple or branched, subhyaline to brown, ellipsoid-ovoid, subcylindrical-fusoid, or obclavate, aseptate to multi-septate, hila somewhat thickened and darkened.

Type species: *Ragnhildiana agerati* (F. Stevens) F. Stevens & Solheim (≡ *Cercospora agerati* F. Stevens) = *Ragnhildiana perfoliati* (Ellis & Everh.) U. Braun, C. Nakash., Videira & Crous

Ragnhildiana ampelopsidis (Peck) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822787. Fig. 32.
Basionym: *Cercospora ampelopsidis* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 30: 55. 1877.
Synonyms: *Passalora ampelopsidis* (Peck) U. Braun, Trudy Bot. Inst. im. V.L. Komarova 20: 38. 1997.
Cercospora pustula Cooke, Grevillea 12: 30. 1883.
Cercospora psedericola Tehon, Mycologia 16: 139. 1924.
Descriptions and illustrations: Chupp (1954), Braun & Mel'nik (1997).

Description in vitro (on V8; CBS 249.67): *Mycelium* composed of hyaline to pale brown hyphae, smooth to verruculose, uniform in width, 1.5–2.5 µm. *Conidiophores* micro- or macronematous, pale olivaceous brown, smooth to verruculose, simple or branched, strongly geniculated at the apex, 70–160 × 2.5–4 µm. *Conidiogenous cells* terminal, subhyaline to pale olivaceous brown, smooth, strongly geniculated at the apex, proliferating sympodially, polyblastic, with conidiogenous loci thickened, darkened and protruding, 2 µm diam. *Conidia* solitary or catenate, in simple or branching chains, subhyaline to pale olivaceous brown, smooth, obovoid, clavate to obclavate, cylindrical, straight or slightly curved, (16–)27–33(–48) × (2.5–)3(–4) µm, 1–4-euseptate, hila thickened, darkened and protruding, 1.5–2 µm diam.

Materials examined: **Romania**, Simeria, on *Parthenocissus tricuspidata*, 6 May 1965, unkown collector, isol. O. Constantinescu, culture CBS 249.67 = IMI 124968. **USA**, New York, Albany, Bethlehem, on *Ampelopsis quinquefolia*, July, C.H. Peck (**holotype** NYS-F-000244).

Notes: Braun & Melnik (1997) examined the holotype specimen of *Cercospora ampelopsidis*, and noted that the conidiophores can occasionally form synnema-like fascicles [20–130 × 3.5–5(–7) µm], and the conidia are formed singly [(20–)30–60(–140) × 4–8 µm]. In culture (CBS 249.67), synnema-like conidiophores were not observed and conidia were catenate and smaller (Fig. 32). Phylogenetically, *Ragnhildiana ampelopsidis* clusters in the *Ragnhildiana* clade (Fig. 1, clade 60; Fig. 3, clade 24) as a single-strain lineage.

Fig. 32. *Ragnhildiana ampelopsidis* (CBS 249.67). A–E. Observations *in vitro*. A. Culture on V8. B. Partial conidiophore, conidiogenous cell and catenate conidia. C. Conidiogenous cell and conidia. D, E. Catenate conidia. Scale bars = 10 µm.

Ragnhildiana diffusa (Heald & F.A. Wolf) Videira & Crous, **comb. nov.** MycoBank MB822788.
Basionym: *Clasterosporium diffusum* Heald & F.A. Wolf, Mycologia 3: 21. 1911.
Synonym: *Cercospora fusca* F.V. Rand, J. Agric. Res. 1: 318. 1914, nom. nov., non *C. diffusa* Ellis & Everh., 1888.
Sirosporium diffusum (Heald & F.A. Wolf) Deighton, in Ellis, More Dematiaceous Hyphomycetes: 299. 1976.

Descriptions and illustrations: Chupp (1954), Ellis (1976), Poletto *et al.* (2017).

Material examined: **USA**, Georgia, Baconton, on *Carya illlinoinensis*, 29 Aug. 1911, dep. F.V. Rand, culture CBS 106.14; Texas, Gonzales, on *Carya illinoinensis*, 10 Sep. 1909, F.D. Heald & F.F. Wolf 2695 (**holotype** of *Clasterosporium diffusum* [≡ *Cercospora fusca*], BPI 436535; isotypes CUP 3946, NEB 47510).

Notes: This pathogen is reported to cause reddish brown angular to round spots on leaves of *Carya* spp. in Cuba, Malawi, Mexico, Mozambique, South Africa, USA, and Venezuela (Ellis 1976, Crous & Braun 2003). It has recently been reported from Brazil (Poletto *et al.* 2017) where it was freshly collected from the same host and examined morphologically and genetically. Both the ITS and *tef1*-α sequences were identical to the respective sequences of *Sirosporium diffusum* (CBS 106.14). This culture is an authentic representative of *Cercospora fusca*, isolated in pure culture by F.V. Rand, on 29 Aug. 1911, from *Carya illinoinensis* in Baconton, Georgia, USA (Rand 1914). Although this isolate was never observed sporulating in culture, the specimen it was isolated from was compared to the type of *Clasterosporium diffusum* (basionym to the current name *Ragnhildiana diffusa*) and considered identical (Rand 1914). Morphologically, the description based on the Brazilian isolate fits well with the published description. Phylogenetically, this strain clusters among *Ragnhildiana* isolates (Fig. 1, clade 60; Fig. 3, clade 24) that produce catenate conidia, while *Sirosporium diffusum* produces solitary conidia that are very long and sometimes slightly constricted at the septa. The phylogenetic position of the type species of *Sirosporium*, *Sirosporium antenniforme*, is still undetermined (see section Genera of the *Mycosphaerellaceae* below).

Ragnhildiana ferruginea (Fuckel) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822791. Fig. 33.
Basionym: *Cercospora ferruginea* Fuckel, Hedwigia 2(15): 134. 1863 and Fuckel, Fungi Rhen. Exs., Fasc. II: no. 120. 1863.
Synonyms: *Mycovellosiella ferruginea* (Fuckel) Deighton, Mycol. Pap. 144: 14. 1979.
Passalora ferruginea (Fuckel) U. Braun & Crous, CBS Biodiversity Ser.: 183. 2003.
Cercospora olivacea G.H. Otth, Mitth. Naturf. Ges. Bern 654-683 (1868): 65. 1869.
Helminthosporium absinthii Peck, Rep. (Annual) New York State Mus. Nat. Hist. 30: 54. 1878.
Cercospora absinthii (Peck) Sacc., Syll. Fung. 4: 444. 1886.
Ramularia absinthii Laubert, Centralbl. Bacteriol., 2. Abt., 52: 242. 1920.
Cercosporidium artemisiae Sawada, Rep. Gov. Agric. Res. Inst. Taiwan 86: 164. 1943 (*nom. inval*.).

Descriptions and illustrations: Deighton (1979), Shin & Kim (2001).

Description in vitro (on V8; CBS 546.71): *Mycelium* composed of hyaline to brown hyphae, smooth to rough, uniform in width, 2–3 µm. *Conidiophores* micro- or macronematous, pale brown to brown, smooth to faintly verruculose, simple or branched, straight to sinuous, sometimes geniculate-sinuous at the apex, 5–200 × 2.5–5 µm. *Conidiogenous cells* terminal

Fig. 33. *Ragnhildiana ferruginea* (CPC 10075). A–F. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Conidiophores. D, E. Partial conidiophore, conidiogenous cell and conidium. F. Conidia. G–K. Observations *in vitro*. G. Culture on V8. H, I. Conidiophore, conidiogenous cell and conidia. J. Partial conidiogenous cell with single and catenate conidia. K. Single conidia. Scale bars = 10 µm.

or intercalary, subhyaline to brown, smooth, geniculate to geniculate-sinuous, proliferating sympodially, polyblastic, with conidiogenous loci thickened, darkened and protruding, 1.5–2 µm diam. *Conidia* solitary, ocasionally catenate in simple chains, subhyaline to brown, smooth, obovoid, long-obclavate, cylindrical, base long-obconically truncate, apex rounded, straight to mildly curved, 20–75 × 2.5–5 µm, 0–5-euseptate, hila thickened, darkened and protruding, 1.5–2 µm diam.

Materials examined: **Germany**, Altersand vs. Hostrichiam (Nassau, Oestrich), on *Artemisia vulgaris*, 1863, Fuckel, Fungi Rhen. Exs. 120 (**lectotype**, designated here, MBT378582, HAL; isolectotypes, Fuckel, Fungi Rhen. Exs. 120, e.g. BPI 436287, F-C0003573F, FH-01012187, G, S F199142, 267462). **Romania**, Bucuresti, on *Artemisia vulgaris*, unknown collector, isol. O. Constantinescu, 6 Apr. 1965, CBS H-9838, culture CBS 255.67 = IMI 124973; unknown host and collector, isol. O. Constantinescu, 20 Jul. 1970, CBS H-9839, culture CBS 546.71. **Republic of Korea**, Pochon, on *Artemisia sylvatica*, 23 Oct. 2002, H.D. Shin, cultures CPC 10014, CPC 10075.

Notes: *Ragnhildiana ferruginea* has a worldwide distribution on hosts from the genera *Ambrosia* and *Artemisia* (*Asteraceae*) (Crous & Braun 2003). It produces mostly single conidia and only rarely catenate conidia in short unbranched chains (Fig. 33) (Shin & Kim 2001). Based on the phylogenetic analyses, *Ragnhildiana ferruginea* clusters among *Ragnhildiana* species (Fig. 1, clade 60; Fig. 3, clade 24) in a well-supported clade. Based on a BLAST comparison against the alignment, *Ragnhildiana ferruginea* CBS 546.71 shared 93 % (441/474) similarity based on ITS and 90 % (674/750) similarity based on *rpb2* with *Ragnhildiana ampelopsidis* CBS 249.67. In addition, it shared only 85 % (664/780) similarity with *Ragnhildiana perfoliati* CBS 125419 based on *rpb2*.

Ragnhildiana gnaphaliacea (Cooke) Videira, H.D. Shin, C. Nakash. & Crous, **comb. nov.** MB822795. Fig. 34.
Basionym: *Cercospora gnaphaliacea* Cooke, J. Linn. Soc., Bot. 17: 142. 1880.
Synonyms: *Phaeoisariopsis gnaphaliacea* (Cooke) Morgan-Jones, Canad. J. Bot. 52: 2635. 1974.
Passalora gnaphaliacea (Cooke) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser.: 201. 2003.
Cercospora gnaphalii Harkn., Bull. Calif. Acad. Sci. Bull. 1: 38. 1884.

Description in vivo (CBS H-22952): *Leaf spots* yellowish to brownish, without definite margin, subcircular to irregular, 3–20 mm. *Mycelium* internal and external, composed of pale brown to brown hyphae that are septate and smooth to verruculose. *Stromata* hypophyllous epidermal, submerged, stomatal or erumpent from epidermal cells, small composed of few brown cells to well-developed, pale to dark brown, up to 180 µm diam. *Conidiophores* solitary to densely fasciculate, emerging from stromata, brown to pale brown, paler towards apex, smooth to verruculose, straight to sinuous-geniculate, simple or branched, 46–75(–240) × 4–6.5 µm. *Conidiogenous cells* terminal and intercalary, polyblastic, proliferating sympodially, with rim-like conidiogenous loci, thickened and darkened, 2–2.5 µm diam. *Conidia* solitary or rarely catenate, hyaline to pale olivaceous brown, obovoid, cylindrical, straight or mildly curved, base obconicaly truncate, apex rounded, 18–70 × 6–10 µm, 0–4-euseptate, occasionally constricted at the septa, hila thickened and darkened.

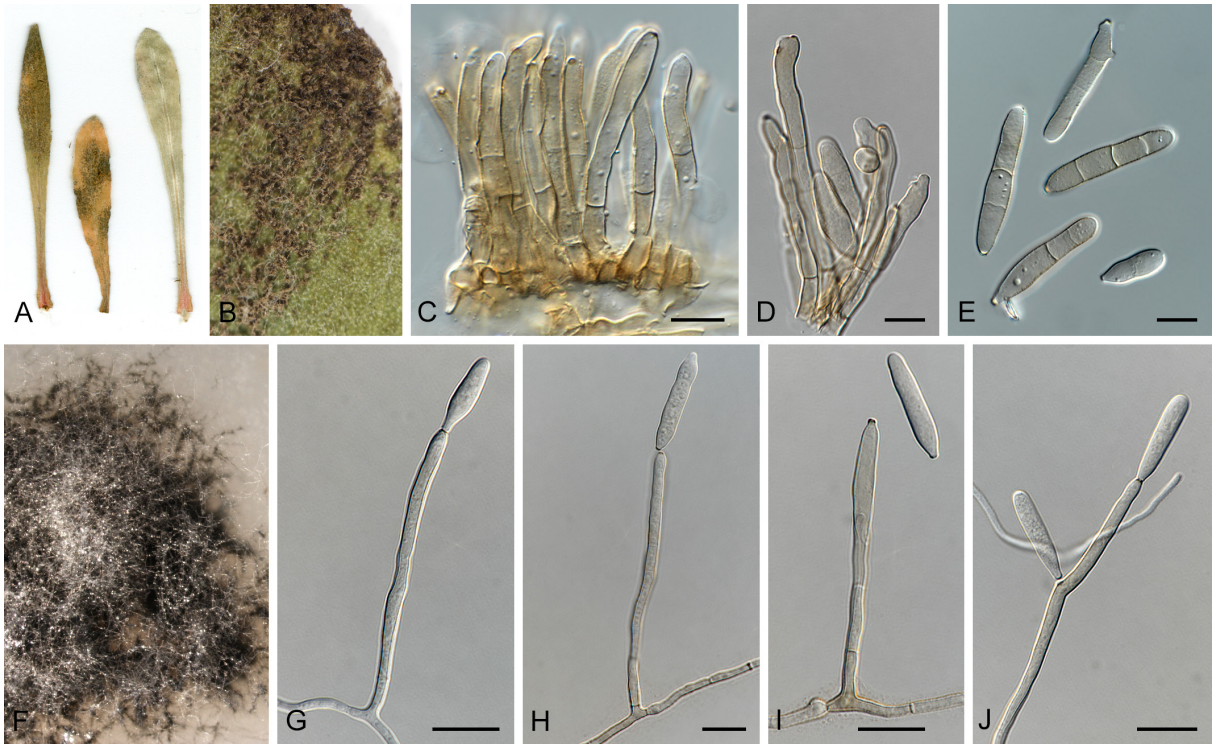


Fig. 34. *Ragnhildiana gnaphaliacea* (CPC 12517). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Conidiophores. D. Conidiophores, conidiogenous cells and conidia. E. Catenate conidia and single conidia. F–J. Observations *in vitro*. F. Culture on OA. G–I. Conidiophore, conidiogenous cell and conidia. J. Partial conidiophore, conidiogenous cell and conidia. Scale bars = 10 µm.

Description in vitro (on SNA; CPC 12517): *Mycelium* hyaline to olivaceous brown, smooth to verruculose. *Conidiophores* macronematous, hyaline to pale brown, simple, septate, cylindrical, straight to slightly curved, 30–88 × 2.5–3 µm. *Conidiogenous cells* integrated, terminal or intercalary, monoblastic, cylindrical, conically truncate at the apex or geniculate-sinuous, determinate or proliferating sympodially, with conidiogenous locus thickened and darkened, located on the shoulder or at the apex, 1.5–2.5 µm diam. *Conidia* solitary, hyaline to pale brown, smooth to verruculose, long-obovoid, cylindrical to long-obclavate, base obconically truncate, apex rounded, straight to slightly curved, 20–75 × 2.5–5 µm, 0–5-euseptate, sometimes mildly constricted at septa, hila thickened and darkened, 1.5–2.5 µm diam.

Materials examined: **Republic of Korea**, Jeju, on *Gnaphalium affine*, May 2005, H.D. Shin, CBS H-22952, culture CBS 142181 = CPC 12517; *idem*., cultures CPC 10882, CPC 10883. **USA**, Texas, Houston, *Gnaphalium* sp., 17 Apr. 1869, H.W. Ravenel 283 (**lectotype** designated here BPI 436721, MycoBank MBT378599).

Notes: This is the first report of *Ragnhildiana gnaphaliacea* in Korea (based on Crous & Braun 2003, Shin & Kim 2001 and https://nt.ars-grin.gov/fungaldatabases/). Morphologically, the observed isolate description *in vivo* varies slightly from the one available in literature by producing longer conidiophores (60–90 × 4–5 µm; Morgan-Jones 1974) and shorter conidia [40–65 × 4–5 µm, (2–)3(–5)-septate; Morgan-Jones 1974] (Fig. 34). Phylogenetically, it clusters in the *Ragnhildiana* clade (Fig. 1, clade 60; Fig. 3, clade 24).

Ragnhildiana perfoliati (Ellis & Everh.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822824.
Basionym: *Cercospora perfoliati* Ellis & Everh., J. Mycol. 5: 71. 1889.
Synonyms: *Cercospora agerati* F. Stevens, Bull. Bern. Bishop Mus. 19: 154. 1925.
Ragnhildiana agerati (F. Stevens) F. Stevens & Solheim, Mycologia 23: 402. 1931.
Cercospora assamensis S. Chowdhury, Lloydia 20(2): 134. 1957.
Passalora perfoliati (Ellis & Everh.) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. 1: 314. 2003.
Passalora assamensis (S. Chowdhury) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser. 1: 69. 2003.
Passalora ageratinae Crous & A.R. Wood, Stud. Mycol. 64: 34. 2009.

Description and illustrations: Crous *et al.* (2009c).

Description in vitro (on V8; CBS 125419): *Mycelium* hyaline to brown, smooth, uniform in width, 2.5–3 µm diam. *Conidiophores* micro- to macronematous, cylindrical, subhyaline to brown, smooth, uniform in width, straight to slightly curved, simple, 25–150 × 2.5–5 µm. *Conidiogenous cells* integrated, apical, mostly monoblastic but sometimes polyblastic, usually determinate but occasionally proliferating sympodially, conically truncate at the apex, with conidiogenous loci slightly but clearly thickened loci at the apex, 2–2.5 µm diam. *Conidia* catenate, in simple chains, rarely in branched chains, hyaline to brown, smooth to verruculose, variable in shape, long-obovoid, cylindrical to long-obclavate, straight to curved, base and apex short- to medium-obconically truncate in intermediate conidia, apex rounded in terminal conidia, 20–80 × 2.5–5 µm, 0–5-euseptate, occasionally constricted at septa, hila thickened, darkened and refractive, 2–2.5 µm diam. Strain CPC 15366 on V8 agar produces *conidiophores* that often form synnematous fascicles and are longer, 10–300 × 2.2–6 µm. Strain CPC 17321 on V8 agar produces conidiophores that are finely verruculose, longer and wider, 20–275 × 2.5–7.5 µm, and wider conidia 26–70 × 3–7.5 µm.

Materials examined: **Guatemala**, on *Ageratina adenophora*, unknown date, M.J. Morris, MJM 1506, dep. A. den Breeÿen, culture CBS 113613 = MJM 1506 = C486. **Laos**, Luang Prabang, on *Chromolaena odorata*, 17 Jun. 2006, P. Pheng, NOUL P101, culture CBS 142180 = CPC 17321. **New Zealand**, Cmoromandel, Thames, on *Ageratina adenophora*, unknown collector and date, isol. CF Hill, MAFF, Auckland, Feb. 2004, culture CBS 115119. **South Africa**, KwaZulu-Natal Province, Hilton, on leaves of *Ageratina adenophora*, 28 May 2008, A.R. Wood (**holotype** of *Passalora ageratinae* CBS H-20336, ex-type culture CBS 125419 = CPC 15365); *idem*. CPC 15366, CPC 15367.

Notes: *Ragnhildiana* was reduced to synonymy with *Mycovellosiella* by Muntañola (1960), and later both genera were placed in synonymy with *Passalora* by Crous & Braun (2003). With the recollection of the type species of *Passalora*, *Passalora bacilligera*, these three genera were found to be phylogenetically distinct, and hence the name *Ragnhildiana* is resurrected for this clade of passalora-like fungi. The type of *Ragnhildiana*, *Ragnhildiana agerati* was described from *Ageratum conyzoides* in Hawaii (**syntype**: ILL00010589, **lectotype**: ILL00010590). *Passalora ageratinae* was described from the host *Ageratina adenophora* from Mexico, and was transported into Hawaii, Australia and South Africa in association with a stem galling fly that was introduced as biocontrol agent for the invasive weed *Ageratina adenophora* (Dodd

1961, Morris 1989, Wang *et al.* 1997, Zhu *et al.* 2007, Muniappan *et al.* 2009). *Passalora ageratinae*, is similar to "*Passalora*" *assamensis*, except for the amphigenous nature of the colonies, the absence of external mycelium and the production of shorter conidiophores. Type material of "*Passalora*" *assamensis* was not available for re-examination but other specimens from the same location and host (India, Nepal, *Ageratina adenophora*) were examined and found to be compatible with the description (Crous & Braun 2003). Based on the phylogenetic analyses, the available strains cluster together in a clade that has a well supported basal branch (Fig. 3, clade 24) and is included in the *Ragnhildiana* clade (Fig. 1, clade 60). In addition, using a BLAST comparison against the alignment, "*Passalora*" *assamensis* CBS 115119 shares 99 % (469/475) similarity on ITS and 99 % (656/657) similarity on *rpb2* with "*Passalora*" *ageratinae* CBS 125419. The morphological description of "*Passalora*" *perfoliati* is also similar to that of "*Passalora*" *ageratinae* and, based on a BLAST comparison against the alignment, "*Passalora*" *perfoliati* CPC 17321 shares 99 % (468/475) similarity on ITS and 100 % (780/780) similarity on *rpb2* with "*Passalora*" *ageratinae* CBS 125419. Therefore, we consider them all to be synonyms.

Ragnhildiana pseudotithoniae (Crous & Cheew.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822797.
Basionym: *Passalora pseudotithoniae* Crous & Cheew., Persoonia 31: 261. 2013.

Description and illustration: Crous *et al.* (2013b).

Description (from Crous *et al.* 2013b): *Leaf spots* amphigenous, brown, angular, confined by leaf veins, 2–5 mm diam. *Conidiophores* amphigenous, fasciculate, 40–100 µm tall, 3–4 µm wide, straight to geniculate-sinuous, mostly unbranched, subcylindrical, 1–3-septate, brown, smooth to finely verruculose, arising from a weakly developed brown stroma, up to 50 µm wide and 60 µm tall. *Conidiogenous cells* integrated, brown, smooth to finely verruculose, terminal, subcylindrical to once geniculate, 15–35 × 3–4.5 µm, with thickened and darkened loci, 2 µm diam, mostly solitary and terminal, but also lateral on conidiogenous cells. *Conidia* occurring in long branched chains, brown, granular, smooth, subcylindrical to narrowly obclavate, (30–)40–65(–130) × (4–)5(–5.5) µm, 1–6-septate, apex obtuse to truncate, base obconically truncate, thickened and darkened, 2 µm diam.

Materials examined: **Thailand**, N18°09024.800 E98°23019.600, Royal Project, on leaves of *Tithonia diversifolia* (*Asteraceae*), 5 Nov. 2012, P.W. Crous (**holotype** CBS H-21453, ex-type culture CBS 136442 = CPC 21688).

Notes: Phylogenetically, *Ragnhildiana pseudotithonia* clusters in the *Ragnhildiana* clade (Fig. 1, clade 60; Fig. 3, clade 24) in a single-strain lineage. One other species has been recently described from the same host but originary from Brazil, *Passalora stromatica* (Fernandes *et al.* 2013). Based on a BLAST comparison against the alignment, the ITS sequence of *Passalora stromatica* GenBank KF275128 was closest to *Ragnhildiana pseudotithonia* CBS 136442, with which it shared 96 % (467/484) similarity, including 2 % (10/484) gaps. Based on the morphological and DNA differences, these are not the same species.

Clade 61: *Phaeoramularia*

Phaeoramularia Munt.-Cvetk., Lilloa 30: 182. 1960.

Description (from Braun 1998): Phytopathogenic, usually forming leaf spots, occasionally almost symptomless. *Mycelium* internal, composed of subhyaline to pigmented hyphae, septate, branched, smooth to rough. *Stromata* almost absent to well-developed, pigmented. *Conidiophores* macronematous, mononematous, in small to large fascicles, rarely solitary, arising from internal hyphae or stromata, emerging through stomata or erumpent through the cuticle, erect, straight, subcylindrical to flexuous, geniculate-sinuous, simple, rarely branched, continuous to septate, pale yellowish green, olivaceous to brown, smooth to rough, thin-walled. *Conidiogenous cells* integrated, terminal, occasionally intercalary, sometimes conidiophores reduced to a single conidiogenous cell, polyblastic, proliferation sympodial, rarely percurrent, conidiogenous loci thickened and darkened. *Conidia* catenate, sometimes in branched chains, ellipsoid-ovoid, subcylindrical, fusiform, continuous to euseptate, subhyaline to pigmented, smooth to rough, ends obtuse, truncate or subacute; hila thickened and darkened; conidial secession schizolytic.

Type species: *Phaeoramularia gomphrenicola* (Speg.) Munt.-Cvetk. (≡ *Cercospora gomphrenicola* Speg.).

Phaeoramularia capsicicola (Vassiljevsky) Deighton, More Dematiaceous Hyphomycetes: 323. 1976.
Basionym: *Cercospora capsicicola* Vassiljevsky, Fungi imperfecti Parasitici. I. Hyphomycetes: 344. 1937.
Synonyms: *Cercospora capsici* E.J. Marchal & Steyaert, Bull. Soc. Roy. Bot. Belgique 61: 167. 1929.
Cladosporium capsici Kovatsch., Z. Pflanzenkrankh. Pflanzenschutz 48(7): 335. 1938.
Cercospora unamunoi Castell., Rivista Agric. Subtrop. Trop. 42: 20. 1948.
Passalora capsicicola (Vassiljevsky) U. Braun & F.O. Freire, Cryptog. Mycol. 23: 299. 2002.
For additional synonyms see Crous & Braun (2003).

Descriptions and illustrations: Kovachevsky (1939), Muntañola (1954), Ellis (1976), Deighton (1976b).

Materials examined: **Italy**, on *Capsicum annuum*, unknown collector and date, dep. A. Matta, 1962, culture CBS 156.62. **Jamaica**, on *Chromolaena odorata*, 2006?, coll. M.J. Morris, dep. A. den Breeÿen, culture CBS 113384 = C499. **USA**, on *C. odorata*, 2006?, coll. M.J. Morris, dep. A. den Breeÿen, culture CBS 113382 = C460.

Notes: In August 2011, the occurrence of *Passalora capsicicola*, the causal agent of a foliar disease on sweet pepper, was reported for the first time in Austria but unfortunately no DNA was extracted (Bedlan *et al.* 2012). The species *Passalora capsicicola* is reported to infect hosts of *Capsicum* sp. (*Solanaceae*) in tropical and subtropical countries including the USA, Brazil, Romania, Tanzania, China and many others (Crous & Braun 2003). The strains CBS 113384 and CBS 113382 were not described due to the cultures being sterile and the herbarium specimens not being preserved (Breeÿen *et al.* 2006). There is no previous report of *Passalora*

capsicicola being isolated from the host *Chromolaena odorata* (*Asteraceae*) (Farr & Rossman, retrieved June 22, 2017, from https://nt.ars-grin.gov/fungaldatabases/). The strain CBS 156.62, identified as *Passalora capsicicola*, was also sterile in culture and the herbarium specimen could not be traced. Based on the phylogenetic analysis, *Passalora capsicicola* clusters in the *Phaeoramularia* clade (Fig. 1, clade 61; Fig. 3, clade 25) in a well supported clade. In addition, based on a BLAST comparison against the alignment, CBS 148.38 shared 99 % (465/472) similarity on ITS and 92 % (587/639) similarity on *rpb2* with *Phaeoramularia gomphrenicola* CPC 23248.

Phaeoramularia gomphrenicola (Speg.) Munt.-Cvetk., Lilloa 30: 209. 1960. Fig. 35.
Basionym: *Cercospora gomphrenicola* Speg., An. Soc. Cient. Argent. 13(1): 29. 1882.

Description in vivo (CBS H-22954): *Mycelium* internal, composed of hyaline to pale brown hyphae, smooth to finely verruculose. *Stromata* hypophyllous, epidermal, stomatal, brown to reddish brown, small to well-developed, 20–50 µm diam. *Conidiophores* emerging from upper part of stromata in dense fascicles, pale brown to brown, smooth to finely verruculose, straight to sinuous, simple or occasionally branched, 25–125(–200) × 5–7.5 µm. *Conidiogenous cells* integrated, terminal or intercalary, pale brown, smooth to finely verruculose, mono- or polyblastic, proliferating sympodially, with rim-like conidiogenous loci that are thickened and darkened, 2–2.5 µm diam. *Conidia* catenate, in simple or branched chains, with microcyclic conidiation, pale brown, smooth to finely verruculose, obclavate to cylindrical, base obconically truncate, apex conically truncated in intercalary conidia and rounded in terminal conidia, 20–75 × 5–7.5 µm, (0–)1–3(–4)-septate, hila thickened and darkened, 2–2.5 µm diam.

Description in vitro (on V8; CPC 23248): *Mycelium* composed of hyaline to olivaceous brown hyphae, smooth to finely verruculose, often constricted at septa, irregular in width, 2.5–7.5 µm. *Conidiophores* micro- or macronematous, pale brown to pale olivaceous brown, smooth to finely verruculose, constricted at septa, simple or branched, straight or mildly sinuous, 50–250 × 2.5–7.5 µm. *Conidiogenous cells* integrated, terminal or intercalary, smooth to finely verruculose, mono- or polyblastic, proliferating sympodially, conically truncate at the apex or geniculate-sinuous, with rim-like conidiogenous loci that are slightly thickened and darkened, 2–2.5 µm diam. *Conidia* catenate in simple chains, rarely in branched chains, pale to pale olivaceous brown, smooth to finely verruculose, obovate, allantoid, cylindrical, base obconically truncate, apex conically truncate in intermediate conidia and rounded in terminal conidia, irregular in width, 18–125 × 3.5–5 µm, 0–4-septate, occasionally constricted at septa, hila slightly thickened and darkened, 2–2.5 µm diam.

Materials examined: **Argentina**, Buenos Aires, Palermo, on *Pfaffia glomerata* (as *Gomphrena glauca*), Feb. 1881, C. Spegazzini (**holotype** LPS 914; isotypes Speg., Hongos Sud-Amer., Dec. Mycol. Argent. 45, e.g. BPI 436740, 722393, FH, PAD, PDD 25866; IMI 7706, slide ex holotype). **Brazil**, Minas Gerais, Viçosa, on *P. glomerata*, 29 Oct. 2012, R.W. Barreto (**epitype** designated here: CBS H-22954, MBT378603, ex-epitype culture CBS 142182 = CPC 23248 = COAD570); *idem*., culture CPC 23249 = COAD571.

Notes: *Phaeoramularia* resembles *Ramularia* by producing catenate conidia but differs by producing pigmented conidiophores and conidia (Braun 1998). In addition, the conidiogenous loci are thickened and rim-like and not coronate. This genus is no longer considered a synonym

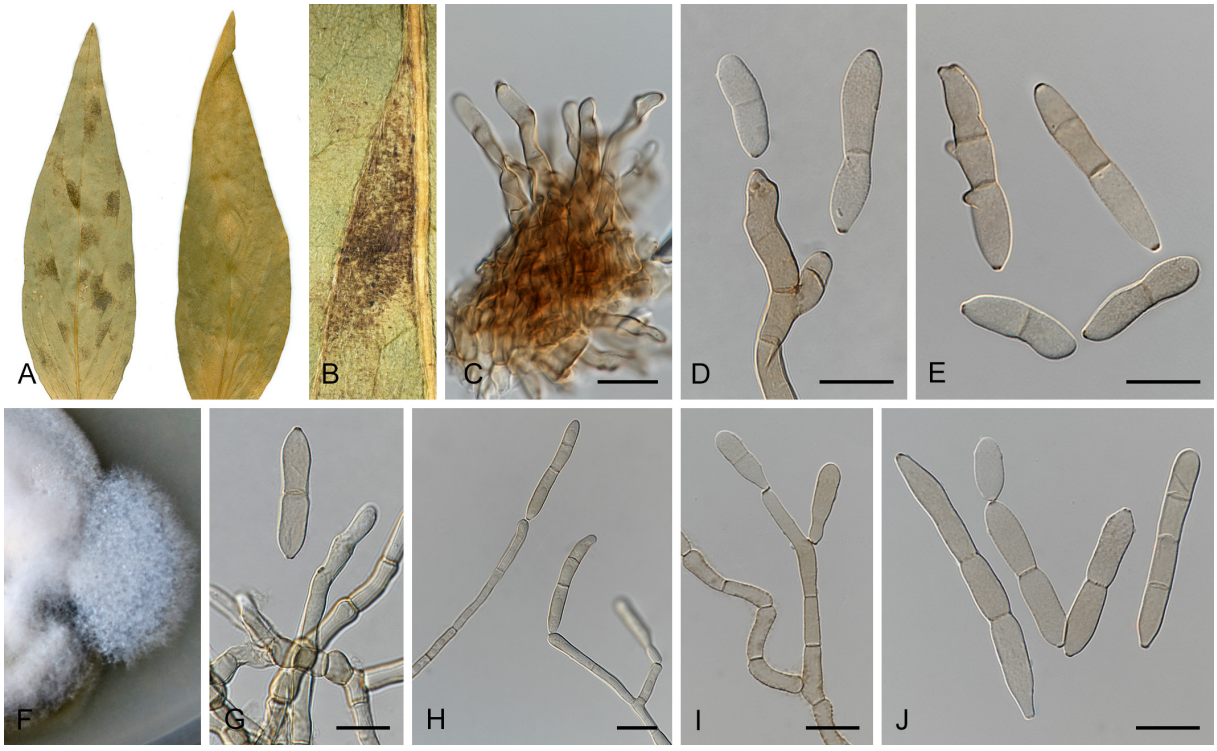


Fig. 35. *Phaeoramularia gomphrenicola* (CPC 23248). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Conidiophores. D. Partial conidiophore, conidiogenous cells and conidia. E. Catenate conidia. F–J. Observations *in vitro*. F. Culture on OA. G–I. Partial conidiophore, conidiogenous cell and conidia. J. Single and catenate conidia. Scale bars = 10 µm.

of *Passalora* since the type, *Phaeoramularia gomphrenicola* (Fig. 1, clade 61), clusters apart from the type of *Passalora*, *Passalora bacilligera* (Fig. 1, clade 34). Phylogenetically, *Phaeoramularia* clusters in a clade well-supported by all three phylogenetic methods (Fig. 1, clade 61, Fig. 3, clade 25) and is closely related to *Ragnhildiana*. Morphologically, it can be distinguished from *Ragnhildiana* by forming broader conidiophores and conidia, and its conidia can generate new conidia from any segment (Fig. 35). The single-gene trees indicate that both LSU and ITS can distinguish this genus but *rpb2* is more reliable. The previously applied phaeoramularioid habit, i.e. internal mycelium *in vivo*, fasciculate conidiophores and catenate conidia, is not diagnostic any longer since species with this morphology belong to different clades within the *Mycosphaerellaceae*. Therefore, phylogenetically unproven species should tentatively be maintained in *Passalora s. lat*.

Clade 62: *Deightonomyces*

Deightonomyces Videira & Crous, **gen. nov.** MycoBank MB822586.

Etymology: Name composed of Deighton (F.C. Deighton, British mycologist and pioneer of modern taxonomy of cercosporoid fungi) and -myces (fungus).

Description: *Mycelium* immersed, hyphae pigmented. *Stromata* immersed, composed of brown, thick-walled hyphal cells. *Conidiophores* in dense fascicles, arising from stromata, olivaceous brown, smooth, simple, straight, subcylindrical, slightly geniculate-sinuous. *Conidiogenous*

cells terminal, subhyaline to pale olivaceous, smooth, proliferating sympodially, conidiogenous loci conspicuous, slightly thickened and darkened. *Conidia* solitary, ellipsoid-ovoid, obclavate-fusiform, subcylindrical, aseptate or septate, subhyaline to pale olivaceous, smooth to verruculose, apex obtuse or subacute, base obconically truncate, hila hardly thickened and somewhat darkened.

Type species: *Deightonomyces daleae* (Ellis & Kellerm.) Videira & Crous (≡ *Cercospora daleae* Ellis & Kellerm.).

Deightonomyces daleae (Ellis & Kellerm.) Videira & Crous, **comb. nov.** MycoBank MB822753.
Basionym: *Cercospora daleae* Ellis & Kellerm., J. Mycol. 4: 6. 1888.
Synonym: *Passalora daleae* (Ellis & Kellerm.) U. Braun, Sydowia 48: 208. 1996.

Description and illustration: Braun (1996).

Materials examined: **Mexico**, Baja California Norte, Catarina, on bark of *Dalea spinosa*, Apr. 2003, L.B. Sparrius, isol. Aptroot, 2003, culture CBS 113031. **USA**, Kansas, on stems of *Dalea enneandra* (= *Dalea laxiflora*), 10 Dec. 1887, Kellerman 954 (**holotype** NY00838299).

Notes: The strain of *Passalora daleae* used in this study forms a single-strain lineage in the phylogenetic analyses (Fig. 1, clade 62; Fig. 4, clade 26). Both morphologically and phylogenetically, this species is not a true *Passalora* as circumscribed in this study, and therefore a new genus is introduced to accommodate it. When blasted against the individual gene alignments, *Deightonomyces daleae* CBS 113301 shares 98 % (465/474) similarity with *Dothistroma pini* CBS 116486 on ITS, 99 % (724/726) similarity with *Dothistroma septosporum* CBS 128282 on LSU, and only 81 % (633/784) similarity with *Phaeoramularia* sp. CBS 113382 on *rpb2*.

Clade 63: *Pleopassalora*

Pleopassalora Videira & Crous, **gen. nov.** MycoBank MB822608.

Etymology: Named after its pleomorphic morphology (Greek pleon = more), and its resemblance to *Passalora*.

Description (adapted from Beilharz *et al.* 2004): Pleoanamorphic, phytopathogenic, causing leaf spots. *Mycelium* internal, hyphae smooth, branched, septate, brown. *Stromata* medium brown, erumpent, protuberant and pulvinate, composed of *textura angularis*. *Conidiomata* amphigenous, eustromatic, bearing Type 1 conidiophores and conidia, Type 2 conidiophores and conidia, or both. Type 1 synasexual morph: *Conidiophores* occasionally solitary, usually in fascicles arising from stromata, pale to medium brown, smooth to rugose, subcylindrical, branched or unbranched, walls slightly thickened, straight to variously curved or geniculate-sinuous, septate. *Conidiogenous cells* terminal, verruculose or rugose, unbranched, subcylindrical, tapering to rounded apices proliferating sympodially, conidiogenous loci slightly thickened and darkened, refractive, flat or sometimes protuberant. *Conidia* solitary, pale olivaceous, dry, smooth, rarely finely verruculose, straight or curved, narrowly obclavate to subcylindrical, tapering gradually to an obtuse apex and to a rounded base, often constricted

at one or more septa, hila slightly but distinctly thickened, darkened and refractive. Type 2 synasexual morph: *Conidiophores* reduced, hyaline to sub-hyaline, aseptate or 1-septate, lining a stroma. *Conidia* hyaline to pale olivaceous, cylindrical, rounded at the apex, truncate at the base, smooth, aseptate to 3-septate, occasionally constricted at septa, hila broad, truncate to slightly convex, not darkened, unthickened, non-refractive. Type 3 synasexual morph: Type 2 conidia develop thick-walled hyphal swellings (reminiscent of chlamydospores), ellipsoid and hyaline, aseptate to 1-septate, that burst free from the cells of the Type 2 conidia, frequently carrying remnants of the conidial wall attached to their hyaline walls.

Type species: *Pleopassalora perplexa* (Beilharz *et al.*) Videira & Crous (≡ *Passalora perplexa* Beilharz *et al.*).

Pleopassalora perplexa (Beilharz *et al.*) Videira & Crous, **comb. nov.** MycoBank MB822776. Fig. 36.
Basionym: *Passalora perplexa* Beilharz *et al.*, Stud. Mycol. 50: 473. 2004.

Description and illustrations: Beilharz *et al.* (2004).

Materials examined: **Indonesia**, South Sumatra, Kerinci, on *Acacia crassicarpa*, Feb. 2004, M.J. Wingfield (**holotype** CBS H-9907, culture ex-type CBS 116363 = CPC 11147–11149);

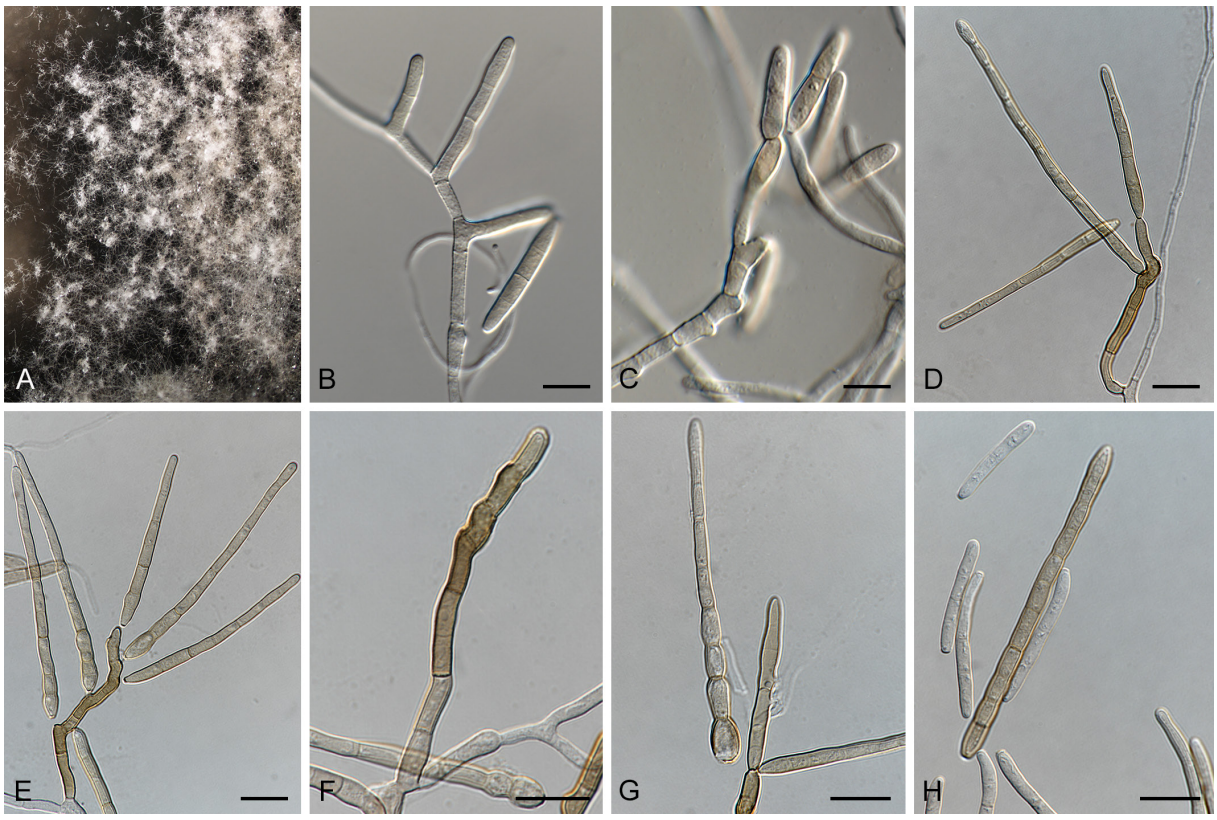


Fig. 36. *Pleopassalora perplexa* (CPC 12168). A–H. Observations *in vitro*. A. Culture on OA. B, C. Conidiophore and conidia type II. D, E. Conidiophore and conidia type I. F. Conidiophore type I. G. Conidia type I, slightly constricted at the septa and swollen cells at the base, and type II, smaller and narrower. H. Conidia type I and type II. Scale bars = 10 µm.

idem. CBS H-9908, CBS H-9909, CBS H-9911, cultures derived from CBS H-9911, CBS 116364 = CPC 11150–11151; *idem*., 1 Mar. 2004, M.J. Wingfield, culture CPC 11152; *idem*., *Acacia* sp., 1 May 2005, M.J. Wingfield, cultures CPC 12168, CPC 12170.

Notes: *Passalora perplexa* is the causal agent of leaf blight in *Acacia crassicarpa* both in Australia where it is native and also in plantations in Indonesia to where it spread. It is one of few pleoanamorphic cercosporoid fungi described with one morph characterised as a hyphomycete, a second morph described as a coelomycete, and a third morph representing a resting spore form on natural substrates and artificial media (Beilharz *et al.* 2004). The available strains of *Passalora perplexa* cluster together in a well-supported clade in the phylogenetic analyses (Fig. 1, clade 63; Fig. 3, clade 27). The phylogenetic analyses support a clade including strains from *Passalora perplexa*, *Passalora* sp. 1, *Passalora juniperina and Phaeocercospora colophospermi*, but these species vary too significantly in their morphology to be assigned to the same genus.

"*Passalora*" sp. 1

Description in vitro (V8; CBS 122466): *Mycelium* composed of hyaline to pale brown hyphae, smooth, uniform in width, 2–2.5 µm. *Conidiophores* micro- or macronematous, pale to pale brown, simple, rough, straight to mildly sinuous, long to medium conically truncate at the apex, 10–40 × 2.5 µm. *Conidiogenous cells* integrated, apical, polyblastic, proliferating sympodially, with slightly protruding conidiogenous loci that are somewhat thickened and darkened, 2 µm in diam. *Conidia* solitary, hyaline to pale brown, finely verruculose, cylindrical to obclavate, base obconically truncate, rounded at the apex, 25–40 × 2–2.5 µm, multi-euseptate, septa indistinct, hila somewhat thickened and darkened, 2 µm diam.

Material examined: **USA**, Florida, on *Citrus* sp., unknown date, R.C. Ploetz, culture CBS 122466.

Notes: Phylogenetically, the present species forms a single strain lineage closely related to *Pleopassalora* (Fig. 1, clade 63; Fig. 3, clade 27). The present strain was initially identified as *Passalora loranthi* (Arzanlou *et al.* 2008) since its DNA was identical to a sequence of *Passalora loranthi* available on GenBank (GenBank AY348311). Although there is no publication associated with that accession number, many subsequent authors followed this identification (Crous *et al.* 2004b, Beilharz *et al.*, 2004, Arzanlou *et al.* 2008, Douanla-Meli *et al.* 2013, Huang *et al.* 2015). A description based on the observation of strain CBS 122466 in culture is presented. Unfortunately, the culture became sterile and thus fresh material needs to be collected to fully clarify the taxonomy of this species, which appears to have a wide host range.

Clade 64: *Phaeocercospora*

Phaeocercospora Crous, Persoonia 28: 171. 2012.

Description (from Crous *et al.* 2012b): Foliicolous, associated with leaf spots. *Caespituli* amphigenous, subepidermal, arising from subepidermal, globular fruiting bodies (immature structures with undefined white contents); wall of 2–3 layers of *textura angularis*, bursting through epidermis, forming grey sporodochia with densely aggregated conidiophores.

Conidiophores subcylindrical to ampulliform, brown, finely verruculose, aggregated, 0–2-septate. *Conidiogenous cells* terminal, brown, finely verruculose, ampulliform, tapering to a truncate apex, proliferating several times percurrently at apex (proliferations irregular, rough), or sympodially. *Conidia* solitary, brown, finely verruculose, guttulate, subcylindrical to narrowly obclavate, straight to mildly curved, apex subobtuse, base truncate with marginal frill, transversely septate; hila and scars not thickened, nor darkened or refractive.

Type species: *Phaeocercospora colophospermi* Crous.

Phaeocercospora colophospermi Crous, Persoonia 28: 171. 2012.

Descriptions and illustrations: Crous *et al.* (2012b).

Material examined: **South Africa**, Mpumalanga, Kruger Game Reserve, Satara rest camp, on leaves of *Colophospermum mopane*, 11 Jul. 2011, P.W. Crous & K.L. Crous (**holotype** CBS H-20966, culture ex-type CBS 132687 = CPC 19812).

Notes: *Phaeocercospora* is a recently introduced genus that was established to accommodate *Phaeocercospora colophospermi* (Crous *et al.* 2012b). In the present phylogenetic analyses, *Phaeocercospora colophospermi* is represented by a single-strain lineage (Fig. 1, clade 64; Fig. 3, clade 28) closely related to *Pleopassalora*.

Phaeocercospora juniperina (Georgescu & Badea) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822825. Fig. 37.
Basionym: *Cercospora juniperina* Georgescu & Badea, Analele Inst. Cercet. Exp. Forest. Bucharest I: 37. 1937.
Synonyms: *Stigmina juniperina* (Georgescu & Badea) M.B. Ellis, Mycol. Pap. 72: 67. 1959.
Sciniatosporium juniperinum (Georgescu & Badea) Morgan-Jones, Canad. J. Bot. 49: 998. 1971.
Asperisporium juniperinum (Georgescu & Badea) B. Sutton & Hodges, Mycologia 82: 317. 1990.
Passalora juniperina (Georgescu & Badea) H. Solheim, Agarica 34: 110. 2014.
Camarosporium juniperinum Georgescu & Badea, Rev. Padurilor, Bucharest: 1. 1935.

Description in vivo (CBS H-22955): *Mycelium* internal, composed of brown hyphae, septate, branched. *Stromata* well-developed, brown to dark brown, often with a cavity filled with spermatia, single or aggregate, wall composed of *textura angularis*, 80–340 µm diam. *Conidiophores* sporodochial, densely fasciculate, pale brown to brown, smooth, aseptate or septate, cylindrical to geniculate, 16–50 × 4–9 µm, often reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, polyblastic, proliferating percurrently or sympodially, with conidiogenous loci not thickened and not darkened, apical or lateral at the apex, 2–2.5 µm diam. *Conidia* solitary, pale to pale olivaceous brown, smooth to thinly verruculose, cylindrical to long-obclavate, straight to slightly curved, base obconically truncate, apex rounded, 18–56 × 2.5–3.5 µm, 1–4-septate, hila not thickened and not darkened at the base, 2–2.5 µm diam.

Description in vitro (on SNA; CPC 11258): *Mycelium* composed of pale brown hyphae, smooth, septate, branched. *Stromata* absent. *Conidiophores* emerging from hyphae, pale

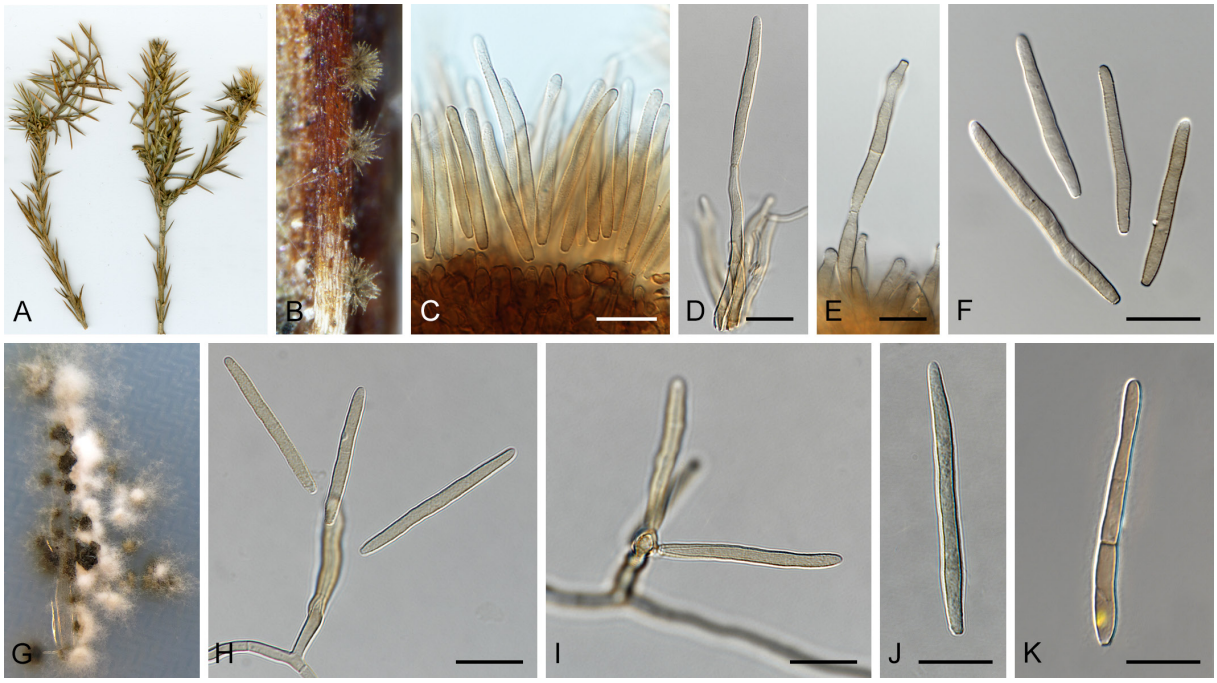


Fig. 37. *Phaeocercospora juniperina* (CPC 11258). A–F. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores and conidia on the lesions. C, E. Conidiogenous cells and conidia. D. Conidiophores and conidia. F. Conidia. G–K. Observations *in vitro*. G. Culture on SNA. H, I. Conidiophore and conidia. J, K. Conidia. Scale bars = 10 µm.

brown, smooth, erect, cylindrical to geniculate, septate, 11–55 × 3–6 µm. *Conidiogenous cells* integrated, terminal, polyblastic, proliferating sympodially, conically truncate or geniculate at the apex, with conidiogenous loci not thickened or darkened, apical or lateral at the apex, 2 µm diam. *Conidia* solitary, pale brown, smooth to thinly verruculose, cylindrical to long-obclavate, straight to slightly curved, base obconically truncate, apex rounded, 25–54 × 2.5–4 µm, 1–4-septate, hila not thickened and not darkened, 2–2.5 µm diam.

Material examined: **USA**, North Carolina, on *Juniperus virginiana*, 1 Mar. 2004, C.S. Hodges, CBS H-22955, culture CBS 142238 = CPC 11258.

Notes: Both specimen and culture materials were examined and this fungus has conidiogenous cells proliferating both percurrently with annellations and sympodially with rim-like loci (Fig. 37). Phylogenetically, this strain forms a single-strain lineage closely related to *Phaeocercospora colophospermi* (Fig. 1, clade 64; Fig. 3, clade 28). Given the phylogenetical proximity and morphological similarities, a combination is proposed in *Phaeocercospora* until further evidence becomes available.

Clade 65: *Rosisphaerella*

Rosisphaerella Videira & Crous, **gen. nov.** MycoBank MB822703.

Etymology: Mycosphaerella-like species from the host genus *Rosa*.

Description: Phytopathogenic, foliicolous. *Mycelium* internal, composed of subhyaline to brown hyphae, smooth, septate, branching. *Stromata* lacking or small, epidermal, substomatal, brown to dark brown. *Conidiophores* emerging from stromata or few brown cells, solitary to fasciculate, often synnematous, dark olivaceous brown near base and paler toward the tip, smooth, simple, multiseptate, straight to sinuous, usually geniculate-sinuous. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, rarely proliferating percurrently, with rim-like conidiogenous loci, somewhat thickened, darkened and protuberant. *Conidia* solitary, pale to medium olivaceous brown, smooth to finely verruculose, cylindrical to obclavate, straight to mildly curved, septate, obconically truncate at base and rounded at apex, hila somewhat thickened and darkened.

Type species: *Rosisphaerella rosicola* (Pass.) U. Braun, *et al.* (≡ *Cercospora rosicola* Pass.).

Rosisphaerella rosicola (Pass.) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822800. Fig. 38.
Basionym: *Cercospora rosicola* Pass., in Thüm., Herb. Mycol. Oecon., Fasc. VII: no. 333. 1875.
Synonyms: *Passalora rosicola* (Pass.) U. Braun, Mycotaxon 55: 234. 1995.
Cercospora rosicola var. *undosa* Davis, Trans. Wisconsin Acad. Sci. 20: 405. 1921.
Cercospora rosae J.M. Hook, Proc. Indiana Acad. Sci. 38: 131. 1929.
Cercospora rosae-indianensis J.M. Hook, Proc. Indiana Acad. Sci. 39: 82. 1930.
Mycosphaerella rosicola B.H. Davis, Mycologia 30: 296. 1938.

Description in vivo (CBS H-22956): *Leaf spots* scattered, circular or irregular when coalescing, singly 1–4 mm diam, uniformly purplish or reddish brown, or greysh white to pale brown

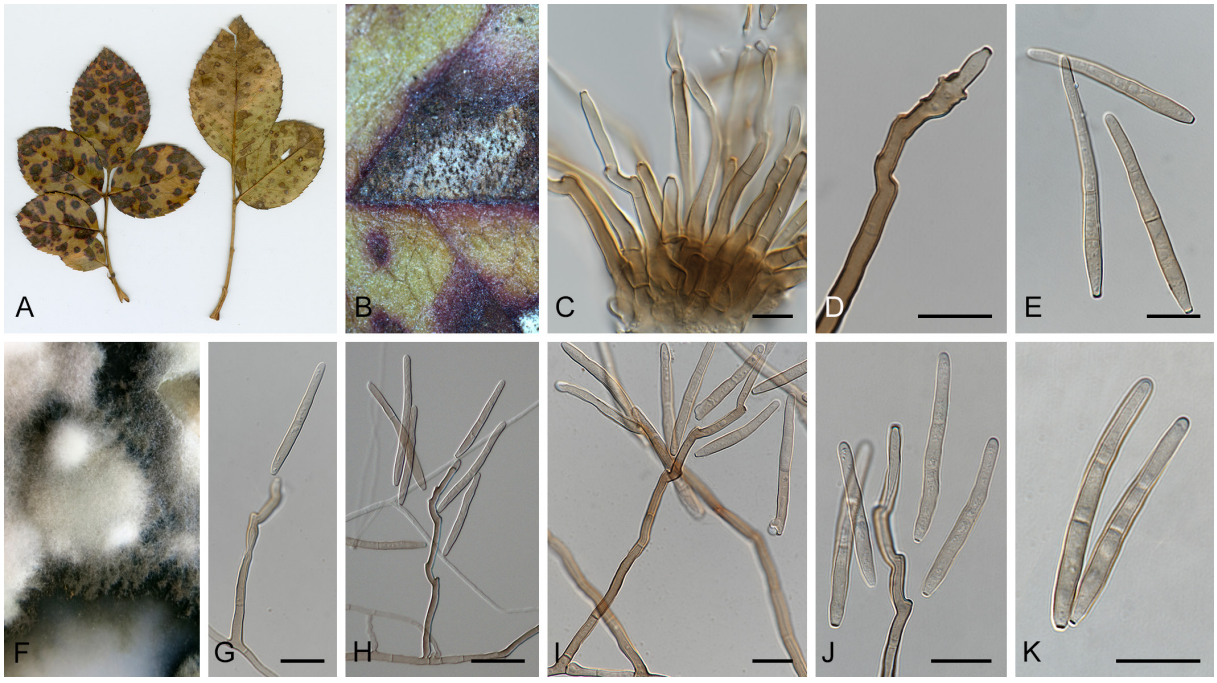


Fig. 38. *Rosisphaerella rosicola* (CPC 12548). A–E. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C, D. Conidiophores and conidiogenous cells. E. Single conidia. F–K. Observations *in vitro*. F. Culture on OA. G–I. Conidiophore, conidiogenous cells and conidia. J. Partial conidiophore, conidiogenous cells and conidia. K. Conidia. Scale bars = 10 µm.

at the centre, indistinct on lower leaf surface. *Mycelium* internal, composed of hyaline and pale brown to brown hyphae, septate, branching, 3–4 µm diam. *Stromata* lacking or small, epidermal, substomatal, brown to dark brown, 25–52 µm diam. *Conidiophores* emerging from stromata or agglomerates of a few brown cells, solitary or in fascicles, fascicles loose or dense, often synnematous, dark olivaceous brown near base, paler towards the tip, smooth, simple, multiseptate, straight or sinuous, usually geniculate-sinuous, 20–156 × 3–6 µm. *Conidiogenous cells* integrated, terminal and intercalary, proliferating sympodially, rarely proliferating percurrently, with rim-like conidiogenous loci, somewhat thickened and darkened, 2–4 µm diam. *Conidia* solitary, pale to medium olivaceous brown, smooth to finely verruculose, cylindrical to obclavate, straight to mildly curved, base long-obconically truncate, apex rounded, 20–98 × 3–5 µm, 1–6-septate, hila somewhat thickened and darkened, 2–4 µm diam.

Description in vitro (on SNA; CPC 12548): *Mycelium* composed of pale brown to brown hyphae, uniform in width, 2–3 µm. *Conidiophores* micro- or macronematous, pale brown to brown, paler at the apex, smooth, erect, simple, septate, geniculate-sinuous, 10–280 × 2.5–5 µm. *Conidiogenous cells* integrated, terminal and intercalary, pale brown to brown, smooth, mono- or polyblastic, proliferating sympodially, conically truncate at the apex or geniculate-sinuous, with conidiogenous loci thickened and darkened, located protruding at the apex and shoulders, 2–2.5 µm diam. *Conidia* solitary, subhyaline to pale brown, smooth to finely verruculose, cylindrical to long obclavate, straight or mildly curved, base short obconically truncate, apex rounded, 1–4-euseptate, 20–63 × 2.5–5 µm, hila refractive and slightly thickened and darkened.

Materials examined: **Italy**, Parma, on *Rosa* sp. cult., 1874, G. Passerini, Thümen, Herb. Mycol. Oecon. 333 (**lectotype** designated here, BPI 440506, MBT378584; isolectotypes Thümen, Herb. Mycol. Oecon. 333, e.g. B, K, S). **USA**, North Carolina, on *Rosa* sp. hybrid, 2005, C.S. Hodges, CBS H-22956, culture CBS 142183 = CPC 12548; unknown state/city, host, collector and date, dep. LM Massey, 1935, culture CBS 138.35 = ATCC 52313.

Notes: *Passalora rosicola* is known to cause leaf spot disease on rose worldwide (Davis 1938). Morphologically, the specimens examined (Fig. 38) fit the description available in the literature (Braun 1995). Morphologically, the strain CBS 142183 is a good representative of the species and was isolated from the same host as the type specimen. However, since it was isolated from a different continent, we refrain from proposing an epitype. Phylogenetically, the observed strains cluster in a well-supported clade (Fig. 1, clade 65; Fig. 3 clade 29) closely related to *Phaeocercospora* and *Pleopassalora*. When single gene sequences are BLASTed against the alignment, CPC 12548 shares 80 % (623/ 778) similarity on *rpb2* with CPC 11258 *Phaeocercospora juniperina*, 91 % (438/479) similarity on ITS and 96 % (700/727) similarity on LSU. In *Passalora rosicola* we did not observe pleomorphic asexual states as in *Pleopassalora*, nor percurrent conidiation as in *Phaeocercospora*. Given both the morphological and phylogenetic differences from the closest related genera, we introduce the genus *Rosisphaerella* to accommodate this species.

Clade 66: *Exutisphaerella*

Exutisphaerella Videira & Crous, **gen. nov.** MycoBank MB822590.

Etymology: exutus- meaning "cast off" or "shed" like the disease symptom + *sphaerella* because of the globose ascomata.

Description: *Ascomata* pseudothecial, globose to slightly elongated or elliptical, emerging through the epidermis, solitary or gregarious, ostiole apical. *Asci* club-shaped, stipitate, 8-spored. *Ascospores* hyaline, oblong, fusiform-elliptical, straight or slightly curved, 1-septate, not constricted at septa, with cells of equal size. Asexual morph acervular-like. *Conidiophores* ampulliform, in compact bunches. *Conidia* hyaline, bacillar to allantoid, rounded at the tip, truncate at the base, straight to slightly curved, aseptate to multiseptate. *Spermagonia* in stromata, barely erumpent to completely exposed, globose to oval or pyriform, apical ostiole. *Spermatia* bacillar to pyriform.

Type species: *Exutisphaerella laricina* Videira & Crous (≡ *Sphaerella laricina* R. Hartig).

Exutisphaerella laricina (R. Hartig) Videira & Crous, **comb. nov.** MycoBank MB822758.
Basionym: *Sphaerella laricina* R. Hartig, Forstl.-Naturwiss. Z. 4: 445. 1895.
Synonym: *Mycosphaerella laricina* (R. Hartig) Mig., Krypt.-Fl. Deutschl. Österr. Schweiz. 3(1): 301. 1912.

Descriptions and illustrations: Hartig (1895), Patton *et al.* (1983).

Description in vivo (adapted from Hartig 1895 and Patton 1983): *Ascomata* pseudothecial, globose to slightly elongated or elliptical, emerging through the epidermis, solitary or gregarious, 100–150 µm diam, ostiole apical. *Asci* club-shaped, stipitate, 40–60 µm long, 8-spored. *Ascospores* hyaline, oblong, fusiform-elliptical, straight or slightly curved, 1-septate, not constricted at septa, with cells of equal size, 11–17 × 2.5–3 µm. *Asexual morph* acervulum-like. *Conidiophores* ampulliform, in compact bunches. *Conidia* hyaline, bacillar to allantoid, rounded at the tip, truncate at the base, straight to slightly curved, 25–46 × 2–4 µm, (0–)1–4-septate. *Spermagonia* in stromata, barely erumpent to completely exposed, globose to oval or pyriform, occasionally two spermagonial cavities occur in a single stroma, apical ostiole. *Spermatia* bacillar to pyriform, 1–3 × 0.5 µm.

Material examined: **Switzerland**, Kt. Zurich, Horgenberg, on *Larix decidua*, unknown date and collector, isol. E. Müller, 27 May 1952 (**neotype** designated here as metabolically inactive culture CBS 326.52, MBT378624).

Notes: *Mycosphaerella laricina* was first observed infecting the host *Larix europaea* (*Pinaceae*) in Germany, and is the causative agent of needle cast disease of European larch wherever it is cultivated. Unfortunately, the type could not be located in any fungaria and a neotype is necessary (Aptroot 2006). The asexual morph is reported as a *Cercoseptoria* (fide D.F. Farr *et al.* 1989, Corlett 1991), currently treated as synonym of *Pseudocercospora* (needs confirmation based on DNA), or a *Leptostroma* (fide Tomilin 1979). The asexual morph is characterised by acervular conidiomata, lined with ampulliform conidiophores with truncate apices, producing hyaline and bacillar conidia, 1–4-septate (Patton 1983). The strain used in this study was unfortunately sterile and morphological comparison was impossible. Phylogenetically, this strain forms a single-strain lineage closely related to *Rosisphaerella* (Fig. 1, clade 66; Fig. 3 clade 30). When the single genes are BLASTed against the alignment, CBS 326.52 shares 90 % (700/774) similarity on *rpb2* and 99 % (717/726) similarity on LSU with CPC 12548 *Rosiphaerella rosicola*, and 98 % (470/480) similarity on ITS with CBS 122466 (*Passalora* sp.1). Based on the phylogenetic results and the morphological differences in comparison to the

closest related species *Rosisphaerella rosicola*, we introduce this new genus to accommodate the present species.

Clade 67: *Brunswickiella*, *Cytostagonospora, Devonomyces and Phaeophleospora*

Brunswickiella Videira & Crous **gen. nov.** MycoBank MB822694.

Etymology: Named after the nature reserve it was collected from.

Description: Phytopathogenic. *Conidiomata* pycnidial, epiphyllous, immersed, black and with central ostiole, outer layer with irregular, brown, verruculose hyphae; basal stroma brown, verruculose, giving rise to conidiophores; basal cells brown, verruculose, upper cells hyaline, smooth, septate, subcylindrical, branched below. *Conidiogenous cells* hyaline, smooth, subcylindrical, terminal and lateral, proliferating percurrently at apex, or with periclinal thickening, intermixed among paraphyses that are branched, similar in length and at times become fertile. *Conidia* solitary, hyaline, smooth, guttulate, subcylindrical to narrowly fusoid-ellipsoidal, straight to slightly curved, widest in the middle, tapering to subobtuse apex and truncate hilum.

Type species: *Brunswickiella parsonsiae* (Crous & Summerell) Videira & Crous.

Brunswickiella parsonsiae (Crous & Summerell) Videira & Crous **comb. nov.** MycoBank MB822740.
Basionym: Phaeophleospora parsonsiae Crous & Summerell (as "*parsoniae*"), Persoonia 32: 217. 2014.

Description and illustration: Crous *et al.* (2014a).

Material examined: **Australia**, New South Wales, Brunswick Heads Nature Reserve, S28°31090.800 E153°32057.000, on *Parsonsia straminea* leaves, 9 Mar. 2013, B.A. Summerell (**holotype** CBS H-21691, culture ex-type CBS 137979 = CPC 22537).

Notes: *Brunswickiella parsonsiae* forms pycnidial conidiomata with hyaline conidiogenous cells that proliferate percurrently and produce hyaline fusoid-ellipsoid aseptate conidia. At the time it was described, Crous *et al.* (2014a) assumed it represented a microconidial state of *Phaeophleospora*. The phylogenetic position of the present strain is outside the *Phaeopleospora* clade, sitting in a single-strain lineage (Fig. 4, clade 6-II) sister to the clade of *Lecanosticta*. Based on the morphological differences between this strain and the closest genera and its phylogenetic position we place it in a new genus.

Cytostagonospora Bubák, Ann. Mycol. 14: 150. 1916.

Description (from Sutton 1980): *Mycelium* immersed, dark brown, branched, septate. *Conidiomata* pycnidial, amphigenous, separate, globose, dark brown to black, immersed, unilocular, thick-walled, clypeate; walls of dark brown, thick-walled *textura angularis* to *textura globulosa*, becoming hyaline towards the conidiogenous region, extending in the upper part to become a circular clypeus of similar thickness to the wall. *Ostiole* central, circular, papillate

to short rostrate, depressed, situated immersed within the clypeus. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, determinate, discrete, lageniform, hyaline, smooth, formed from the inner cells of the pycnidial wall. *Conidia* hyaline, 0–2-euseptate, not constricted at septa, base truncate, apex obtuse, thin-walled, eguttulate, smooth, filiform, often curved.

Type species: *Cytostagonospora photiniicola* Bubák.

Cytostagonospora martiniana (Sacc.) B. Sutton & H.J. Swart, Trans. Br. mycol. Soc. 87: 99. 1986.
Basionym: *Septoria martiniana* Sacc., Syll. Fung. (Abellini) 10: 351. 1892.
Synonym: *Septoria phyllodiorum* Cooke & Massee, Grevillea 19: 47. 1890, non *S. phyllodiorum* Sacc., Hedwigia 29: 156. 1890.

Description and illlustration: Sutton & Swart (1986), Quaedvlieg *et al.* (2013).

Materials examined: **Australia**, Victoria, Warneet close to Melbourne, S38º13037.800 E145º18025.400, on leaves of *Acacia pycnantha*, 21 Oct. 2009, P.W. Crous (**epitype** designated here CBS H-21297, MBT378691, culture CBS 135102 = CPC 17727); Victoria, on phyllodes of *Acacia longifolia*, Mrs. Martin 432 (**holotype** K, slide as IMI 299337).

Notes: According to the phylogenetic analyses in the present study, the strain of *Cytostagonospora martiniana* forms a single strain lineage (Fig. 1, clade 66; Fig. 4, clade 5-III) closely related to *Phaeopleospora* species. *Cytostagonospora martiniana* forms pycnidial to acervular conidiomata, hyaline conidiogenous cells that are polyphialidic with periclinal thickening, proliferate percurrently and produce hyaline, 1–3-septate, scolecosporous conidia (Quaedvlieg *et al.* 2014). These morphological characters are distinct from the typical generic characters of *Phaeophleospora*.

Cytostagonospora photiniicola Bubák, Ann. Mycol. 14(3–4): 150. 1916.
Synonym: *Cytostaganis photiniicola* (Bubák) Clem. & Shear, The genera of Fungi: 367. 1931.

Description and illustration: Quaedvlieg *et al.* (2013).

Notes: The phylogenetic position of *Cytostagonospora* (Bubák 1916) is still unclear since material representing the type species, *Cytostagonospora photiniicola*, has not yet been sequenced. The only *Cytostagonospora* species of which a strain is available is *Cytostagonospora martiniana*, which forms a single strain lineage in the phylogenetic analysis (Fig. 4, clade 5-III).

Devonomyces Videira & Crous, **gen. nov.** MycoBank MB822695.

Etymology: Named after Devon Valley, Stellenbosch, where this taxon was first collected.

Description: Phytopathogenic, foliicolous. *Ascomata* pseudothecial, amphigenous, subepidermal, becoming erumpent, subglobose to globose, with apical, papillate ostiole; walls of 2–3 layers of medium brown *textura angularis*, subhymenium of 1–2 layers of hyaline cells. *Asci* fasciculate, bitunicate, cylindrical to narrowly obovoid, straight or slightly incurved, 8-spored. *Ascospores*

bi- to triseriate, overlapping, hyaline, guttulate, thin-walled, straight, fusoid-ellipsoidal with obtuse ends, medianly 1-septate. *Mycelium* internal, consisting of septate, branched, hyaline to brown, smooth to verruculose hyphae. *Caespituli* sporodochial, situated on a brown stroma consisting of verruculose, brown, globose cells and hyphal elements. *Conidiophores* rarely pigmented and verruculose in lower part, mostly hyaline and smooth throughout, thick-walled, cylindrical, straight to irregularly curved, septate. *Conidiogenous cells* terminal, hyaline, smooth, unbranched, straight or slightly curved, proliferating sympodially. *Conidia* solitary, hyaline, smooth, narrowly obclavate, septate, irregularly curved, rarely straight, apex obtuse, base long obconic-truncate, lateral branches common, secondary conidia forming on most mature primary conidia; conidia aggregated in slimy masses.

Type species: *Devonomyces endophyticus* (Crous & H. Sm. ter) Videira & Crous.

Devonomyces endophyticus (Crous & H. Sm. ter) Videira & Crous, **comb. nov.** MycoBank MB822754.
Basionym: *Mycosphaerella endophytica* Crous & H. Sm. ter, Mycol. Mem. 21: 54. 1998.
Synonym: *Pseudocercosporella endophytica* Crous & H. Sm. ter, Mycol. Mem. 21: 55. 1998.

Descriptions and illustrations: Crous (1998).

Materials examined: **Australia**, Western Australia, Esperance, Chips Plantation (ITC), on *Eucalyptus globulus*, 15 Dec. 2000, A. Maxwell, MURU0011, culture CBS 110501 = CMW 14462; Pemberton, Steward Road, *Banksia* woodland, on *Hakea undulata*, 2 Aug. 2008, A.R. Wood, culture CPC 15580. **South Africa**, Western Cape Province, De Hoop Nature Reserve, *Eucalyptus cladocalyx*, 22 Sep. 1995, A.R. Wood, culture CBS 111167 = CPC 1225; Stellenbosch, Devon Valley, on leaves of *Eucalyptus* sp., Jun. 1995, P.W. Crous (**holotype** of *Mycosphaerella endophytica* PREM 54398, culture ex-type CBS 114662 = CPC 1193); Kwazulu-Natal, on *Eucalyptus nitens*, unknown collector and date, isol. G.C. Hunter, Jun. 2000, culture CBS 114709 = CMW 9099.

Notes: Based on the phylogenetic analyses *Devonomyces endophyticus* (Fig. 4, clade 5-I) is closely related to *Phaeophleospora eugeniae*, as observed in a previous study (Quaedvlieg *et al.* 2014). The pseudocercosporella-like morph of *Devonomyces endophyticus* is however morphologically distinct from *Phaeophleospora* (Crous 1998), and thus has to be accommodated in a different genus. The strain CBS 114709 was originally named as *Mycosphaerella pseudoellipsoidea* but no details of the species description could be found. The strain is currently sterile and is included in *Devonomyces endophyticus* based on molecular data. The strain CPC 15580 was isolated from the same herbarium material as *Periconiella hakeae* (CPC 15577), which indicates they may be co-existing in the same lesions.

Phaeophleospora Rangel, Arq. Mus. Nac., Rio de Janeiro 18: 162. 1916.

Description: Foliicolous, plant pathogenic. *Conidiomata* pycnidial, aggregated or separate, becoming erumpent, lifting the epidermis, pycnidia black, subglobose, unilocular, wall of brown *textura epidermoidea* in surface view, and of *textura angularis* to *textura intricata* in vertical section, base of 2–3 layers, ostiole irregular, central. *Conidiophores* mostly reduced to conidiogenous cells. *Conidiogenous cells* terminal, discrete, brown, verruculose, subcylindrical

or doliiform, proliferating percurrently, with inconspicuous percurrent proliferations, or at times proliferating sympodially. *Conidia* solitary, exuded in cirrhus, hyaline to medium brown, smooth to verruculose, granular, thick-walled, subcylindrical to obclavate, straight to irregularly curved, base obconically truncate, apex obtuse, euseptate, hila with a minute marginal frill. *Spermatogenous cells* developing in conidiomata before the development of conidia, hyaline, ampulliform. *Spermatia* hyaline, smooth, rod-shaped.

Type species: *Phaeophleospora eugeniae* Rangel.

Phaeophleospora eugeniae Rangel, Decheniana 18: 162. 1916.

Description and illustration: Crous *et al.* (1997).

Description in vitro (on V8; CPC 15143): *Mycelium* hyaline, smooth, uniform in width, 2.5 µm diam. *Conidiomata* pycnidial, aggregated on mycelial colonies, pale brown, forming 1-layered conidiomatal wall composed of large brown cells (*textura intricata*), 100–300 µm diam. *Conidiogenous cells* lining the inner cavity, hyaline to pale brown, ampulliform, monoblastic, determinate or proliferating percurrently, 5–20 × 2.5–3.8 µm, without distinguished loci. *Conidia* solitary, pale brown to pale olivaceous brown, darker in the center and paler towards both ends, scolecosporous, obclavate, straight or sinuous, base long-obconical, apex pointed, 30–150 × 5–8 µm, 6–25-euseptate, with frill-like hila.

Materials examined: **Brazil**, Minas Gerais, Viçosa University campus, living leaves of *Eugenia uniflora*, 8 Jul. 1996, F.A. Ferreira (**neotype** IMI 372655, designated in Crous *et al.* 1997; isoneotype PREM 55275, cultures ex-type CPC 1453, CPC 1454); same location and host, 15 Jun. 1990, F.A. Ferreira, PREM 55276; same location and host, 20 Jun. 1989, F.A. Ferreira, PREM 55277; Viçosa, Paraiso, on *Eugenia uniflora*, 1 Mar. 2008, A.C. Alfenas, CBS H-22957, culture CBS 142184 = CPC 15143; Guaiba, on *Eugenia uniflora*, 1 Apr. 2008, A.C. Alfenas, culture CPC 15159.

Notes: The genus *Phaeophleospora*, based on *Phaeophleospora eugeniae* (on *Eugenia uniflora*, Brazil), includes species that form pycnidia lined with percurrently proliferating brown conidiogenous cells that give rise to brown, multiseptate, scolecosporous conidia (Crous *et al.* 1997, 2007a). Based on phylogenetic analyses, *Phaeophleospora* belongs to the *Mycosphaerellaceae* (Crous *et al.* 1997, 2009b; present study Fig. 1, clade 67), and clusters in a well supported clade by the Bayesian analyses (Fig. 4, clade 5-II), being closely related to *Lecanosticta*. The genus *Kirramyces*, initially considered a synonym of *Phaeophleospora* (Crous *et al.* 1997), is currently considered the asexual morph of *Teratosphaeria*. The taxa *Phaeophleospora scytalidii* and *Phaeophleospora stramenti* were allocated to *Phaeophleospora* based on phylogenetic inference since only the sexual morph is known (Quaedvlieg *et al.* 2014). Recently described species in the genus are morphologically variable [e.g. *Phaeophleospora pteridivora* has a sporodochial hyphomycete asexual morph (Guatimosim *et al.* 2016); *Phaeophleospora hymenocallidis* and *Phaeophleospora hymenocallidicola* produce hyaline conidia (Crous *et al.* 2015d)], suggesting that this genus needs to be revised.

Clade 68: *Lecanosticta*

Lecanosticta Syd., Ann. Mycol. 20: 211. 1922.

Description (from Sutton 1980): *Mycelium* immersed, branched, septate, pale brown. *Conidiomata* acervular, subepidermal, separate, formed of brown, thin- or thick-walled *textura angularis*. Dehiscence by pushing back a flap of epidermis that remains attached. *Conidiophores* hyaline to pale brown, branched, septate, smooth, formed from the upper cells of the pseudoparenchyma. *Conidiogenous cells* holoblastic, integrated or discrete, indeterminate, cylindrical, hyaline, with 1–2 often widely spaced percurrent proliferations. *Conidia* acrogenous, straight or curved, fusiform, tapered to the rounded apex and truncate base, l–3-euseptate, continuous, pale brown, verrucose.

Type species: *Lecanosticta acicola* (Thüm.) Syd. (≡ *Cryptosporium acicola* Thüm.).

Lecanosticta acicola (Thüm.) Syd., Ann. Mycol. 22: 400. 1924.
Basionym: *Cryptosporium acicola* Thüm., Flora (Regensburg) 61: 178. 1878.
Synonyms: *Septoria acicola* (Thüm.) Sacc., Syll. Fung. 3: 507. 1884.
Dothistroma acicola (Thüm.) Schischkina & Tzanava, Novosti Sist. Nizsh. Rast. 1967: 277. 1967.
Lecanosticta pini Syd., Ann. Mycol. 20: 211. 1922.
Oligostroma acicola Dearn., Mycologia 18: 251. 1926.
Scirrhia acicola (Dearn.) Sigg., Phytopathology 29: 1076. 1939.
Systremma acicola (Dearn.) F.A. Wolf & Barbour, Phytopathology 31: 70. 1941.
Mycosphaerella dearnessii M.E. Barr, Contr. Univ. Michigan Herb. 9: 587. 1972.

Description and illustration: Quaedvlieg *et al.* (2012).

Materials examined: **France**, Gironde, Le Teich, on needles of *Pinus radiata*, Apr. 1995, M. Morelet, CBS H-21114, culture CBS 871.95. **Lithuania**, on needles of *Pinus mugo*, 2009, S. Markovskaja, A. Kačergius & A. Treigienė, CBS H-21109, cultures LA773A & LA773B = CBS 133790. **Mexico**, on needles of a *Pinus* sp., 30 Nov. 2009, M. de Jesús Yáñez-Morales, CBS H-21112, culture CPC 17822 = CBS 133789. **USA**, South Carolina, Aiken, needles of *Pinus caribaea*, 1876, H.W. Ravenel (**lectotype** designated here IMI 91340, MBT378589, isotype of *Cryptosporium acicula* ex Padova No. 1484); Arkansas, Pike City, alt. 700 ft, needles of *Pinus* (*palustris* or *taeda*), 24 Apr. 1918, coll. J.A. Hughes, det. Sydow (**syntypes** of *Lecanostricta pini*, BPI 393329, BPI 393331); Florida, Silver Spring, needles of *P. palustris*, 27 Feb. 1919, coll. Geo G. Hedgcock, det. J. Dearness (**syntype** of *Oligostroma acicola*, BPI 643015); Maine, Bethel, on needles of *Pinus strobus*, 14 Jun. 2011, coll. B. Ostrofsky, det. K. Broders, WPF4.12; *idem*., on needles of *P. strobus*, 15 Jun. 2011, coll. B. Ostrofsky, det. K. Broders, WPF13.12; New Hampshire, Blackwater, on needles of *P. strobus*, 15 Jun. 2011, coll. B. Ostrofsky, det. K. Broders (**epitype** of *Cryptosporium acicola* designated here: CBS H-21113, MBT378591, culture ex-epitype CBS 133791).

Notes: The genus *Lecanosticta* is closely related to *Phaeophleospora* based on phylogenetic analyses (Crous *et al.* 2009c). The phylogenetic analyses in the present study corroborated the previous findings, placing *Lecanosticta* species in a well-supported clade (Fig. 1, clade 68; Fig.

4, clade 6-I) sister to *Phaeophleospora*. Species of *Lecanosticta* have typical phaeophleospora-like conidia, but form acervular conidiomata instead of pycnidial conidiomata. *Lecanosticta acicola* is the causal agent of brown spot needle blight on *Pinus* spp. worldwide, a serious disease that leads to defoliation, dieback and finally tree death. For this reason, it is included on the European quarantine list. *Lecanosticta acicola* was shown to represent a species complex, including *Lecanosticta brevispora* and *Lecanosticta guatemalensis* (Quaedvlieg *et al.* 2012). The epitypification presented by Quaedvlieg *et al.* was not compliant with the code (Art. 9.8) and a new epitypification is therefore proposed.

Lecanosticta brevispora Quaedvlieg & Crous, Persoonia 29: 109. 2012.

Descriptions and illustrations: Quaedvlieg *et al.* (2012).

Materials examined: **Mexico**, on needles of a *Pinus* sp., 24 Oct. 2009, M. de Jesús Yáñez-Morales (**holotype** CBS H-21110, cultures ex-type CBS 133601 = CPC 18092).

Notes: *Lecanosticta brevispora* produces smaller conidia than *Lecanosticta acicula* (Quaedvlieg *et al.* 2012). Based on the phylogenetic analyses, *Lecanosticta brevispora* clusters in the *Lecanosticta* clade (Fig. 1, clade 68; Fig. 4, clade 6-I) as observed in a previous phylogenetic study (Quaedvlieg *et al.* 2012).

Lecanosticta longispora Marm., Mycotaxon 76: 395. 2000.

Description and illustration: Quaedvlieg *et al.* (2012).

Materials examined: **Mexico**, Nuevo León, Galeana, Cerro del Potosí, on *Pinus culminicola*, 6 Jun. 1993, J.G. Marmolejo (**holotype** CFNL); Michoacán State, Zinapecuaro area, on needles of a *Pinus* sp., 24 Oct. 2009, M. de Jesús Yáñez-Morales & C. Méndez-Inocencio (**epitype** designated by Quaedvlieg *et al.* 2012: CBS H-21111, cultures ex-epitype CBS 133602 = CPC 17940); *idem*., culture CPC 17941.

Notes: *Lecanosticta longispora* produces conidia of the same size as *Lecanosticta acicola* but conidia have only 1–3 septa (Marmolejo 2000). Phylogenetically, *Lecanosticta longispora* clusters in the *Lecanosticta* clade (Fig. 1, clade 68; Fig. 4, clade 6-I) as observed in a previous phylogenetic study (Quaedvlieg *et al.* 2012).

Clade 69: *Zasmidium complex* (*Periconiella*, ramichloridium-like, rasutoria-like, stenella-like, *Verrucisporota*, *Zasmidium*)

Zasmidium Fr., Summa Veg. Scand. 2: 407. 1849.
Synonyms: *Periconiella* Sacc., Atti Ist. Veneto Sci. Lett. Arti 3: 727. 1885 (*type species*: *Periconiella velutina* (G. Winter) Sacc. 1885).
Biharia Thirum. & Mishra, Sydowia 7: 79. 1953 (*type species*: *Biharia vangueriae* Thirum. & Mishra 1953).
Stenellopsis B. Huguenin, Bull. Trimestriel Soc. Mycol. France 81: 695. 1966 (*type species*: *Stenellopsis fagraeae* B. Huguenin 1966).
Verrucisporota D.E. Shaw & Alcorn, Austral. Syst. Bot. 6: 273. 1993 (*type species*: *Verrucisporota*

proteacearum (D.E. Shaw & Alcorn) D.E. Shaw & Alcorn 1993).
Verrucispora D.E. Shaw & Alcorn, Proc. Linn. Soc. New South Wales 92: 171. 1967, nom. illeg. (Art. 53.1).

Description (from Braun *et al.* 2013): Hyphomycetous (asexual morphs or asexual holomorphs) or *Zasmidium* with mycosphaerella-like sexual morphs; saprobic or mostly biotrophic, usually foliicolous, symptomless or causing various lesions, ranging from yellowish discolorations to distinct leaf spots. In plant pathogenic species, mycelium mostly immersed as well as superficial, rarely only immersed; hyphae branched, septate, hyaline or almost so to pigmented, pale olivaceous to brown, wall thin to somewhat thickened, immersed hyphae smooth or almost so to faintly rough, external hyphae distinctly verruculose to verrucose (in culture immersed hyphae usually smooth or almost so, aerial hyphae verruculose). *Stromata* lacking to well-developed, pigmented. *Conidiophores* solitary, arising from superficial hyphae, lateral, occasionally terminal, *in vivo* (in plant pathogenic taxa) sometimes also fasciculate, arising from internal hyphae or stromata, semimacronematous to macronematous, in culture occasionally micronematous, cylindrical, filiform, subuliform, straight to strongly geniculate-sinuous, mostly unbranched, aseptate, i.e. reduced to conidiogenous cells, to pluriseptate, subhyaline to pigmented, pale olivaceous to medium dark brown, wall thin to somewhat thickened, smooth to verruculose; *conidiogenous cells* integrated, terminal, occasionally intercalary, rarely pleurogenous, or conidiophores reduced to conidiogenous cells, mostly polyblastic, sympodial, with conspicuous, somewhat thickened and darkened-refractive, planate loci. *Conidia* solitary or catenate, in simple or branched acropetal chains, shape and size variable, ranging from amero- to scolecosporous, aseptate to transversely plurieuseptate, subhyaline to pigmented, pale olivaceous to brown, wall thin to somewhat thickened, smooth or almost so to usually distinctly verruculose (in plant pathogenic species without superficial mycelium always verruculose), hila somewhat thickened and darkened-refractive, planate, conidial secession schizolytic.

Type species: *Zasmidium cellare* (Pers.) Fr. (≡ *Racodium cellare* Pers.).

Zasmidium angulare Batzer & Crous, Persoonia 28: 123. 2012.

Description and illustration: Li *et al.* (2012).

Materials examined: **USA**, Georgia, on fruit surface of *Malus domestica*, Aug. 2005, M. Wheeler (**holotype** CBS H-20931, ex-type culture CBS 132094 = CPC 19042 = GA227B1a).

Notes: *Zasmidium angulare* was the first *Zasmidium* species described in association with sooty blotch and flyspeck symptoms on apple. Phylogenetically, it is closely related to *Zasmidium nocoxi* (Fig. 4, clade 1, Fig. 5, clade I) but can morphologically be distinguished in having shorter conidiophores (Li *et al.* 2012).

Zasmidium anthuriicola (U. Braun & C.F. Hill) Crous & U. Braun, Persoonia 23: 104. 2009.
Basionym: *Stenella anthuriicola* U. Braun & C.F. Hill, Fungal Diversity 22: 33. 2006.

Description and illustration: Braun *et al.* (2006).

Materials examined: **Thailand**, (intercepted at Auckland International Airport, New Zealand), on *Anthurium* sp., 3 Aug. 2005, C.F. Hill 1235 (**holotype** HAL 1870 F, ex-type culture CBS 118742).

Note: In the present study *Zasmidium anthuriicola* is phylogenetically close to *Zasmidium citrigriseum* (Fig. 4, clade 1; Fig. 5, clade III).

Zasmidium arcuatum (Arzanlou *et al.*) Videira & Crous, **comb. nov.** MycoBank MB822807.
Basionym: *Periconiella arcuata* Arzanlou *et al.*, Stud. Mycol. 58: 65. 2007.

Description and illustration: Arzanlou *et al.* (2007).

Materials examined: **South Africa**, Western Cape Province, Kogelberg, on dead culms of *Ischyrolepis subverticillata*, May 2001, S. Lee (**holotype** CBS H-19927, culture ex-type CBS 113477).

Notes: The present species was previously known as *Periconiella arcuata*, but the type of *Periconiella*, *Periconiella velutina*, is combined into *Zasmidium* in the present study based on morphology and phylogenetic data (see notes under *Zasmidium cellare*). Based on the phylogenetic analysis, the present species is represented by a single-strain lineage (Fig. 4, clade 1, Fig. 5, clade VIII). It is unique in producing large obclavate conidia that are pale olive, coarsely verrucose and straight to curved (Arzanlou *et al.* 2007).

Zasmidium aucklandicum (U. Braun & C.F. Hill) U. Braun, Polish Bot. J. 55: 289. 2010.
Basionym: *Stenella aucklandica* U. Braun & C.F. Hill, Australas. Pl. Pathol. 32: 96. 2003.

Description and illustration: Braun *et al.* (2003b).

Materials examined: **New Zealand**, on *Geniostoma rupestre*, 15 Oct. 2005, C.F. Hill 6000, culture CPC 13569; Auckland, Grey Lynn, Western Springs Park, on *Geniostoma rupestre*, 14 Apr. 2001, C.F. Hill 402-A (**holotype** HAL 1726 F).

Note: Based on the phylogenetic analyses, *Zasmidium aucklandicum* is closely related to *Zasmidium pittospori* (Fig. 4, clade 1; Fig. 5, clade VII), which is also found in New Zealand but on a different host (*Pittosporum tenuifolium*; *Pittosporaceae*).

Zasmidium biverticillatum (Arzanlou & Crous) Videira & Crous, **comb. nov.** MycoBank MB822827.
Basionym: *Ramichloridium biverticillatum* Arzanlou & Crous, Stud. Mycol. 58: 72. 2007.
Synonyms: *Ramichloridium musae* Stahel, Trop. Agric., Trinidad 14: 43. 1937, nom. inval., Art. 36.
Periconiella musae Stahel ex M.B. Ellis, Mycol. Pap. 111: 5. 1967, non *Zasmidium musae* (Arzanlou & Crous) Crous & U. Braun, 2010.
Ramichloridium musae (Stahel ex M.B. Ellis) de Hoog, Stud. Mycol. 15: 62. 1977.

Description and illustration: Arzanlou *et al.* (2007).

Materials examined: **Surinam**, on *Musa sapientum*, isol. and dep. G. Stahel, Aug. 1936, culture CBS 335.36.

Notes: The genus *Ramichloridium*, based on the type *Ramichloridium apiculatum*, belongs to the *Dissoconiaceae* (Fig. 1, clade 95; Fig. 4, clade 31). Based on the phylogenetic analyses, the current species belongs to the genus *Zasmidium* (Fig. 4, clade 1; Fig. 5, clade V). *Zasmidium biverticillatum* is closely related to *Zasmidium musigenum* (= *Ramichloridium musae*), but produces profusely branched conidiophores and smaller conidia (Arzanlou *et al.* 2007).

Zasmidium cellare (Pers.) Fr., Summa Veg. Scand. 2: 407. 1849.
Basionym: *Racodium cellare* Pers., Neues Mag. Bot. 1: 123. 1794.
Synonyms: *Antennaria cellaris* (Pers.) Fr., Syst. Mycol. 3: 229. 1829.
Cladosporium cellare (Pers.) Schanderl, Arch. Hyg. Bakteriol.: 117. 1936.
Rhinocladiella cellaris (Pers.) M.B. Ellis, Dematiaceous Hyphomycetes: 248. 1971.
Rhinocladiella ellisii D. Hawksw., Taxon 26: 208. 1977.

Description and illustration: Arzanlou *et al.* (2007).

Materials examined: **Europe**, on wall in wine cellar, unknown collector and date, isol. and dep. H. Schanderl, Jun. 1936 (**neotype** designated here, preserved as metabolically inactive, CBS 146.36, MBT378698) duplicate cultures are ATCC 36951 = IFO 4862 = IMI 44943 = LCP 52.402 = LSHB BB274 = MUCL 10089, MBT378698; **Germany**, Lorch am Rhein, on wall in wine cellar, Aug. 1985, M. Schlag, CBS H-3980, culture CBS 892.85.

Notes: *Zasmidium* was introduced for the stenella-like fungi belonging to the *Mycosphaerellaceae*, since the type species of *Stenella* (*Stenella araguata*) clustered in the *Teratosphaeriaceae* (Arzanlou *et al.* 2007, Braun *et al.* 2010a, b, Kamal 2010, present study Fig. 1, clade 98; Fig. 4, clade 33). The type specimen of *Zasmidium cellare* (based on *Racodium cellare*, from wine cellars in Europe and America) could not be located and the species needed to be neotypified. Morphologically, *Stenella* and *Zasmidium* species are very similar and are usually distinguished by the shape of the conidiogenous loci, which is planate in *Zasmidium* and more pileate in *Stenella* (Braun *et al.* 2013).

Based on the phylogenetic analyses of dataset 4, several terminal branches are highly supported but the backbone is usually poorly supported except for a very basal branch that includes various other genera like *Verrucisporota*, *Ramichloridium*, *Rasutoria*, *Stenella* and *Periconiella* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clades I–IX). In order to improve the tree resolution, supplementary phylogenetic analyses were performed including these zasmidium-like and closest related species in dataset 4 (Fig. 4, clades 1–7), using both Bayesian and parsimony methods (PBS), and including three genes (LSU, ITS and *rpb2*). Based on these analysis, there is strong support from both Bayesian and parsimony methods for keeping these species together (Fig. 5, clades I-IX). Based on the parsimony analysis these clades (Fig. 5, clades I–VIII) cluster in a basal polytomy, with one clade being excluded but closely related (Fig. 5, clade IX). Morphologically, there was also not a clear pattern that could be observed based on the most strongly supported terminal branches that justified the division of this generic complex in multiple genera. Species with a simple conidiophore are more common than with branched conidiophores, a characteristic only found in Fig. 5, clades V (e.g. *Zasmidium biverticillatum*) and VIII (e.g. *Zasmidium velutinum*). Conidiogenous cells terminal and forming rachis can be

found in Fig. 5, clades I (e.g. *Zasmidium cerophilum*) and V (e.g. *Zasmidium musae-banksii*) while conidiogenous cells both terminal and intercalary forming rachis can be found in Fig. 5, clades IV (e.g. *Z. strelitziae*), V (e.g. *Z. musigenum*) and VIII (e.g. *Zasmidium arcuata*). Species with short and catenate conidia are only found on Fig. 5, clades I (e.g. *Zasmidium fructicola*) and II (e.g. *Zasmidium pseudoparkii*) while species with shorter but single conidia can be found in Fig. 5, clades I (e.g. *Zasmidium syzygii*), IV (e.g. *Zasmidium strelitziae*), V (e.g. *Zasmidium musigenum*), VIII (e.g. *Zasmidium hakeae*) and IX (e.g. *Zasmidium iteae*). Species with single and long-obclavate conidia are less common in Fig. 5, clade I (e.g. *Zasmidium angulare*) but appear often in Fig. 5, clades III (e.g. *Zasmidium citri-griseum*), VI (*Zasmidium grevilleae*), VII (e.g. *Zasmidium pittospori*), VIII (e.g. *Zasmidium daviesiae*) and IX (e.g. *Zasmidium queenslandicum*).

Species of the genus *Verrucisporota* (Shaw & Alcorn 1993, Beilharz & Pascoe 2002) are barely distinguishable from *Zasmidium* based on morphological traits and phylogenetically cluster with *Zasmidium* strains (Crous *et al.* 2009a; present study, Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade VI, clade VIII). Although the exact phylogenetic position of the type species, *Verrucisporota proteacearum*, is unknown, the fact that a representative strain clustered among *Zasmidium* species led previous authors to consider the genus *Verrucisporota* as a synonym of *Zasmidium* (Braun *et al.* 2013). Therefore, we propose the combination of these names into *Zasmidium*.

The genus *Ramichloridium* was phylogenetically delimited with the sequencing of the type species (*Ramichloridium apiculatum*) that clustered in *Dissoconiaceae* (Arzanlou *et al.* 2007; this study Fig. 1, clade 95; Fig. 4, clade 31). New combinations are proposed for the *Ramichloridium* species that cluster within the *Zasmidium* clade, among which are included two species involved in the banana speckle disease, namely *Ramichloridium musae* and *Ramichloridium biverticillatum* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade V).

The genus *Periconiella* is based on *Periconiella velutina*, isolated from *Brabejum stellatifolium* (South Africa), and is known to be a polyphyletic genus (Arzanlou *et al.* 2007; present study Fig. 1, clade 69, 70, 85; Fig. 4, clade 1, 2, 21; Fig. 5, clades VIII, X). Morphologically, *Periconiella* species are zasmidium-like with pigmented conidiophores and conidia, smooth to verruculose, with conidiogenous cells polyblastic and with planate scars and were usually distinguished by producing conidiophores that are prominently branched in the upper part (Arzanlou *et al.* 2007). Based on the phylogenetic position of the type species *Periconiella velutina* and the morphological characters of the genus, we propose to reduce *Periconiella* to synonymy under *Zasmidium*, which is the older name.

Rasutoria was established by Barr (1987), based on *Rasutoria abietis* (on *Abies amabilis*, USA), to accommodate species with hyaline to brown ascospores occurring on *Gymnospermae*. The genus currently accommodates four species that are only known from their sexual morph. *Rasutoria tsugae* and *Rasutoria pseudotsugae*, which are important pathogens of Douglas-fir (Winton *et al.* 2007), have hyaline ascospores, while *Rasutoria abietis* and *Rasutoria terrieri* have pale brown to brown ascospores. Hyaline ascospores is a typical morphological characteristic in the *Mycosphaerellaceae* (Aptroot 2006). Only *Rasutoria pseudotsugae* and *Rasutoria tsugae* have cultures and DNA sequences available that place them among *Zasmidium* species (Fig. 1, clade 69; Fig. 4, clade 1, Fig. 5, clade VIII), and closely related to *Zasmidium pseudovespa* (= *Mycosphaerella pseudovespa*), which also produces hyaline ascospores (Carnegie *et al.* 2007). Therefore, these two species are placed in the genus *Zasmidium*, while *Rasutoria abietis* and *Rasutoria terrieri* need to be recollected in order to determine their correct phylogenetic position, as well as the position of the genus *Rasutoria*.

The clade at the bottom of the *Zasmidium* complex (Fig. 5, clade IX) includes species that are mostly ramichloridium-like, with a straight conidiophore and polyblastic intercalary and terminal conidiogenous cells producing single or short catenate obovoid conidia. However, the species *Zasmidium queenslandicum* in this clade has a typical *Zasmidium* morphology, similar to *Zasmidium musicola* (Fig. 5, clade III) and *Zasmidium musae* (Fig. 5, clade VIII). Therefore, based on phylogenetic support and morphological similarities these species are considered part of the genus *Zasmidium*.

Zasmidium cerophilum (Tubaki) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822808.
Basionym: *Acrotheca cerophila* Tubaki, J. Hattori Bot. Lab. 20: 143. 1958.
Synonyms: *Cladosporium cerophilum* (Tubaki) Matsush., Icones Microfungorum a Matsushima lectorum: 34. 1975.
Ramichloridium cerophilum (Tubaki) de Hoog, Stud. Mycol. 15: 74. 1977.
Description and illustration: Arzanlou *et al.* (2007).

Material examined: **Japan**, on *Sasa* sp., May 1955, K. Tubaki (**holotype** preserved in Nagao Institute, culture ex-type of *Acrotheca cerophila* CBS 103.59 = MUCL 10034).

Notes: The present species is phylogenetically placed within the *Zasmidium* clade (Fig. 4, clade 1; Fig. 5, clade I) among typical *Zasmidium* species. *Zasmidium cerophilum* is closely related to *Zasmidium fructigenum*, but is more similar morphologically to *Zasmidium eucalypticola* by producing terminal and short rachis-like conidiogenous cells and secondary conidia (Arzanlou *et al.* 2007). *Zasmidium cerophilum* can be morphologically distinguished from *Z. musigenum*, *Zasmidium musae-banksii* and *Zasmidium biverticillatum* by the production of secondary conidia and its distinct conidial hila.

Zasmidium citri-griseum (F.E. Fisher) U. Braun & Crous, IMA Fungus 5: 337. 2014.
Basionym: *Cercospora citri-grisea* F.E. Fisher, Phytopathology 51: 300. 1961.
Synonyms: *Stenella citri-grisea* (F.E. Fisher) Sivan., Bitunicate Ascomycetes and their Anamorphs: 226. 1984.
?*Mycosphaerella citri* Whiteside, Phytopathology 62: 263. 1972.
?*Zasmidium citri* (Whiteside) Crous, Persoonia 23: 105. 2009.

Descriptions and illustrations: Braun *et al.* (2014), Huang *et al.* 2015).

Materials examined: **China**, Yunnan prov., Mengdian, on leaves with yellow spot of *Citrus limon*, Jul. 2011, L. Zhu, cultures ZJUM 103 = CPC 24500, ZJUM 104 = CPC 24501; on leaf with yellow spot of *Citrus aurantifolia*, Jul. 2011, L. Zhu, culture ZJUM 105 = CPC 24502; Zhejiang prov., Cangnan, on leaf with yellow spot of *Citrus grandis*, Dec. 2009, L. Zhu, culture ZJUM 5 = CPC 24464; Changshan, on leaves of *Citrus paradisi* × *Citrus* sp., May 2009, L. Zhu, culture ZJUM 25 = CPC 24468, ZJUM 27 = CPC 24469; Nov. 2011, L. Zhu, culture ZJUM 54 = CPC 24474; Huangyan, on leaf with big round spot of *Citrus reticulata*, Apr. 2010, L. Zhu, culture ZJUM 81 = CPC 24488; Yuhuan, on leaf with greasy spot of *C. grandis*, Nov. 2011, L. Zhu, culture ZJUM 97 = CPC 24497; Jiangshan, on leaf with brown small round spot of *C. paradisi* × *Citrus* sp., Apr. 2013, F. Huang, culture ZJUM 127 = CPC 24504. Thailand, on living leaves of *Eucalyptus* sp., 2006, W. Himaman, culture CPC 13467; Chonburi, on living

leaves of seedlings of *Acacia mangium*, 19 Nov. 2002, M.J. Wingfield, culture CPC 10522 = CBS 116366. **USA**, Florida, Polk County, Babson Park, on *C. limon*, 15 Jan. 1958, F.E. Fisher (presumably lost); single ascospore isolates, associated with citrus greasy leaf spot disease symptoms, *Citrus* sp. 2003, R.C. Ploetz, cultures CPC 15289, CPC 15290 = CBS 122455, CPC 15294, CPC 15285, CPC 15291, CPC 15293; on leaves of *Musa* sp., 2003, J. Cavaletto, culture CBS 116426; Florida, Lake Alfred & Haines City, on *Citrus* sp., May 1970, F.E. Fisher (**neotype** designated by Braun *et al.* 2014: IMI 148810); single ascospore isolates, associated with citrus greasy leaf spot disease symptoms, *Citrus* sp., 2003, S.N. Mondal (**epitype** designated by Huang *et al.* 2015: CBS H-22176, culture ex-epitype CBS 139467 = CPC 15296).

Notes: See Braun *et al.* (2014) for the detailed description of the neotype and Huang *et al.* (2015) for the epitype details. Based on the phylogenetic analyses, *Zasmidium citri-griseum* clusters within the *Zasmidium* clade (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade III) and is closely related to *Zasmidium anthuricola*.

Zasmidium daviesiae (Cooke & Massee) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822828.
Basionym: *Cercospora daviesiae* Cooke & Massee, Grevillea 18: 7. 1889.
Synonyms: *Verrucisporota daviesiae* (Cooke & Massee) Beilharz & Pascoe, Mycotaxon 82: 360. 2002.
Mycosphaerella daviesiicola Beilharz & Pascoe, Mycotaxon 82: 364. 2002.

Description and illustration: Chupp (1954), Beilharz & Pascoe (2002).

Materials examined: **Australia**, Victoria, on road from Merimbah to Circuit road, 3.4 km short of Mt. Stirling, on *Daviesia mimosoides* (= *D. cormybosa* var. *mimosoides*), 30 Dec. 2003, V. & R. Beilharz, culture VPRI 31767 = CBS 116002.

Notes: The type of *Zasmidium daviesiae*, based on *Cercospora daviesiae*, was isolated from leaves of *Daviesia latifolia* (Victoria, Australia, K) which is a different host from the examined strain. Phylogenetically, the present specimen clusters among *Zasmidium* species (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade VIII), as defined in the present study, and is closely related to *Zasmidium velutinum* (= *Periconiella velutinae*), but the latter species produces branched conidiophores with terminal polyblastic conidiogenous cells and shorter conidia (Arzanlou *et al.* 2007). Morphologically, the examined material is similar to *Zasmidium* spp. by producing polyblastic, intercalary and terminal conidiogenous cells with conidiogenous loci darkened and planate, which give rise to long-obclavate, multiseptate, verruculose conidia (Beilharz & Pascoe 2002).

Zasmidium elaeocarpi U. Braun, C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822718. Fig. 39.

Etymology: Derived from the host genus on which it occurs, *Elaeocarpus*.

Description in vitro (on SNA): *Mycelium* composed of hyaline and pale brown to dark blackish brown hyphae, verruculose, septate, branching, uniform in width, 2.5 µm. *Conidiophores* arising from hyphae, micro- to macronematous, pale olivaceous brown to pale blackish brown, finely

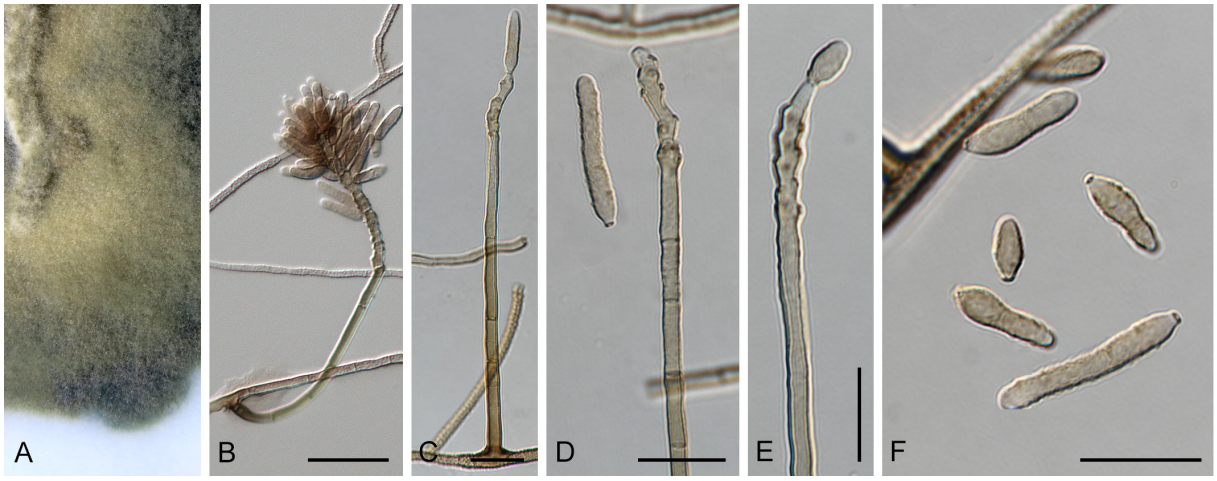


Fig. 39. *Zasmidium elaeocarpi* (CPC 16640). A–F. Observations *in vitro*. A. Culture on OA. B, C. Conidiophore, conidiogenous cells and conidia. D, E. Partial conidiophore, conidiogenous cells and conidia. F. Conidia. Scale bars = 10 µm.

verruculose, straight or slightly curved, frequently geniculate, rugged or rugose at the upper part, 25–450 × 3.5–5 µm. *Conidiogenous cells* integrated, apical or intercalary, polyblastic, proliferating sympodially, with numerous rim-like conidiogenous loci, thickened and darkened, dispersed through the entire cells, forming a single or multicelled rachis (ramichloridium-like), 1–1.5 µm diam. *Conidia* solitary, occasionally catenate, pale blackish brown to pale olivaceous brown, verruculose, ellipsoidal, cylindrical to obclavate, base obconically truncate and apex rounded, straight or curved, 10–75 × 2.5–4 µm, 0-7-euseptate, sometimes constricted at septa, with hila thickened and darkened, 1–1.5 µm diam.

Materials examined: **Australia**, New South Wales, north-west of Grafton, North Washpool State Forest, on *Elaeocarpus kirtonii*, 1 Mar. 2009, B. Summerell (**holotype** CBS H-22960, ex-type culture CBS 142187 = CPC 16642); *idem*. culture CPC 16640.

Notes: *Zasmidium elaeocarpi* is morphologically similar to *Zasmidium iteae* by producing ramichloridium-like polyblastic conidiogenous cells on a short rachis with thickened and darkened scars, and verruculose conidia that are solitary or catenate. *Zasmidium elaeocarpi* can be distinguished by producing longer conidiophores and longer and wider conidia than *Zasmidium iteae* (Kirschner *et al.* 2004). Based on the phylogenetic analysis, these two species are closely related and cluster in the same clade within the *Zasmidium* complex (Fig. 4, clade 1; Fig. 5, clade IX).

Zasmidium eucalypticola U. Braun, C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822724. Fig. 40.

Etymology: Composed of *Eucalyptus* (host genus) and -cola (dweller).

Description in vitro (on SNA; CPC 15149): *Mycelium* composed of hyaline, subhyaline, or pale olivaceous brown hyphae, smooth to rough, uniform in width 2–2.5 µm. *Conidiophores* micro- to macronematous, arising from hyphae, pale olivaceous brown to olivaceous brown, somewhat paler towards the apex, verruculose, simple, septate, straight to slightly curved, uniform in

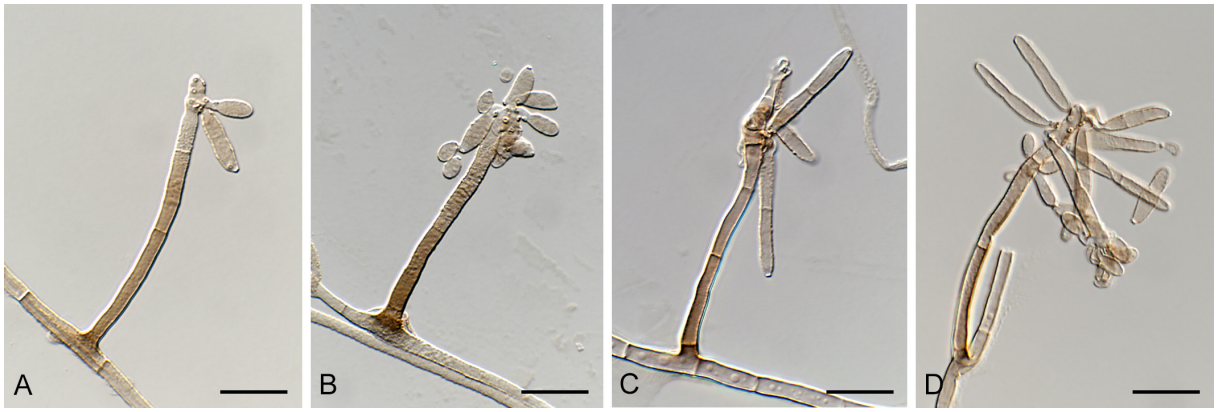


Fig. 40. *Zasmidium eucalypticola* (CPC 15149). A–D. Conidiophores and conidia observed *in vivo*. Scale bars = 10 µm.

width, rugged or geniculate at the apex, 38–63 × 3–3.5 µm. *Conidiogenous cells* integrated, apical, polyblastic, proliferating sympodially, with rim-like conidiogenous loci, thickened and darkened, located apically and lateraly as in a short rachis (ramichloridium-like), 1.5–2 µm diam. *Conidia* solitary, sometimes bearing conidia by microcyclic conidiation, pale olivaceous brown, verruculose, ovoid to cylindrical, base obconically truncate and apex rounded, 7.5–20 × 2.5–4 µm, 0–1-septate, hila thickened and darkened.

Material examined: **Brazil**, Minas Gerais, Viçosa, Paraíso, on *Eucalyptus* sp., 1 Mar. 2008, coll. A.C. Alfenas, isol. P.W. Crous (**holotype** CBS H-22959, ex-type culture CBS 142186 = CPC 15149).

Notes: Phylogenetically, the present species is closely related to *Zasmidium syzygii* (Fig. 4 clade 1; Fig. 5, clade I) but they are morphologically distinct. *Zasmidium eucalypticola* produces conidiogenous cells that are rachis-like with broader scars and smaller ovoid conidia. *Zasmidium syzygii* produces conidiogenous cells with smaller scars and multiseptate conidia that are longer and narrowly obclavate (Crous *et al.* 2012a). Based on a BLAST comparison against the alignment, *Zasmidium eucalypticola* shares 99 % (481/486) similarity on ITS and 97 % (714/737) similarity on *rpb2* with *Zasmidium syzygii*.

Zasmidium eucalyptorum (Crous & M.J. Wingf.) Quaedvlieg & Crous, Persoonia 33: 24. 2014. *Basionym*: *Mycosphaerella eucalyptorum* Crous & M.J. Wingf., Stud. Mycol. 55: 112. 2006.

Description and illustration: Crous *et al.* (2006c).

Material examined: **Indonesia**, on leaves of *Eucalyptus urophylla*, Mar. 2004, M.J. Wingfield (**holotype** CBS H-19689, ex-type culture CBS 118500 = CPC 11174).

Notes: The present species is only known from its sexual morph that is mycosphaerella-like and produces ascospores (12–17 × 3.5–4.5 µm) that germinate in a Type B germination pattern (Crous *et al.* 2006c). Based on the phylogenetic analyses *Zasmidium eucalyptorum* is closely related to *Zasmidium pseudoparkii* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade II), which is also a pathogen of *Eucalyptus* but was originally described from Colombia.

Zasmidium fructicola Crous *et al.*, Mycologia 107: 1165. 2015.

Description and illustration: Huang *et al.* (2015).

Materials examined: **China**, Zhejiang Prov., Huangyan, on fruit of *Citrus reticulata*, Jan. 2010, X.H. Wang, **holotype** CBS H-22177, culture ex-type ZJUM 80 = CPC 24487 = CBS 139625; Huangyan, on fruit with citrus black spot of *Citrus unshiu*, Jan. 2010, X.H. Wang, culture ZJUM 84 = CPC 24489; Cangnan, on fruit with greasy spot of *Citrus grandis*, Oct. 2010, L. Zhu, culture ZJUM 9 = CPC 24465; Changshan, on fruit with yellow spot of *Citrus paradisi* × *Citrus* sp., Nov. 2010, L. Zhu, cultures ZJUM 48 = CPC 24472, ZJUM 50 = CPC 24473; on fruit with black dot of *C. paradisi* × *Citrus* sp., Dec. 2010, L. Zhu, culture ZJUM 55 = CPC 24475; Linhai, on fruit with black dot of *C. sinensis*, Nov. 2010, G.Q. Chen, culture ZJUM 89 = CPC 24494); Fujian Prov., on fruit with greasy spot of *C. grandis*, Nov. 2010, L. Zhu, culture ZJUM 58 = CPC 24477; Nanjing, on fruit with greasy spot of *C. grandis*, Nov. 2009, L. Zhu, culture ZJUM 90 = CPC 24495; Guangdong Prov., Pingyuan, on fruit with citrus black spot of *Citrus sinensis*, Nov. 2009, X.H. Wang, culture ZJUM 68 = CPC 24479; Hunan Prov., Jishou, on fruits of *C. reticulata*, Nov. 2011, X.H. Wang, cultures ZJUM 77 = CPC 24484, ZJUM 78 = CPC 24485, ZJUM 79 = CPC 24486.

Notes: Based on the phylogenetic analyses, *Zasmidium fructicola* is closely related to *Zasmidium fructigenum* (Fig. 4, clade 1; Fig. 5, clade I) which agrees with the original assessment by Huang *et al.* (2015). These two species are morphologically similar, but *Zasmidium fructicola* produces darker and wider conidia than *Zasmidium fructigenum* (conidia pale brown, 5–15 × 2 µm; Huang *et al.* 2015).

Zasmidium fructigenum Crous *et al.*, Mycologia 107: 1165. 2015.

Description and illustration: Huang *et al.* (2015).

Materials examined: **China**, Zhejiang Prov., Changshan, on fruit with greasy spot of *Citrus paradisi* × *Citrus* sp., Nov. 2009, L. Zhu (**holotype** CBS H-22178, culture ex-type ZJUM 36 = CPC 24471 = CBS 139626); Yuhuan, on fruits with greasy spot of *Citrus grandis*, Nov. 2010, L. Zhu, cultures ZJUM 99 = CPC 24498, ZJUM 100 = CPC 24499; Linhai, on fruit with black dot of *Citrus reticulata* (= *Citrus unshiu*), Nov. 2010, G.Q. Chen, culture ZJUM 88 = CPC 24493; Jiangxi Prov., on fruit with citrus black spot of *Citrus reticulata*, Nov. 2010, X.H. Wang, cultures ZJUM 86 = CPC 24491, ZJUM 87 = CPC 24492.

Note: See notes on *Zasmidium fructicola*.

Zasmidium grevilleae Crous & Summerell, **sp. nov.** MycoBank MB822721.
Basionym: *Verrucisporota grevilleae* Crous & Summerell, Persoonia 22: 155. 2009, nom. inval. (Art. 40.6).

Etymology: Derived from the host genus on which it occurs, *Grevillea*.

Description and illustration: Crous *et al.* (2009a).

Materials examined: **Australia**, Northern Territory, Emerald Springs, on leaves of *Grevillea decurrens*, 22 Sep. 2007, B. Summerell (**holotype** CBS H-20205, ex-type culture CBS 124107 = CPC 14761); *idem*. cultures CPC 14762, CPC 14763.

Notes: Crous *et al.* (2009a) proposed the new species *Verrucisporota grevilleae* but did not designate the type specimen at the time, making it an invalid name according to Art. 40.6 (Melbourne). Herewith we designate the original specimen as the holotype for *Zasmidium grevilleae*. *Verrucisporota* is currently considered a synonym of *Zasmidium* based on morphological and phylogenetical evidence (Braun *et al.* 2013). The present species clusters within the genus *Zasmidium* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade VI) as circumscribed in the present study. *Zasmidium grevilleae* can be distinguished from its closest relative, *Verrucisporota proteacearum*, by producing shorter conidiophores and narrower and longer conidia (Shaw & Alcorn 1967; Crous *et al.* 2009a).

Zasmidium gupoyu (R. Kirschner) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822809.
Basionym: *Parastenella gupoyu* R. Kirschner, Fungal Diversity 40: 42. 2010.

Description and illustration: Kirschner & Chen (2010).

Material examined: **Taiwan**, Nantou County, Chitou, ca. 1200 m, on senescent lower leaf of *Alocasia odora*, 19 Mar. 2007, R. Kirschner & S.-H. Wu, 2990-B (**holotype** TNM, isotypes BPI 878812, FR); Taipei County, Wulai, 300 m, on senescent lower leaf of *Alocasia odora*, 22 Feb. 2005, R. Kirschner & C.-J. Chen 2279, 3022 (TNM), culture CBS 122099 = RoKi 3022.

Notes: The present species was originally described in the genus *Parastenella*. However, judging from the SEM photographs (Kirschner & Chen 2010), its loci were distinctly thickened, which is not a character typical of the generic description of *Parastenella*. *Parastenella gupoyu* produces erect, unbranched conidiophores and verruculose hyphae and conidia, characters typical of *Zasmidium s. lat.* The genus *Parastenella* is based on *Parastenella magnolia* (on leaves of *Magnolia grandiflora*, USA) and its current phylogenetic position is unknown because there are no sequence data available. Based on the phylogenetic analyses, the present species clusters in *Zasmidium* (Fig. 1, clade 63; Fig. 4 clade 1; Fig. 5, clade IX) and is closely related to *Zasmidium elaeocarpi*. Morphologically, *Zasmidium gupoyo* can be distinguished from *Zasmidium elaeocarpi* by producing the conidia in short shoulders mostly in the apical area of the conidiogenous cells and by producing long and single conidia.

Zasmidium hakeae U. Braun, C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822723. Fig. 41.

Etymology: Derived from the host genus on which it occurs, *Hakea*.

Description in vitro (on SNA; CPC 15577): *Mycelium* composed of hyaline to subhyaline hyphae, smooth to rough, septate, branching. *Conidiophores* emerging from hyphae, micro- to macronematous, brown to olivaceous brown, paler towards the apex, verruculose, rugose, straight to slightly curved, simple, strongly geniculate at the apex, 200–250 × 2.5–3.8 µm. *Conidiogenous cells* integrated, apical, polyblastic, proliferating sympodially, sometimes also

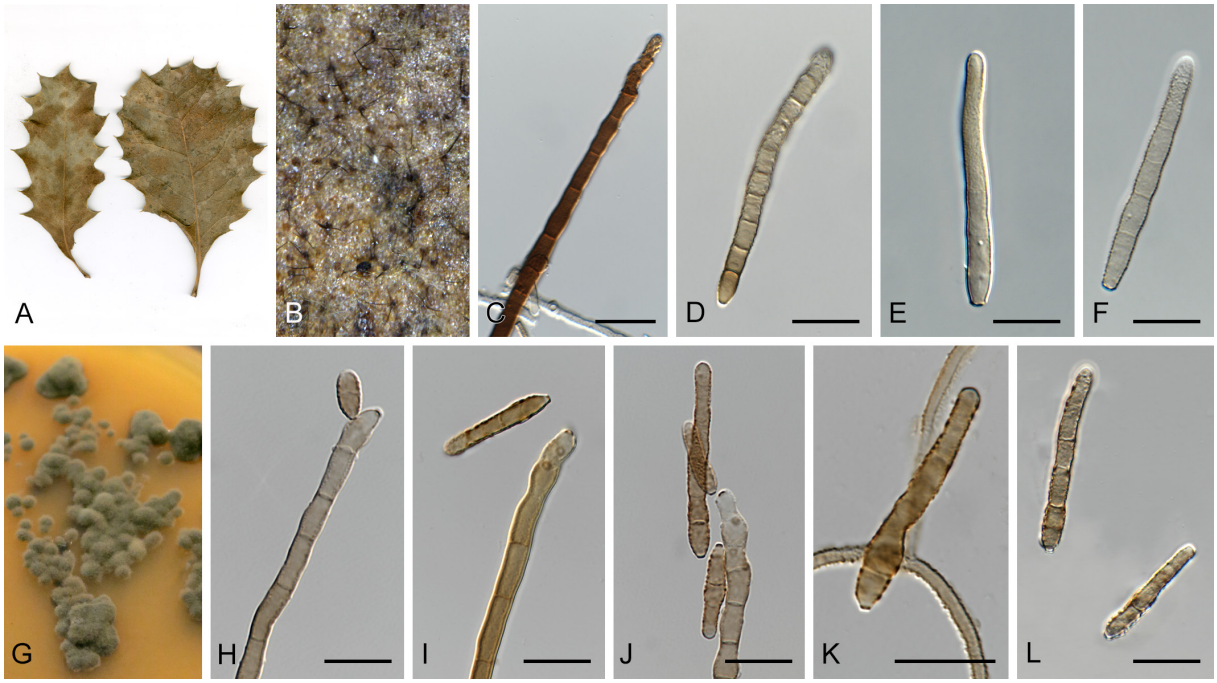


Fig. 41. *Zasmidium hakeae* (CPC 15577). A–F. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Partial conidiophore and conidiogenous cells. D–F. Conidia. G–L. Observations *in vitro*. G. Culture on V8. H–J. Partial conidiophore, conidiogenous cells and conidia. K, L. Conidia. Scale bars = 10 µm.

percurrently, with rim-like conidiogenous loci, thickened and darkened, located apically and laterally in a short rachis, 1.5–2 µm diam. *Conidia* solitary, pale to pale olivaceous brown, verruculose, ellipsoid to obclavate, straight to mildly sinuous, obconically truncate at the base, rounded at the apex, 8–32.5 × 2.5–5 µm, 1–9-septate, hila thickened and darkened, 1.5–2 µm diam.

Materials examined: **Australia**, Western Australia, Pemberton, Steward Road, *Banksia* woodland, on *Hakea undulata*, 2 Aug. 2008, A.R. Wood (**holotype** CBS H-22958, ex-type culture CBS 142185 = CPC 15577); *idem*., culture CPC 15583; Queensland, Norta Nature Reserve, leaves in shop (Loma tea), 13 Jul. 2009, P.W. Crous, culture CPC 17213.

Notes: Based on the phylogenetic analyses, the present species clusters in *Zasmidium* (Fig. 4, clade 1; Fig. 5, clade VIII), and is closely related to *Zasmidium daviesiae*. Morphologically, *Zasmidium hakeae* produces longer and narrower conidiophores and shorter and narrower conidia with more septa than *Zasmidium daviesiae* (conidiophores 16–65 × 5–7 µm, conidia 18–56 × 4.5–7 µm, 0–6-septate; Beilharz & Pascoe 2002). There were two different species isolated from the same herbarium specimen in this study, *Zasmidium hakeae* (CPC 15577) and *Devonomyces endophyticus* (CPC 15580) which indicates they may be co-existing in the same lesions.

Zasmidium indonesianum Crous *et al.*, Mycologia 107: 1166. 2015.

Description and illustration: Huang *et al.* (2015).

Materials examined: **Indonesia**, on leaf spots of *Citrus* sp., 2004, M. Arzanlou (**holotype** CBS H-22179, culture ex-type CBS 139627 = CPC 15300); *idem*., cultures CPC 15301, CPC 15302.

Notes: Based on the phylogenetic analyses, *Zasmidium indonesianum* clusters in the *Zasmidium* clade (Fig. 4, clade 1; Fig. 5, clade III), which is in agreement with the original observations by Huang *et al.* (2015), and is closely related to *Zasmidium musicola*, a pathogen of *Musa* sp. *Zasmidium indonesianum* is a pathogen of *Citrus* sp. and differs from *Zasmidium citri-griseum* by producing shorter and narrower conidiophores and conidia (Braun *et al.* 2014, Huang *et al.* 2015).

Zasmidium iteae (R. Kirschner) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822810.
Basionym: *Stenella iteae* R. Kirschner, Fungal Diversity 17: 58. 2004.

Description and illustration: Kirschner *et al.* (2004).

Materials examined: **Taiwan**, Pingtung, Nanrenshan, on leaves of *Itea parviflora*, 2 Jun. 2002, R. Kirschner & C.-J. Chen (**holotype** TNM, culture ex-type CBS 113094 = RoKi 1279).

Notes: The present species was originally described in the genus *Stenella* (Kirschner *et al.* 2004), which is currently accommodated in *Teratosphaeriaceae* (Fig. 1, clade 98). As a consequence of the circumscription of the genus *Stenella* based on its type, several stenella-like species in the *Mycosphaerellaceae* were assigned to the genus *Zasmidium* (Braun *et al.* 2010a). Based on the phylogenetic analysis, the present species clusters in *Zasmidium* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade IX), and is closely related to *Zasmidium elaeocarpi*. Morphologically, *Zasmidium iteae* can be distinguished from *Zasmidium elaeocarpi* by producing shorter conidiophores and shorter and narrower conidia (Kirschner *et al.* 2004).

Zasmidium lonicericola (Y.H. He & Z.Y. Zhang) Crous & U. Braun, Persoonia 23: 140. 2009.
Basionym: *Cladosporium lonicericola* Yong H. He & Z.Y. Zhang, Mycosystema 20: 469. 2001.
Synonyms: *Stenella lonicericola* (Yong H. He & Z.Y. Zhang) K. Schub. *et al.*, Fungal Diversity 20: 204. 2005.
Cladosporium lonicerae Sawada, Rep. Gov. Res. Inst. Formosa 86: 163. 1943, nom. inval. (Art. 39.1).

Description and illustrations: See Crous *et al.* (2009d).

Materials examined: **Republic of Korea**, Yangpyong, on leaves of *Lonicera japonica*, 23 Jul. 2004, H.D. Shin, herb. HAL 3240 F; Hongchon, on leaves of *Lonicera japonica*, 30 Oct. 2004, H.D. Shin [**epitype** of *Cladosporium lonicericola* designated here: CBS H-20271, MBT378604, (**holotype** MHYAU 03533), culture ex-epitype CBS 125008 = CPC 11671]; *idem*., cultures CPC 11672, CPC11673. **Taiwan**, Taipei, on leaves of *Lonicera japonica* var. *sempervillosa*, 20 Dec. 1914, K. Sawada (authentic material of *Cladosporium lonicerae*, BPI 427243).

Notes: The taxonomic history of the present species was addressed by several authors (Zhang *et al.* 2003, Schubert & Braun 2005, Crous *et al.* 2009d). The epitypification of *Cladosporium lonicericola* by Crous *et al.* (2009d) was not compliant with the code (Art. 9.8) since the holotype

was not cited. Based on the phylogenetic analyses this species clusters in *Zasmidium* (Fig. 4, clade 1; Fig. 5, clade I), and is closely related to *Zasmidium cerophilum*. The morphological characteristics and scar type (planate instead of pileate), of this species confirms its placement in *Zasmidium*.

Zasmidium musae (Arzanlou & Crous) Crous & U. Braun, Schlechtendalia 20: 102. 2010.
Basionym: *Stenella musae* Arzanlou & Crous, Persoonia 20: 31. 2008.

Description and illustration: Arzanlou *et al.* (2008).

Materials examined: **France**, Martinique, on *Musa* sp., unknown collector and date, culture CBS 121384 = CIRAD 41 = X877. **Tonga**, Aciar Plot, Tongatapu, on *Musa* cv. TU8 AAAA, Mar. 1990, R.A. Fullerton (**holotype** of *Stenella musae*, CBS H-20047, ex-type culture X745 = CBS 122477). **Netherlands Antilles**, Windward Islands, St Lucia, on *Musa* cv., 2003, E. Reid, culture X47 = CBS 122476; St. Lucia, on *Musa* cv., 2003, E. Reid, culture CBS 122478 = X70.

Note: Based on the phylogenetic analyses *Zasmidium musae* clusters in the *Zasmidium* clade (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade VII), and is closely related to *Zasmidium aucklandicum*, which agrees with previous observations by Arzanlou *et al.* (2008).

Zasmidium musae-banksii Videira & Crous, **nom. nov.** MycoBank MB822830.
Replaced synonym: Ramichloridium australiense Arzanlou & Crous, Stud. Mycol. 58: 69. 2007, non *Zasmidium australiense* (J.L. Mulder) U. Braun & Crous 2010.

Description and illustration: Arzanlou *et al.* (2007).

Material examined: **Australia**, Queensland, Mount Lewis, Mount Lewis Road, 16°34047.200 S, 145°190700 E, 538 m alt., on *Musa banksii* leaf, Aug. 2006, P.W. Crous & B. Summerell (**holotype** CBS H-19928, culture ex-type CBS 121710).

Notes: Based on the phylogenetic analyses and morphological characters, the present species belongs to the genus *Zasmidium* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade V). The phylogenetic position of *Ramichloridium* is defined by the type, *Ramichloridium apiculatum*, in *Dissoconiaceae* (Fig. 1, clade 83; Fig. 4, clade 28).

Zasmidium musicola (Arzanlou & Crous) Crous & U. Braun, Schlechtendalia 20: 102. 2010.
Basionym: *Stenella musicola* Arzanlou & Crous, Persoonia 20: 33. 2008.

Description and illustration: Arzanlou *et al.* (2008).

Material examined: **India**, Tamil Nadu, Tiruchirapally, on leaf of *Musa* cv. Grand Nain AAA (Cav.), 23 Feb. 2005, I. Buddenhagen (**holotype** CBS H-20046, culture ex-type CBS 122479 = X1019).

Notes: *Zasmidium musicola* (as *Stenella musicola*) was described from *Musa* sp. and found to be both phylogenetically and morphologically close to *Zasmidium citri-griseum* (Arzanlou *et*

al. 2008). These results are corroborated by the phylogenetic analyses in the present study (Fig. 4, clade 1; Fig. 5, clade III).

Zasmidium musigenum Videira & Crous, **nom. nov.** MycoBank MB822831.
Replaced synonym: *Veronaea musae* Stahel ex M.B. Ellis, in Ellis, More Dematiaceous Hyphomycetes: 209. 1976, non *Zasmidium musae* (Arzanlou & Crous) Crous & U. Braun 2010.
Synonyms: *Chloridium musae* Stahel, Trop. Agric., Trinidad 14: 43. 1937, *nom. inval*. (Art. 39.1).
Ramichloridium musae (Stahel ex M.B. Ellis) de Hoog, Stud. Mycol. 15: 62. 1977.
Misapplied name: *Chloridium indicum* Subram., sensu Batista & Vital, Anais Soc. Biol. Pernambuco 15: 379. 1957.

Description and illustration: Arzanlou *et al.* (2007).

Materials examined: **Cameroon**, from *Musa sapientum*, J.E. Heron, culture CBS 169.61 = ATCC 15681 = IMI 079492 = DAOM 84655 = MUCL 2689. **Suriname**, Paramaribo, from *Musa sapientum* leaf, G. Stahel (authentic material of *Chloridium musae*, CBS H-19933, culture CBS 365.36 = JCM 6973 = MUCL 9556). **Unknown**, from *Musa sapientum*, J. Brun, culture CBS 190.63 = MUCL 9557.

Notes: The type specimen of *Zasmidium musigenum*, based on *Veronaea musae*, was isolated from *Musa sapientum* from Jamaica (type IMI 23006), which is a different location from the examined strains. Based on the phylogenetic analysis, *Zasmidium musigenum* belongs to *Zasmidium* as circumscribed in the present study (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade V), and is closely related to *Zasmidium musae-banksii*. *Zasmidium musigenum* and *Zasmidium musae-banksii* are both pathogens of *Musa* sp. and are morphologically similar, but *Zasmidium musigenum* produces shorter conidiophores and conidia (Arzanlou *et al.* 2007).

Zasmidium nocoxi Crous, Persoonia 23: 141. 2009.

Description and illustration: See Crous *et al.* (2009d).

Material examined: **USA**, Virginia, Front Royal, on twig debris, 14 May 2007, P.W. Crous (**holotype** CBS H-20272, cultures ex-type CBS 125009 = CPC 14044).

Note: *Zasmidium nocoxi* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade I) produces a synasexual morph similar to *Hyalozasmidium aerohyalinosporium* (Fig. 4, clade 21), revealing this synasexual morph to not be exclusive to the genus *Zasmidium*.

Zasmidium pittospori (U. Braun) U. Braun, Schlechtendalia 20: 102. 2010.
Basionym: *Stenella pittospori* U. Braun, Fungal Diversity 26: 68. 2007.

Description and illustration: See Braun & Crous (2007).

Material examined: **New Zealand**, Auckland, Mt. Albert, on *Pittosporum tenuifolium*, 15 Jul. 2007, C.F. Hill, culture CBS 122274 = ICMP 17098. **China**, Sichuan, Dujiangyan, on *Pittosporum podocarpum*, 20 Sep. 2006, S. Both (**holotype** HAL 1945 F).

Notes: Based on the phylogenetic analyses *Zasmidium pittospori* is closely related to *Zasmidium aucklandicum* and *Zasmidium musae* (Fig. 4, clade 1; Fig. 5, clade VII). Morphologically, it can be distinguished from *Zasmidium musae* by producing longer conidiophores, and longer and wider verruculose conidia (Braun & Crous 2007, Arzanlou 2008).

Zasmidium proteacearum (D.E. Shaw & Alcorn) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822812.
Basionym: *Verrucispora proteacearum* D.E. Shaw & Alcorn, Proc. Linn. Soc. New South Wales. 92: 171. 1967.
Synonym: *Verrucisporota proteacearum* (D.E. Shaw & Alcorn) D.E. Shaw & Alcorn, Austral. Syst. Bot. 6: 273. 1993.

Description and illustrations: Crous *et al.* (2009a).

Material examined: **Australia**, Queensland, Indooroopilly, on *Grevillea* sp., 3 Feb. 2004, J.L. Alcorn, dep. V. Beilharz, culture CBS 116003 = VPRI 31812.

Notes: The type of *Verrucisporota*, *Verrucisporota proteacearum*, was described from the host *Finschia chloroxantha* from Papua New Guinea (**holotype** IMI 77905, fide Shaw & Alcorn 1967). The present strain was isolated from a different host and originates from a different country. In addition, it produced wider conidia than those in the original description (Crous *et al.* 2009a). Therefore, this may be a different species and the precise phylogenetic position of the type of *Verrucisporota* remains unresolved. Nevertheless, given the morphological similarities with *Zasmidium* and phylogenetic placement of the existing strains (Fig. 4, clade 1; Fig. 5, clade VI), *Verrucisporota* was tentatively synonymised with *Zasmidium* (Braun *et al.* 2013).

Zasmidium pseudoparkii (Crous & M.J. Wingf.) Crous & U. Braun, Schlechtendalia 20: 102. 2010.
Basionym: *Stenella pseudoparkii* Crous & M.J. Wingf., Stud. Mycol. 55: 128. 2006.

Description and illustrations: Crous *et al.* (2006c).

Materials examined: **Colombia**, Sinai, on leaves of *Eucalyptus grandis*, May 1995, M.J. Wingfield, culture CBS 110988 = CPC 1090; on leaves of *Eucalyptus* sp., 1995, M.J. Wingfield (**holotype** CBS H-19702, culture ex-holotype CBS 110999 = CPC 1087).

Notes: Phylogenetically, *Zasmidium pseudoparkii* is closely related to *Zasmidium eucalyptorum* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade II). *Zasmidium eucalyptorum* is only known from its sexual morph and produces ascospores that germinate in a Type C pattern (Crous 1998), while ascospores of *Zasmidium pseudoparkii* germinate with a Type D pattern (Crous *et al.* 2006c). The asexual morph of *Zasmidium pseudoparkii* is morphologically similar to *Pseudozasmidium parkii* (Fig. 1, clade 94; Fig. 4, clade 27).

Zasmidium pseudotsugae (V.A.M. Mill. & Bonar) Videira & Crous, **comb. nov.** MycoBank MB822813.
Basionym: *Dimeriella pseudotsugae* V.A.M. Mill. & Bonar, Univ. Calif. Publ. Bot. 19: 405. 1941.

Synonyms: *Epipolaeum pseudotsugae* (V.A.M. Mill. & Bonar) Shoemaker, Canad. J. Bot. 43: 637. 1965.
Rasutoria pseudotsugae (V.A.M. Mill. & Bonar) M.E. Barr, Mycotaxon 29: 502. 1987.

Description and illustration: Farr (1963), Shoemaker (1965).

Description in vivo (adapted from Shoemaker 1965): *Perithecia* clustered on hypophyllous superficial mycelium, spherical, 60–80 µm diam, setose; beak rarely perceptible, usually a paler coloured circular area, 10–15 µm diam, composed of 5–8×3 µm convergent yellow hyphae; wall 10–15 µm wide, of 2 layers of polygonal cells, 9 × 12 µm. *Asci* in a basal cluster, bitunicate, saccate to cylindrical, aparaphysate, 30–40 × 6–10 µm, with 8 biseriate ascospores. *Ascospores* hyaline, smooth, without sheath, 1-septate at middle, wider at upper cell, both cells uninucleate, 9–12(–15) × 2.5–3.5 µm.

Notes: The type specimen of *Zasmidium pseudotsugae*, based on *Dimeriella pseudotsugae*, was isolated from *Pseudotsuga menziesii* from California, USA (**holotype** UC498795, isotypes in CUP, F, NY, BPI, GAM, ILL, MICH, TENN and WIS). The DNA sequences of *Rasutoria pseudotsugae* used in this study were available on GenBank (Table 1) (Winton *et al.* 2007) and no new sequences were generated. See notes on *Zasmidium cellare*.

Zasmidium pseudovespa (Carnegie) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822814.
Basionym: *Mycosphaerella pseudovespa* Carnegie, Mycologia 99: 468. 2007.

Description and illustration: Carnegie *et al.* (2007).

Materials examined: **Australia**, New South Wales, Urbenville, Reid Plantation, native regeneration within plantation boundary, on living leaves of *Eucalyptus biturbinata*, 14 Apr. 2005, A.J. Carnegie (**holotype** DAR 77432, culture ex-type AC0466 = CBS 121159).

Notes: The species *Mycosphaerella pseudovespa* is commonly associated with wasp galls or leaf spots in *Eucalyptus* (Carnegie *et al.* 2007). It was described based solely on the sexual morph which is mycosphaerella-like and produces hyaline ascospores that germinate in a type I pattern (Crous *et al.* 2008). The phylogenetic analyses showed that it is closely related to *Zasmidium velutinum* (Fig. 1, clade 69; Fig. 4, clade 1; Fig. 5, clade VIII). See notes on *Zasmidium cellare*.

Zasmidium queenslandicum (Arzanlou & Crous) Crous & U. Braun, Schlechtendalia 20: 103. 2010.
Basionym: *Stenella queenslandica* Arzanlou & Crous, Persoonia 20: 34. 2008.

Description and illustration: Arzanlou *et al.* (2008).

Material examined: **Australia**, Queensland, Mount Lewis, Mount Lewis Road, 16° 340 47.200 S, 145° 190 700 E, 538 m alt., on leaf of *Musa banksii*, Aug. 2006, P.W. Crous, W. Gams & B. Summerell (**holotype** CBS H-20050, culture ex-type CBS 122475 = X1084).

Notes: Based on the phylogenetic analyses, the present species clusters among ramichloridium-like species in the *Zasmidium* clade (Fig. 4, clade 1; Fig. 5, clade IX) but it is morphologically more similar to *Zasmidium musae* (Fig. 5, clade VII) and *Zasmidium musicola* (Fig. 5, clade III). It is characterised by short conidiophores with an apical conidiogenous cell, short geniculate, with darkened and thickened conidiogenous loci, producing single cylindrical-oblong conidia (Arzanlou *et al.* 2008). Based on a BLAST comparison, *Zasmidium queenslandicum* shares 97 % (475/491) similarity on ITS with *Zasmidium elaeocarpi* (CPC 16642) and 89 % (656/735) similarity on *rpb2* with *Zasmidium gupoyu* (CBS 122099).

Zasmidium scaevolicola R.G. Shivas *et al.*, Persoonia 24: 133. 2010.

Description and illustration: Shivas *et al.* (2010).

Materials examined: **Australia**, Queensland, Cape Tribulation, 16°0400200 S 145°27050.900 E, on *Scaevola taccada*, 8 Aug. 2009, R.G. Shivas & P.W. Crous (**holotype** BRIP 52795, isotype CBS H-20455, culture ex-type CBS 127009 = CPC 17344); Thornton's Beach, 2 Sep. 1977, J.H. Simmonds, BRIP 12368; same loc., 1 Oct. 1979, J.H. Simmonds, BRIP 13098; Cape Tribulation, 30 Sep. 1979, J.H. Simmonds, BRIP 13097; Potters Creek, Wongaling Beach, Sep. 1993, H.Y. Yip, BRIP 21434; same loc., 27 Nov. 1993, H.Y. Yip, BRIP 21479; same loc., 17 Apr. 1994, H.Y. Yip, BRIP 22037; Cape Tribulation, 18 Dec. 2009, R.G. Shivas & A.R. McTaggart, BRIP 50073.

Notes: *Zasmidium scaevolicola* is morphologically and phylogenetically a *Zasmidium* species (Fig. 4, clade 1; Fig. 5, clade III) as previously observed by Shivas *et al.* (2010). In the present phylogenetic analyses, *Zasmidium scaevolicola* is closely related to *Zasmidium indonesianum*, a recently described species that infects the host *Citrus* sp. (Huang *et al.* 2015). Morphologically, both species produce conidia solitary or catenate, very similar in size and pigmentation, but *Zasmidium scaevolicola* produces longer conidiophores (Shivas *et al.* 2010, Huang *et al.* 2015).

Zasmidium schini U. Braun, C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822726. Fig. 42.

Etymology: Named after the host genus on which it occurs, *Schinus.*

Description in vitro (on V8; CPC 19516): *Mycelium* composed of hyaline, pale olivaceous or pale brown hyphae, rough and uniform in width, 2.5 µm. *Conidiophores* micro- to macronematous, pale brown to brown, paler towards the apex, rough, straight to mildly sinuous, simple, 45–325 × 2.5–5 µm. *Conidiogenous cells* integrated, apical, polyblastic, proliferating percurrently and sympodially, with rim-like conidiogenous loci, thickened and somewhat darkened, 2–2.5 µm diam. *Conidia* solitary, hyaline to pale brown, rough, cylindrical to obclavate, base short-obconically truncate and apex rounded, straight, 17.5–50 × 2.5–4 µm, 0–5-septate, hila darkened and thickened.

Material examined: **Brazil**, Minas Gerais, Viçosa, Mata da Prefeitura, on *Schinus terebinthifolia*, 1 Sep. 2005, A.B.V. Faria (**holotype** CBS H-22961, ex-type culture CBS 142188 = CPC 19516).

Notes: Thus far, only one cercosporoid species was known from this host genus, namely *Pseudocercospora schini* from *Schinus polygama* (Argentina) (Braun *et al.* 2016). The

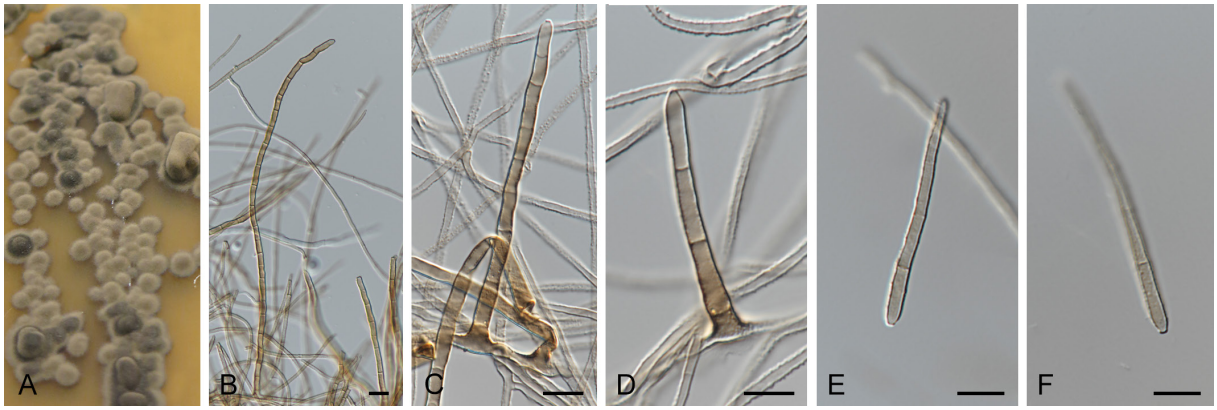


Fig. 42. *Zasmidium schini* (CPC 19516). A–F. Observations *in vitro*. A. Culture on V8. B–D. Conidiophore. E, F. Conidia. Scale bars = 10 µm.

phylogenetic analyses placed the present species in a basal branch to the clade *Zasmidium* (Fig. 4, clade 1; Fig. 5, clade IX). Based on a BLAST comparison, *Zasmidium schini* shares 94 % (463/494) similarity, including 2 % (14/494) gaps, on ITS with *Zasmidium queenslandicum* (CBS 122475) and 84 % (594/708) similarity on *rpb2* with *Zasmidium iteae* (CBS 113094). Morphologically, *Zasmidium schini* can be distinguished from *Zasmidium elaeocarpi*, by producing only apical, polyblastic conidiogenous cells and single conidia that are shorter and paler.

***Zasmidium* sp.**

Material examined: **Colombia**, on *Eucalyptus* sp., 2004, M.J. Wingfield, culture CBS 118494 = CPC 11004.

Notes: The culture observed was sterile and the fungarium material could not be located. Based on the results of the phylogenetic analyses, it is tentatively assigned to the genus *Zasmidium* (Fig. 1, clade 63; Fig. 4, clade 2; Fig. 5, clade IX) until it is recollected and morphologically described.

Zasmidium strelitziae (Arzanlou *et al.*) Videira & Crous, **comb. nov.** MycoBank MB822815. *Basionym*: *Ramichloridium strelitziae* Arzanlou *et al.*, Stud. Mycol. 58: 74. 2007.

Description and illustrations: Arzanlou *et al.* (2007).

Materials examined: **South Africa**, KwaZulu-Natal, Durban, near Réunion, on leaves of *Strelitzia nicolai*, 5 Feb. 2005, W. Gams & H. Glen (**holotype** CBS H-19776, ex-type culture CBS 121711 = X1029).

Notes: *Zasmidium strelitziae* is the only zasmidium-like species described from the host *Strelitzia*, an important plant cultivated for its flowers. Phylogenetically, it clusters within the *Zasmidium* clade (Fig. 4, clade 1; Fig. 5, clade IV) as circumscribed in the present study, and is closely related to *Z. musigenum*.

Zasmidium syzygii Crous, Persoonia 29: 173. 2012.

Description and illustration: Crous *et al.* (2012a).

Material examined: **South Africa**, Mpumalanga, Nelspruit, Lowveld Botanical Garden, on leaves of *Syzygium cordatum*, 16 Jul. 2011, P.W. Crous, M.K. Crous, M. Crous & K.L. Crous (**holotype** CBS H-21082, culture ex-type CBS 133580 = CPC 19792).

Notes: Phylogenetically and morphologically the present species belongs to the genus *Zasmidium* (Fig. 4, clade 1; Fig. 5, clade I). It is closely related to *Zasmidium eucalypticola*, isolated from the host *Eucalyptus* sp. (*Myrtaceae*), but is morphologically distinct (see notes on *Zasmidium eucalypticola*).

Zasmidium tsugae (Dearn.) Videira & Crous, **comb. nov.** MycoBank MB822833.
Basionym: *Dimerosporium tsugae* Dearn., Mycologia 16(4): 153. 1924.
Synonyms: *Dimeriella tsugae* (Dearn.) Petr., Ber. Schweiz. Bot. Ges. 57: 171. 1947.
Epipolaeum tsugae (Dearn.) Shoemaker, Canad. J. Bot. 43: 635. 1965.
Eudimeriolum tsugae (Dearn.) M.L. Farr, Mycologia 76: 801. 1984.
Rasutoria tsugae (Dearn.) M.E. Barr, Mycotaxon 29: 502. 1987.

Description and illustration: Dearness (1924).

Description in vivo (adapted from Dearness 1924): *Mycelium* hypophyllous, growing on the surface of the leaf giving it a smoky cast, branched, 3–4 µm thick. *Perithecia* dark brown, globose, 75–90 µm, gregarious, unappendaged, sometimes with 2 to 3 short rigid mycelioid branches, cells of the wall quadrate, 6–8 µm diam. *Asci* very variable in shape, clavate to cylindrical, 36–60 × 12–25 µm wide. *Ascospores* biseriate to conglobate, hyaline, uniseptate, sometimes nucleate in one or both cells, 13–21 × 3.5–5 µm, upper cell usually larger.

Notes: The type specimen of *Zasmidium tsugae*, based on *Dimerosporium tsugae*, could not be located (USA, Washington, Pierce Co., on leaves of *Tsuga heterophylla*, 25 July 1921, J.S. Boyce 832, fide Dearness 1924). The DNA sequences of *Rasutoria tsugae* used in this study were available on GenBank (Table 1) (Winton *et al.* 2007, Schoch *et al.* 2009) and no new sequences were generated. See notes on *Zasmidium cellare*.

Zasmidium velutinum (G. Winter) Videira & Crous, **comb. nov.** MycoBank MB822816.
Basionym: *Periconia velutina* G. Winter, Hedwigia 23: 174. 1884.
Synonym: *Periconiella velutina* (G. Winter) Sacc., in Saccardo & Berlese, Atti Reale Ist. Veneto Sci. Lett. Arti, Sér. 6, 3: 727. 1885.

Description and illustrations: Arzanlou *et al.* (2007).

Materials examined: **South Africa**, Cape Town, on *Brabejum stellatifolium* (*B. stellatum*), P. MacOwan, G. Winter herbarium (**lectotype** selected by Arzanlou *et al.* 2007: B; isolectotypes PAD, S F42165, S F462166); Stellenbosch, Jonkershoek Nature Reserve, on *Brabejum stellatifolium*, 21 Jan. 1999, J.E. Taylor (**epitype** designated by Arzanlou *et al.* 2007: CBS H-15612, cultures ex-epitype CBS 101948–101950 = CPC 2262–2264).

Note: See notes under *Zasmidium cellare*.

Zasmidium xenoparkii (Crous & M.J. Wingf.) Crous & U. Braun, Schlechtendalia 20: 103. 2010.
Basionym: *Stenella xenoparkii* Crous & M.J. Wingf., Stud. Mycol. 55: 129. 2006.

Description and illustration: Crous *et al.* (2006c).

Materials examined: **Indonesia**, on leaves of *Eucalyptus grandis*, Mar. 1996, M.J. Wingfield (**holotype** PREM 54968, isotype CBS H-19703, culture ex-type CBS 111185 = CPC 1300); *idem*. Cultures CPC 1299, CPC 1301.

Notes: *Zasmidium xenoparkii* belongs to the genus *Zasmidium* both morphologically and phylogenetically (Fig. 4, clade 1; Fig. 5, clade I). In the present phylogenetic analyses, it is closely related to *Zasmidium angulare*, but morphologically it is more similar to *Zasmidium pseudoparkii*, which differs by producing longer and wider conidia (Crous *et al.* 2006c). *Zasmidium xenoparkii* has a mycosphaerella-like sexual morph and produces hyaline ascospores that germinate in a type D pattern (Crous 1998).

Clade 70: *Nothopericoniella*

Nothopericoniella Videira & Crous, **gen. nov.** MycoBank MB822697.

Etymology: From the greek notho-, meaning false, and similarity to the genus *Periconiella*.

Description: Phytopathogenic. *Mycelium* mainly superficial, composed of brown and verrucose hyphae, internal mycelium sparsely developed, intracellular, composed of hyaline to brown hyphae, finely verruculose, septate, branched. *Conidiophores* solitary, arising from superficial hyphae, erect, straight, septate, brown olivaceous, paler at the apex, smooth to verruculose, composed of a main axis with a dichotomously branched apical head, branches terminal, partly lateral, proliferating percurrently and sympodially. *Conidiogenous cells* integrated, terminal and pleurogenous, polyblastic, sympodial, geniculate or subdenticulate, conidiogenous loci slightly thickened and darkened, truncate, without marginal rim or papillae. *Conidia* solitary, rarely in short chains, ellipsoid-ovoid, subcylindrical, verruculose, pale olivaceous, apex rounded, base obconically truncate, hila slightly thickened and darkened.

Type species: *Nothopericoniella perseae-macranthae* (Hosag. & U. Braun) Videira & Crous (≡ *Periconiella perseae-macranthae* Hosag. & U. Braun).

Nothopericoniella perseae-macranthae (Hosag. & U. Braun) Videira & Crous, **comb. nov.** MycoBank MB822767.
Basionym: *Periconiella perseae-macranthae* Hosag. & U. Braun, Indian Phytopathol. 48: 260. 1996 (1995).

Descriptions and illustrations: Hosagoudar & Braun (1995), Kirschner & Chen (2010).

Description (adapted from Hosagoudar & Braun 1996 and Kirschner & Chen 2010): Phytopathogenic, producing diffuse leaf spots, colonies hypophyllous, sometimes large and confluent. *Mycelium* mainly external, composed of superficial brown and verrucose hyphae, internal mycelium sparsely developed, intracellular, hyaline to brown, finely verruculose. *Hyphae* creeping, septate, branched, occasionally anastomosing, (1–)1.5–2.5(–3.5) µm wide, somewhat darker and wider around the conidiophores. *Conidiophores* solitary, arising from creeping hyphae, brown olivaceous, paler at the apex, almost smooth to verruculose, septate, erect, straight or slightly curved, 250–800 × 3–5 µm, composed of a very long main axis (about 200–700 µm long) with a 1–3 dichotomously branched apical head, branches terminal, partly lateral, proliferating percurrently and sympodially. *Conidiogenous cells* integrated, terminal and pleurogenous, often somewhat swollen, polyblastic, sympodial, somewhat geniculate or subdenticulate, conidiogenous loci slightly thickened and darkened, truncate, without marginal rim or papillae. *Conidia* solitary, rarely in short chains, pale olivaceous to olivaceous brown, verruculose, ellipsoid-ovoid, subcylindrical, base slightly obconically truncate and apex rounded, (8–)10–32 × 3–6 µm, (1–)2–3(–4)-septate, hila slightly thickened and darkened.

Materials examined: **India**, Tamil Nadu, Coimbatore, Anamalai, Koomati, on leaves of *Persea macrantha*, 13 Mar. 1994, V.B. Hosagoudar (**holotype** HAL 1627 F). **Taiwan**, Taichung County, Dongshi Forest Park, ca. 500 m, on living leaves of *Machilus zuihoensis*, 18 Mar. 2007, R. Kirschner & C.-J. Chen 2995 (TNM), culture CBS 122097 = RoKi 2995; Taipei County, Wulai, 300 m, 1 Apr. 2007, on living leaves of unidentified *Lauraceae*, R. Kirschner & C.-J. Chen 3030 (TNM), culture CBS 122282 = RoKi 2995.

Notes: Phylogenetically, *Nothopericoniella perseae-macranthae* is more closely related to the type of *Annellosympodiella* (Fig. 1, clade 71; Fig. 4, clade 3) than to the type of *Periconiella*, *Periconiella velutina* (Fig. 4, clade 1), the genus in which it was originally described. Morphologically, it is similar to *Annellosympodiella* by displaying both percurrent and sympodial proliferation, verrucose conidiophores and conidia and conidiogenous scars without marginal rim or papillae but slightly thickened and darkened. *Nothopericoniella perseae-macranthae* differs from *Annellosympodiella nectandrae* by forming longer conidiophores (250–800 × 3–5 µm) that rise singly from the external mycelium and are branched at the top instead of forming straight conidiophores (25–50 × 4–7 µm) rising from stromata in densely aggregated bunches. The conidia of *Nothopericoniella persea-macranthae* are also shorter and narrower (8–32 × 3–6 µm) than those of *Annellosympodiella nectandrae* (30–70 × 5–7 µm) (Hosagoudar & Braun 1996, Crous *et al.* 2014a).

Clade 71: *Annellosympodiella*

Annellosympodiella Crous & Assefa, Persoonia 32: 245. 2014.

Description (from Crous *et al.* 2014a): *Conidiomata* sporodochial on leaflets, arising from an erumpent brown stroma, consisting of brown, subcylindrical cells. *Conidiophores* densely aggregated, subcylindrical, brown, verruculose to warty, rejuvenating percurrently, septate. *Conidiogenous cells* integrated, terminal, brown, verruculose, proliferating percurrently with irregular annellations, and long, brown, tubular collarettes. *Loci* formed by sympodial proliferation are also visible on the tubular collarette, circular, thickened, darkened and

refractive. *Conidia* solitary, brown, verruculose to warty, guttulate, subcylindrical to narrowly obclavate, straight to curved, euseptate; hilum truncate, thickened and slightly darkened.

Type species: *Annellosympodiella juniperi* Crous & Assefa.

Annellosympodiella juniperi Crous & Assefa, Persoonia 32: 245. 2014.

Description and illustration: Crous *et al.* (2014a).

Materials examined: **Ethiopia**, Addis Ababa, Mangadishu Forest, on needles of *Juniperus procera*, 25 Jun. 2013, PW. Crous & A. Assefa (**holotype** CBS H-21706, ex-type culture CBS 137992 = CPC 23276).

Notes: *Annellosympodiella* is a monotypic genus similar to *Annellophragmia* (Ellis 1971) and *Annellosympodia* (McTaggart *et al.* 2007) based on their strange mode of percurrent and sympodial proliferation with darkened, thickened scars (Crous *et al.* 2014a). In the phylogenetic analyses, *Annellosympodiella* is a single-strain lineage closely related to *Neopenidiella* and *Neopericoniella* (Fig. 1, clade 71; Fig. 4, clade 3).

Clade 72: *Neopenidiella*

Neopenidiella Quaedvlieg & Crous, Persoonia 33: 22. 2014.

Description (from Quaedvlieg *et al.* 2014): Foliicolous. *Conidiophores* erect, straight, filiform, pluriseptate throughout, brown, darker below and paler above, thin-walled, smooth, apex penicillate, terminal cell of the conidiophore with short denticle-like loci giving rise to sets of conidiogenous cells or ramoconidia that then form a sequence of new sets of ramoconidia on different levels. *Conidiogenous loci* terminal or subterminal, usually 1–3(–4), subdenticulate, conical, apically truncate, unthickened or almost so, not to somewhat darkened-refractive. *Ramoconidia* with truncate base, barely or distinctly attenuated at the truncate base, aseptate, at the apex with 2–3(–4) subdenticulate hila, subcylindrical, very pale olivaceous, olivaceous brown to brown, thin-walled, smooth to faintly verruculose. *Conidia* in long acropetal chains, narrowly ellipsoid-ovoid, fusiform to cylindrical aseptate, very pale olivaceous, olivaceous brown to brown, thin-walled, smooth to very faintly rough-walled; hila unthickened or almost so, at most slightly darkened-refractive.

Type species: *Neopenidiella nectandrae* (Crous *et al.*) Quaedvlieg & Crous (≡ *Penidiella nectandrae* Crous *et al.*).

Neopenidiella nectandrae (Crous *et al.*) Quaedvlieg & Crous, Persoonia 33: 22. 2014.
Basionym: *Penidiella nectandrae* Crous *et al.*, Stud. Mycol. 58: 20. 2007.
Synonym: *Cladosporium ferrugineum* R.F. Castañeda, Fungi Cubenses II: 4. 1987, *nom. illeg.* (Art. 53.1).

Description and illustrations: Crous *et al.* (2007a).

Material examined: **Cuba**, Matanzas, San Miguel de los Baños, on living leaves of *Nectandrea coriacea*, 24 Jan. 1987, R.F. Castañeda & G. Arnold (**holotype** of *Cladosporium ferrugineum*

INIFAT C87/45, culture ex-type CBS 734.87 = ATCC 200932 = INIFAT 87/45; isotype HAL 2018 F).

Notes: *Neopenidiella* is currently a monotypic genus that was established to accommodate *Neopenidiella nectandrae* since it was not congeneric with the type of *Penidiella*, *P. columbiana* (*Teratosphaeriaceae*) (Quaedvlieg *et al.* 2014). *Neopenidiella* differs from *Penidiella* by forming conidiophores that are long and filiform, with a subdenticulate apical cell where long and narrow penicillate ramoconidia are formed. In the phylogenetic analyses performed in this study it forms a single-strain lineage closely related to *Annellosympodiella* (Fig. 1, clade 72; Fig. 4 clade 4).

Clade 73: *Neoceratosperma*

Neoceratosperma Crous, Persoonia 32: 257. 2014.

Description (from Crous *et al.* 2014a): *Mycelium* consisting of branched, septate, brown, verruculose hyphae turning warty with age. *Conidiophores* reduced to conidiogenous cells, or septate, erect, brown, verruculose, unbranched, subcylindrical, dark brown and smooth at the base. *Conidiogenous cells* subcylindrical, brown, verruculose, but conidiogenous apical area smooth, forming a short rachis that proliferates sympodially, with somewhat thickened and darkened loci. *Conidia* solitary, rarely in unbranched chains, subcylindrical, medium brown, becoming dark brown, verruculose, becoming warty, distoseptate, less obvious when older (dark brown, warty), straight to irregularly curved; apex obtuse, base truncate, but hila somewhat thickened and darkened.

Type species: *Neoceratosperma eucalypti* Crous & Cheew.

Neoceratosperma cyatheae Guatimosim *et al.*, Persoonia 37: 122. 2016.

Description and illustration: Guatimosim *et al.* (2016).

Materials examined: **Brazil**, Rio de Janeiro, Fazenda Barreto II, Rio grandina, on fronds of *Cyathea delgadii*, 11 Feb. 2014, R.W. Barreto (**holotype** CBS H-22074; isotype VIC 42605, culture ex-type CPC 24704; Rio de Janeiro, Nova Friburgo, Macaé de Cima, on fronds of *C. delgadii*, 11 Jul. 2009, R.W. Barreto, CBS H-22078, VIC 42533, cultures CPC 18580 = COAD573.

Notes: *Neoceratosperma cyatheae* was recently described from a fern host, *Cyathea delgadii*, originating from Brazil. Only its asexual morph is known, which can easily be distinguished from *Neoceratosperma eucalypti* by producing smooth conidiophores reduced to conidiogenous cells and solitary conidia (Guatimosim *et al.* 2016). Based on the phylogenetic analyses it forms a single-strain lineage within the *Neoceratosperma* clade (Fig. 1, clade 73; Fig. 4, clade 7).

Neoceratosperma eucalypti Crous & Cheew., Persoonia 32: 257. 2014.

Description and illustration: Crous *et al.* (2014a).

Materials examined: **Thailand**, Chiang Mai, on living leaves of *Eucalyptus* sp., Sep. 2013, R. Cheewangkoon (**holotype** CBS H-21712, culture ex-type CBS 137998 = CPC 23465).

Notes: *Neoceratosperma* has a zasmidium-like morphology except it produces distoseptate conidia. *Neoceratosperma* differs from *Ceratosperma* by forming strongly verruculose conidiophores and conidia, producing conidia in a short sympodial rachis, solitary or in chains and with slightly thickened, darkened hila and scars (Crous *et al.* 2014a). Phylogenetically, *Neoceratospoerma* strains cluster in a well-supported clade by both Bayesian and maximum likelihood analyses (Fig. 1, clade 73; Fig. 4, clade 7) and is closely related to *Xenomycosphaerella*. *Neoceratosperma* was monotypic, but several species have been recently added by Guatimosim *et al.* (2016).

Neoceratosperma legnephoricola U. Braun, C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822715. Fig. 43.

Etymology: Derived from the host genus on which it occurs, *Legnephora.*

Description in vivo (CBS H-22962): *Leaf spots* small, brown to dark brown, angular, 2–3 mm diam, later enlarged, circular to subcircular, with 2–3 dark brown concentric rings, 5–10 mm diam. *Mycelium* internal and external, composed of pale brown to brown hyphae, smooth to

Fig. 43. *Neoceratosperma legnephoricola* (CPC 16411). A–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Partial conidiophore, conidiogenous cells and conidia. C. Conidiophore and conidiogenous cells. D, E. Conidia. F–K. Observations *in vitro*. F. Culture on V8. G. Conidiophore and conidiogenous cell. H, I. Conidiogenous cell and conidia. J, K. Conidia. Scale bars = 10 µm.

verruculose. *Caespituli* hypophyllous, well-developed, visible in concentric rings, yellowish brown. *Stromata* hypophyllous, epidermal, substomatal, 20–54 µm diam. *Conidiophores* often reduced to conidiogenous cells, emerging from stromata and internal/external hyphae, solitary or fasciculate, more than 20, pale brown to brown, verruculose, straight to sinuous, simple, 25–380 × 2–6 µm. *Conidiogenous cells* terminal or intercalary, pale brown to brown, verruculose, polyblastic, proliferating sympodially, with rim-like conidiogenous loci slightly thickened and darkened, 2–3 µm diam. *Conidia* solitary, pale brown to brown, verruculose, cylindrical, obclavate to filiform, straight to curved, obconically truncate at the base and apex rounded, 34–260 × 5–11 µm, 0–23-distoseptate, hila slightly thickened and darkened, 2–3 µm diam.

Description in vitro (on SNA; CPC 16411): *Mycelium* composed of pale brown to olicaveous brown hyphae, smooth to verruculose. *Conidiophores* single, pale brown to olicaveous brown verruculose, erect, straight, simple, often reduced to conidiogenous cells, 3–120 × 4–5 µm. *Conidiogenous cells* terminal in conidiophores or integrated in the mycelium, pale brown to olivaceous brown, verruculose, single or polyblastic, proliferating sympodially, with rim-like conidiogenous loci, slightly thickened and darkened. *Conidia* solitary, occasionally catenate in a single chain, pale brown to olivaceous brown, verruculose, cylindrical, straight or curved, (16–)44–66(–128) × (3.5–)4–5(–5.5) µm, 0–10-distoseptate, obconically truncate at the base and conically truncate at the apex when intercalary, obconically truncate at the base and apex rounded when terminal, hila slightly thickened and darkened, 2–3 µm diam.

Material examined: **Australia**, New South Wales, North Washpool State Forest, on *Legnephora moorei* (≡ *Cocculus moorei*), Mar. 2009, B. Summerell (**holotype** CBS H-22962, ex-type culture CBS 142189 = CPC 16411).

Notes: This is the first time that a fungus has been described in association with the host *Legnephora moorei*, an endemic plant of the Australian rainforest. In the phylogenetic analyses it is closely related to *Neoceratosperma yunnanensis* (Fig. 1, clade 73; Fig. 4, clade 7), but can be morphologically distinguished by producing longer conidiophores and shorter conidia.

Neoceratosperma haldinae U. Braun, C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822716. Fig. 44.

Etymology: Derived from the host genus on which it occurs, *Haldina.*

Description in vitro (on SNA, CPC 19202): *Mycelium* composed of pale olivaceous hyphae, verruculose, 2 µm wide. *Conidiophores* pale olivaceous, finely verruculose, straight, simple, geniculate-sinuous at the apex, (25–)43–53(–76) × 1.5–2 µm, often reduced to conidiogenous cells. *Conidiogenous cells* pale olivaceous, finely veruculose, proliferating sympodially at the apex, polyblastic, withconidiogenouslocislightlythickened and darkened, 1 µm diam. *Conidia* solitary, pale olivaceous, finely verruculose, filiform, cylindrical to longobclavate, baseshort-obconicallytruncate and apex rounded, (5.5–)17–22.5(–30) × (1.5–)2(–3) µm, 1–5-euseptate, with hila slightly thickened but hardly darkened, 1 µm diam.

Materials examined: **Laos**, Vientiane, Xanthany, Dong Makkai, on *Haldina cordifolia*, unknown date, P. Pheng, LC 0408, NUOL P53 (**holotype** CBS H-22963, culture ex-type CBS 142190 = CPC 19202).

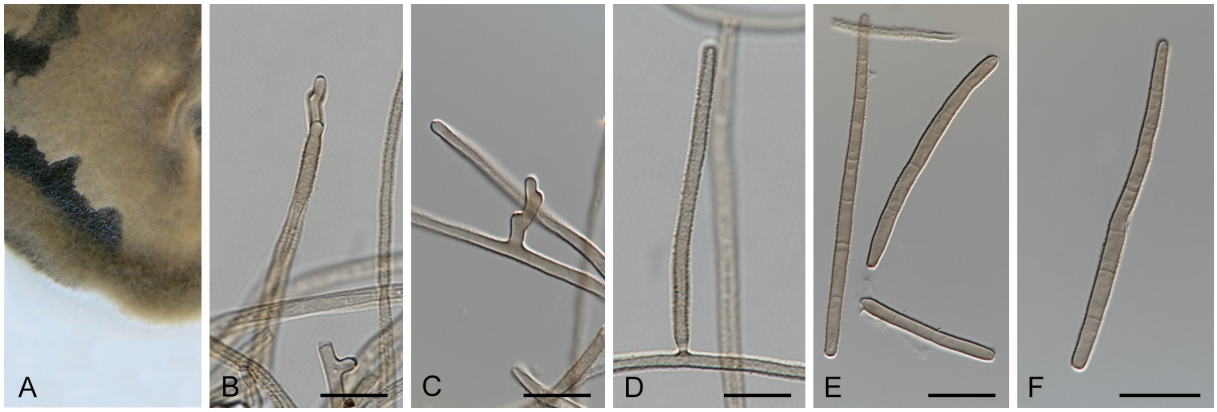


Fig. 44. *Neoceratosperma haldinae* (CPC 19202). A–F. Observations *in vitro*. A. Culture on OA. B, C. Conidiophore and conidiogenous cell. D–F. Conidia. Scale bars = 10 µm.

Notes: *Neoceratosperma haldinae* needs to be compared with *Passalora haldinae*, which was described from *Haldina cordifolia* collected in Thailand (Nakashima *et al.* 2007). The strain CBS 142190 (previously identified as *Passalora haldinae*), sporulated in culture, and proved to be distinct from *Passalora haldinae*, which has wider conidiophores (15–63 × 2.8–3.6 µm) that are occasionally branched, and conidia that are smooth, longer and wider (24–80 × 2.7–5 µm, 1–7-septate; Nakashima *et al.* 2007). Based on the phylogenetic analyses it forms a single-strain lineage within the *Neoceratosperma* clade (Fig. 1, clade 73; Fig. 4, clade 7).

Neoceratosperma yunnanensis (Barber & T.I. Burgess) Guatimosim *et al.*, Persoonia 37: 123. 2016.
Basionym: *Mycosphaerella yunnanensis* Barber & T.I. Burgess, Fungal Diversity 24: 150. 2007.
Synonym: *Xenomycosphaerella yunnanensis* (Barber & T.I. Burgess) Quaedvlieg & Crous, Persoonia 33: 24. 2014.

Description and illustration (sexual morph): Burgess *et al.* (2007).

Description in vitro (on V8; CBS 119975): *Mycelium* composed of hyaline to pale olivaceous hyphae, verruculose, 2.5 µm wide. *Conidiophores* short, reduced to conidiogenous cells, hyaline to pale olivaceous, verruculose, simple, 2.5–5 × 3–4 µm. *Conidiogenous cells* polyblastic, determinate, rarely proliferating sympodially, with rim-like conidiogenous loci that are slightly thickened and darkened, 1–1.5 µm diam. *Conidia* solitary, rarely catenate in a single chain, pale to pale olivaceous, verruculose, cylindrical to long obclavate, filiform, base short-obconical truncate and apex rounded, 30–210 × 3–4 µm, 0–6-eu- or distoseptate, hila slightly thickened and darkened, 1–1.5 µm diam.

Materials examined: **China**, Yunnan, Lancang, on leaves of *Eucalyptus urophylla*, May 2005, B. Dell (**holotype** MURU 407, ex-type culture CBS 119975 = CMW 23443 = MUCC 410 = PAB 05.05 B2).

Notes: Until now, *Mycosphaerella yunnanensis* was only known from its sexual morph, but in this study, we observed the asexual morph in culture using V8 medium with sterilised banana leaves. The morphological features of the asexual morph included short conidiophores

reduced to conidiogenous cells and distoseptate scolecospores, which are in agreement with the description of the genus *Neoceratosperma*. Based on the genes used in this study and the phylogenetic methods employed, *Mycosphaerella yunnanensis* is included in *Neoceratosperma* (Fig. 1, clade 73; Fig. 2, clade 7).

Clade 74: *Xenosonderhenia*

Xenosonderhenia Crous, Persoonia 28: 175. 2012.

Description (from Crous *et al.* 2012b): Foliicolous, associated with leaf spots. *Conidiomata* pycnidial, black, globose, substomatal, erumpent, predominantly epiphyllous, with central ostiole, lined with periphyses; wall of 2–3 layers of brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* lining the inner cavity, subcylindrical to doliiform; finely verruculose, pale brown, proliferating apically with several percurrent proliferations. *Conidia* subcylindrical, brown, finely verruculose, apex obtuse, base truncate with visible scar-like hilum, (1–)3-euseptate, but septa with visible central pore. Conidia of synasexual morph intermingled in same conidioma, but conidiogenous cells proliferating percurrently or sympodially; conidia hyaline to subhyaline, narrowly obclavate, apex subobtuse, base truncate, straight to curved, transversely multi-septate. *Synasexual morph* also hyphomycetous, developing in aerial mycelium; conidiophores subcylindrical, straight to curved, 0–2-septate, hyaline to subhyaline, proliferating sympodially at apex. Conidiophores solitary or fasciculate or forming on a reduced stroma.

Type species: *Xenosonderhenia syzygii* Crous.

Xenosonderhenia eucalypti Crous & M.J. Wingf., Persoonia 33: 241. 2014.

Description and illustration: Crous *et al.* (2014b).

Material examined: **Mozambique**, Forestas de Niassa, leaf spots of *Eucalyptus urophylla*, 2 Feb. 2014, M.J. Wingfield (**holotype** CBS H-21991, culture ex-type CPC 24247 = CBS 138858).

Notes: *Xenosonderhenia eucalypti* was recently described based on the morphological characteristics of the sexual morph. It was placed in *Xenosonderhenia* due to being phylogenetically closest to *Xenosonderhenia syzygii* (Crous *et al.* 2014b). In this study, *Xenosonderhenia eucalypti* formed a single-strain lineage in the phylogenetic analyses (Fig. 1, clade 74; Fig. 4, clade 9) that is closely related to *Xenomycosphaerella elongata* with which it shares 98 % (728/740) similarity on LSU, 94 % (449/477) similarity on ITS, and only 84 % (622/737) similarity on *rpb2*.

Xenosonderhenia syzygii Crous, Persoonia 28: 175. 2012.

Description and illustration: Crous *et al.* (2012b).

Material examined: **South Africa**, Mpumalanga, Nelspruit, Lowveld Botanical Garden, on leaves of *Syzygium cordatum*, 17 Aug. 2011, P.W. Crous, M.K. Crous, M. Crous & K.L. Crous (**holotype** CBS H-20968, ex-type culture CBS 132688 = CPC 19790).

Notes: *Xenosonderhenia* currently accommodates two species, *Xenosonderhenia syzygii* and *Xenosonderhenia eucalypti*. *Xenosonderhenia syzygii* is phylogenetically close to *Xenomycosphaerella elongata* but is unique in being morphologically dimorphic (Crous *et al.* 2012b). *Xenosonderhenia syzygii* is easily distinguished from *Sonderhenia* since species in the latter genus produce distoseptate conidia and form a distinct clade in the *Mycosphaerellaceae* (Fig. 1, clade 28; Fig. 2, clade 34). It can also be separated from *Phaeophleospora* since species in the latter genus produce scolecosporous conidia and form a unique clade in the *Mycosphaerellaceae* (Fig. 1, clade 67; Fig. 4, clade 5). Unfortunately, an *rpb2* sequence was not generated for this strain and it was not included in the phylogenetic trees in this study.

Clade 75: *Xenomycosphaerella*

Xenomycosphaerella Quaedvlieg & Crous, Persoonia 33: 24. 2014.

Description (from Quaedvlieg *et al.* 2014): Foliicolous, plant pathogenic. *Ascomata* pseudothecial, dark brown, subepidermal to erumpent, globose, with an apical ostiole; wall of 2–3 layers of medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid to broadly ellipsoidal, straight to slightly curved, 8-spored. *Ascospores* bi- to multiseriate, overlapping, hyaline, thin- or thick-walled, straight to slightly curved, fusoid-ellipsoidal with obtuse ends, widest in middle of the apical cell, medianly or unequally 1-septate, tapering towards both ends, but more prominently towards the lower end.

Type species: *Xenomycosphaerella elongata* (Crous & M.J. Wingf.) Quaedvlieg & Crous (≡ *Mycosphaerella elongata* Crous & M.J. Wingf.).

Xenomycosphaerella elongata (Crous & M.J. Wingf.) Quaedvlieg & Crous, Persoonia 33: 24. 2014.
Basionym: *Mycosphaerella elongata* Crous & M.J. Wingf., Fungal Diversity 26: 163. 2007.

Description and illustrations: Crous *et al.* (2007c).

Material examined: **Venezuela**, El Piñal Lotes farm near Acarigua, on leaves of *Eucalyptus calmadulensis* × *urophylla*, Oct. 2006, M.J. Wingfield (**holotype** CBS H-19824, ex-type culture CBS 120735 = CPC 13378).

Notes: The genus *Xenomycosphaerella* was introduced to accommodate *Mycosphaerella elongata* and *Mycosphaerella yunnanensis*, both species only known from their mycosphaerella-like sexual morph but that were not congeneric with *Ramularia* (Quaedvlieg *et al.* 2014). Based on a large phylogenetic analysis based on several genes, *Xenomycosphaerella yunnanensis* was later combined into *Neoceratosperma* (Guatimosim *et al.* 2016). In the present phylogenetic analyses, the genus is represented by its type, *Xenomycosphaerella elongata*, in a single-strain lineage (Fig. 1, clade 75; Fig. 4, clade 8) that is closely related to *Xenosonderhenia*. The genera *Xenosonderhenia* and *Xenomycosphaerella* are very close phylogenetically, but due to lacking information related to their morphology and the existing differences observed based on the DNA sequences, they should remain separate until more isolates are available for further analysis. The type of *Xenosonderhenia*, *Xenosonderhenia syzygii*, is only known by its dimorphic asexual morph while the type of *Xenomycosphaerella*, *Xenomycosphaerella*

elongata, is only known from its sexual morph. The other known species of *Xenosonderhenia*, *Xenosonderhenia eucalypti*, is only known from its sexual morph which can be distinguished from *Xenomycosphaerella elongata* by forming ascospores not constricted at the septa and widest at one third of the apex of the apical cell (ascospores constricted at the septum and tapering towards both ends but more prominently towards the lower end in *Xenomycosphaerella elongata*).

Clade 76: *Xenosonderhenioides*

Xenosonderhenioides Videira & Crous, **gen. nov.** MycoBank MB822706.

Etymology: *Xenos*- from the Greek strange + *sonderhenioides* for the phylogenetic proximity to the genus *Sonderhenia.*

Description: *Mycelium* composed of hyaline to pale brown hyphae, smooth, septate, branching. *Conidiophores* micro- to macronematous, subhyaline to pale brown, smooth to rough, simple, sometimes branched, straight to sinuous. *Conidiogenous cells* integrated, terminal or intercalary, hyaline to pale brown, proliferating sympodially, polyblastic, with rim-like conidiogenous loci, slightly thickened and darkened. *Conidia* solitary, rarely catenate in a single chain, hyaline to subhyaline, smooth, oblong, cylindrical to obclavate, straight, base medium-long obconically truncate, apex rounded, aseptate or eu- or distoseptate hila thickened and darkened and protruding at the base or at both ends when catenate.

Type species: *Xenosonderhenioides indonesiana* C. Nakash., Videira & Crous.

Xenosonderhenioides indonesiana C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822728. Fig. 45.

Etymology: Derived from the country where it was collected from, Indonesia.

Description in vitro (on SNA; CPC 15066): *Mycelium* composed of hyaline to pale brown hyphae, smooth, septate, branched, uniform in width, 2–2.5 µm diam. *Conidiophores* micro- to macronematous, subhyaline to pale brown, smooth to finely verruculose, simple, straight to sinuous, sometimes geniculate-sinuous at the apex, 20–75 × 2.5–7.5 µm. *Conidiogenous cells* integrated, terminal and intercalary, hyaline to pale brown, smooth, proliferating sympodially, conical at the apex, mono- or polyblastic, with rim-like conidiogenous loci slightly thickened and darkened, located at the apex or shoulder, sometimes in large number and disperse through the cell, 1.5–2 µm in diam. *Conidia* solitary, rarely catenate in a single chain, hyaline to subhyaline, smooth, oblong, cylindrical to long-obclavate, base medium-long obconically truncate, apex rounded, 15–50 × 5–6 µm, 0–4-septate, eu- or distosepta, sometimes slightly constricted at the septa, hila slightly thickened and darkened.

Material examined: **Indonesia**, on *Eucalyptus* sp., 26 Mar. 2008, M.J. Wingfield (**holotype** CBS H-19824, ex-type culture CBS 142239 = CPC 15066).

Notes: Phylogenetically, the genus *Xenosonderhenioides* is represented by a single-strain lineage (Fig. 1, clade 76; Fig. 4, clade 10) that is closely related to *Xenosonderhenia*. Morphologically,

Fig. 45. *Xenosonderhenioides indonesiana* (CPC 15066). A–E. Observations *in vitro*. A. Culture on OA. B, C. Conidiophore and conidiogenous cell. D. Conidiogenous cell and conidia. E. Conidia. Scale bars = 10 μm.

Xenosonderhenioides indonesiana can easily be distinguished from *Xenosonderhenia syzygii*, which has dimorphic conidia in culture. Due to phylogenetic and morphological differences, we consider that this should represent a unique genus.

Clade 77: *Polyphialoseptoria*

Polyphialoseptoria Quaedvlieg *et al.*, Stud. Mycol. 75: 355. 2013.

Description (from Quaedvlieg *et al.* 2013): Foliicolous, plant pathogenic. *Conidiomata* brown, erumpent, pycnidial (acervular in culture), globose, brown; wall of 3–6 layers of pale brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, subcylindrical to ampulliform, proliferating sympodially at apex, forming polyphialides with minute periclinal thickening, or as solitary loci on superficial mycelium in culture. *Conidia* hyaline, smooth, granular to guttulate, scolecosporous, irregularly curved, apex subobtuse, base long obconically truncate, transversely multi-euseptate, in older cultures disarticulating at septa; microcyclic conidiation also common in older cultures.

Type species: *Polyphialoseptoria terminaliae* Quaedvlieg *et al.*

Polyphialoseptoria terminaliae Quaedvlieg *et al.*, Stud. Mycol. 75: 356. 2013.

Description and illustration: Quaedvlieg *et al.* (2013).

Materials examined: **Brazil**, Minas Gerais, Viçosa, on leaves of *Terminalia catappa*, 18 May 2010, R.W. Barreto (**holotype** CBS H-21298, culture ex-type CBS 135106 = CPC 19611); *idem*. cultures CBS 135475 = CPC 19487.

Notes: *Polyphialoseptoria* currently includes two species, *Polyphialoseptoria terminaliae* and *Polyphialoseptoria tabebuiae-serratifoliae*, both collected from Brazil. It differs from *Septoria* and *Neoseptoria* based on the presence of polyphialides. The phylogenetic analyses performed in this study strongly supported the *Polyphialoseptoria* clade (Fig. 1, clade 77; Fig. 4, clade 11).

Clade 78: *Mycodiella*

Mycodiella Crous, Persoonia 37: 337. 2016.

Description (from Crous *et al.* 2016a): *Ascomata* pseudothecial, brown, erumpent, globose; wall consisting of 2–3 layers of medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid, straight to slightly curved, 8-spored. *Ascospores* multiseriate, overlapping, hyaline, guttulate, thin-walled, straight to slightly curved, fusoid-ellipsoidal with obtuse ends, widest in middle of apical cell, medianly 1-septate.

Type species: *Mycodiella eucalypti* Crous.

Mycodiella eucalypti Crous, Persoonia 37: 337. 2016.

Description and illustration: Crous *et al.* (2016a).

Materials examined: **Australia**, Western Australia, Porongurup, Porongurup National Park, S34°41018.600 E117°5505600, on leaves of *Eucalyptus diversicolor*, 24 Sep. 2015, P.W. Crous (**holotype** CBS H-22885, culture ex-type CBS 142097 = CPC 29226); Western Australia, Denmark, Mount Lindesay Walk Trail, Southern Cross, on leaves of *Xanthosia rotundifolia*, 19 Sep. 2015, P.W. Crous, cultures CBS 142099 = CPC 29525.

Notes: *Mycodiella* was recently introduced to accommodate *Mycodiella eucalypti*, a pathogen on *Eucalyptus* that clustered together with "*Mycosphaerella*" *sumatrensis* on *Eucalyptus* and "*Mycosphaerella*" *laricis-leptolepidis* on *Larix*. All three species are only known from their asexual morph and cluster together in a well-supported clade based on LSU, which supported the combination of all three species into the same genus (Crous *et al.* 2016a). In this study only a representative of *Mycodiella sumatrensis* was used and it forms a single-strain lineage closely related to *Polyphialoseptoria* (Fig. 1, clade 78; Fig. 4, clade 12).

Mycodiella sumatrensis (Crous & M.J. Wingf.) Crous, Persoonia 37: 337. 2016.
Basionym: Mycosphaerella sumatrensis Crous & M.J. Wingf., Stud. Mycol. 55: 124. 2006.

Description and illustration: Crous *et al.* (2006c).

Material examined: **Indonesia**, Northern Sumatra, on leaves of *Eucalyptus* sp., Feb. 2004, M.J. Wingfield (**holotype** CBS H-19704, cultures ex-type CBS 118499 = CPC 11171); *idem*. cultures CBS 118501 = CPC 11175, CBS 118502 = CPC 11178.

Note: See *Mycodiella eucalypti*.

Clade 79: *Australosphaerella*

Australosphaerella Videira & Crous, **gen. nov.** MycoBank MB822579.

Etymology: Derived from the country of origin Australia and mycosphaerella-like sexual morph.

Description: *Ascomata* pseudothecial, black, slightly erumpent, globose. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obclavate to ellipsoidal, straight to incurved, 8-spored. *Ascospores* multiseriate, overlapping, hyaline, straight to rarely curved, fusoid-ellipsoidal with obtuse ends, medianly 1-septate, widest in middle of apical cell, not constricted at septum or only slightly so.

Type species: *Australosphaerella nootherensis* (Carnegie) Videira & Crous.

Australosphaerella nootherensis (Carnegie) Videira & Crous, **comb. nov.** MycoBank MB822739.
Basionym: *Mycosphaerella nootherensis* Carnegie, Austral. Pl. Pathol. 40: 377. 2011.

Description and illustration: Carnegie *et al.* (2011).

Materials examined: **Australia**, Queensland, Noosa Heads, on living leaves of *Corymbia intermedia*, 11 Aug. 2008, A.J. Carnegie (**holotype** BRIP 52584a, ex-type culture CBS 130522).

Notes: This genus is represented by a single-strain lineage in the phylogenetic analyses (Fig. 1, clade 79; Fig. 4, clade 16), closely related to *Mycodiella*, but not strongly supported by any of the phylogenetic methods employed, which indicates that it is quite different even from the closest related species. Based on a BLAST search against the alignment, CBS 130522 shares 89 % (428/483) similarity on ITS, including 2 % (10/483) gaps, with *Xenosonderhenioides indonesiana* CPC 15066 and 76 % (535/ 704) similarity on *rpb2*, including 1 % (12/704) gaps, with *Polyphialoseptoria terminaliae* CBS 135106. Therefore, a new genus is introduced to accommodate this species. Morphologically it is only known from its mycosphaerella-like sexual morph but the ascospores have a distinctive germination pattern with multiple germ tubes growing at various angles from both ends of the ascospore (Carnegie *et al.* 2011).

Clade 80: *Chuppomyces*

Chuppomyces Videira & Crous, **gen. nov.** MycoBank MB822582.

Etymology: In honour of the mycologist Charles Chupp, who produced an extensive work on cercosporoid fungi.

Description: *Mycelium* composed of hyaline to pale olivaceous brown hyphae, smooth to rough. *Conidiophores* macronematous, pale olivaceous brown, rough, straight or strongly geniculate, simple. *Conidiogenous cells* integrated, terminal or intercalary, thickened and darkened, proliferating sympodially, polyblastic, apex short-conically truncate, with rim-like conidiogenous loci, thickened and darkened, located on the apex and shoulders. *Conidia* solitary, hyaline, smooth, cylindrical to obclavate, septate.

Type species: *Chuppomyces handelii* (Bubák) U. Braun *et al.* (≡ *Cercospora handelii* Bubák).

Chuppomyces handelii (Bubák) U. Braun, C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822741. Fig. 46.
Basionym: *Cercospora handelii* Bubák, Ann. Naturhist. Mus.Wien 23: 106. 1909.

Synonyms: *Cercoseptoria handelii* (Bubák) Deighton, Mycol. Pap. 140: 166. 1976.
Cercospora rhododendri Ferraris, Fl. Ital. Cryptog. I: Fungi, Hyphales: 895. 1910.
Cercospora rhododendri Marchal & Verpl., Bull. Soc. Roy. Bot. Belgique 59: 24. 1927 (1926-1927), *nom. illeg.* (Art. 53.1).
Pseudocercospora handelii (Bubák) Deighton, Trans. Brit. Mycol. Soc. 88(3): 390. 1987.
Mycosphaerella handelii Crous & U. Braun, CBS Biodiversity Ser. 1: 211. 2003.

Description and illustrations: Chupp (1954), Ellis (1976), Deighton (1976a), Crous & Braun (2003), present study (Fig. 46).

Description in vitro (on V8; CBS 113302): *Mycelium* composed of hyaline to pale olivaceous brown hyphae, smooth to rough, uniform in width, 2.5–3 µm. *Conidiophores* macronematous, pale olivaceous brown, rough, straight or geniculate-sinuous, simple, 30–80 × 3–6 µm. *Conidiogenous cells* integrated, terminal or intercalary, proliferating sympodially, polyblastic, apex short-conically truncate or geniculate-sinuous, with rim-like conidiogenous loci, thickened and darkened, located on the apex and shoulders, 2–2.5 µm. *Conidia* solitary, hyaline, smooth, cylindrical to obclavate, base medium-long obconically truncate and apex rounded, straight, 25–125 × 3–5 µm, 1–5-septate, hila thickened and darkened.

Materials examined: **Netherlands**, Utrecht, Bilthoven, 28 Evert Comelislaan, on *Rhododendron* sp., 10 Mar. 2003, M. Crous & P.W. Crous (**holotype** of *Mycosphaerella handelii* CBS H-6594, culture ex-type CBS 112681); Utrecht, on *Rhododendron* sp., 2002, P.W. Crous & U. Braun, culture CBS 113302. **Turkey**, Trabzon District, Fol Koei, on *Rhododendron ponticum*, 14 Jul. 1907, Handel-Mazzetti (**holotype** of *Cercospora handelii*, BPI 437020).

Notes: The culture CBS 113302 was deposited as "*Mycosphaerella*" *handelii* (= *Pseudocercospora handelii*). However, the morphological characters on the V-8 medium are different from that of the genus *Pseudocercospora*. In the phylogenetic analyses, the present species is closely related to *Ruptoseptoria unedonis* and *Neoamichloridium pini*, but morphologically is quite distinct from both (Fig. 1, clade 80; Fig. 4, clade 13). *Chuppomyces handelii* (Fig. 1, clade 80; Fig. 4, clade 13) forms sympodially proliferating conidiophores

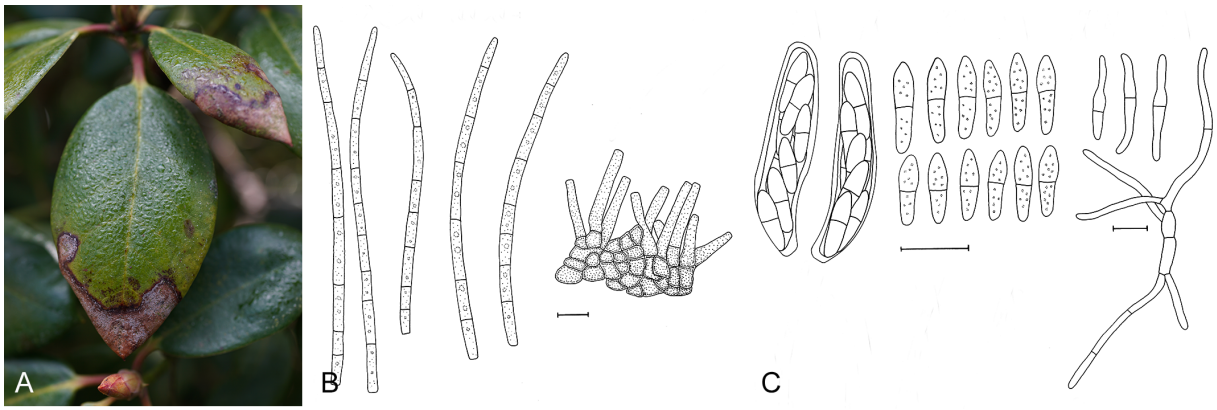


Fig. 46. *Chuppomyces handelii* (CBS 113302). A. Disease symptoms on the host leaves. B. Drawings of the asexual morph (from Crous & Braun 2003). C. Drawings of the sexual morph (from Crous & Braun 2003).

and conidia which are hyaline, solitary, cylindrical and multiseptate. *Ruptoseptoria unedonis* (Fig. 1, clade 81; Fig. 4, clade 14) has convoluted conidiomata that open by irregular rupture and frequently form phialidic conidiogenous cells. *Pachyramichloridium pini* (Fig. 1, clade 82; Fig. 4, clade 15) has simple conidiophores, plurigenous conidiogenous cells with flat to prominent conidiogenous scars, producing conidia hyaline, obovoid, aseptate with darkened hila. *Chuppomyces handelii* shares 98 % (729/747) similarity with *Ruptoseptoria unedonis* and 96 % (712/744) similarity with *Pachyramichloridium pini*, based on LSU; 95 % (450/475) similarity with *Ruptoseptoria unedonis* and 91 % (431/476) similarity with *Pachyramichloridium pini*, based on ITS; 87 % (639/731) similarity with *Ruptoseptoria unedonis* and 80 % (593/737) similarity with *Pachyramichloridium pini*, based on *rpb2*. Despite the strong support on the branch that connects these three strains together based on all three phylogenetic methods employed in this study, the morphological characters are too different to consider joining them in the same genus and, therefore, two new genera are introduced to accommodate them.

Clade 81: *Ruptoseptoria*

Ruptoseptoria Quaedvlieg *et al.*, Stud. Mycol. 75: 356. 2013.

Description (from Quaedvlieg *et al.* 2013): Foliicolous, plant pathogenic. *Conidiomata* black, appressed, elongated, pycnidial, but opening via irregular rupture, convulated; exuding a creamy white conidial mass; outer wall dark brown, crusty, consisting of 6–8 layers of dark brown *textura angularis*; giving rise to 2–3 inner layers of pale brown to hyaline *textura angularis*. *Conidiophores* lining the inner cavity, hyaline, smooth or pale brown, verruculose at base, branched below, septate, subcylindrical. *Conidiogenous cells* integrated, terminal, subcylindrical, smooth; proliferating sympodially at apex, or apex phialidic with minute periclinal thickening. *Conidia* solitary, hyaline, smooth, guttulate, subcylindrical to narrowly obclavate, gently to irregularly curved, apex subobtuse, base truncate to narrowly obovoid, transversely septate.

Type species: *Ruptoseptoria unedonis* (Roberge ex Desm.) Quaedvlieg *et al.* (≡ *Septoria unedonis* Roberge ex Desm.).

Ruptoseptoria unedonis (Roberge ex Desm.) Quaedvlieg, Verkley & Crous, Stud. Mycol. 75: 357. 2013.
Basionym: *Septoria unedonis* Roberge ex Desm., Ann. Sci. Nat., Bot., Sér. 3, 8: 20. 1847.
Synonym: *Sphaerella arbuticola* Peck, Bull. Torrey Bot. Club 10(7): 75. 1883.
For additional synonyms see MycoBank.

Description and illustration: Quaedvlieg *et al.* (2013).

Materials examined: **Croatia**, Rab, city park, leaf spots on *Arbutus unedo*, Jul. 1970, J.A. von Arx, CBS H-18192, culture CBS 755.70. France, on leaves of *Arbutus unedo*, Aug. 1986, H.A. van der Aa, CBS H-14645, culture CBS 355.86.

Notes: Morphologically, *Ruptoseptoria* is very similar to *Septoria* but differs from the later genus in forming convoluted conidiomata that open by irregular rupture and frequently form

phialidic conidiogenous cells. The type species *Ruptoseptoria unedonis* was described from *Arbutus unedo* from France, but the type specimen could not be located. The link between the asexual morph *Septoria unedonis* (CBS 755.70) and the sexual morph *Mycosphaerella arbuticola* (CBS 355.86) was established based on phylogenetic data (Quaedvlieg *et al.* 2013). In this study, based on the phylogenetic analyses, *Ruptoseptoria* forms a single-strain lineage (Fig. 1, clade 81; Fig. 4, clade 14). See also notes on *Chuppomyces handelii*.

Clade 82: *Pachyramichloridium*

Pachyramichloridium Videira & Crous, **gen. nov.** MycoBank MB822600.

Etymology: When noting the differences between *Ramichloridium apiculatum* and *Ramichloridium pini*, Hoog *et al*. (1983) stated it had: "darker, shorter and stout conidiophores". The name is formed by the Greek prefix pachy- (stout), and -*ramichloridium* for its morphological resemblance to the genus.

Description: *Mycelium* composed by dimorphic hyphae, hyaline to pale olivaceous, or olivaceous to dark brown and thick-walled, verrucose often with irregular clumps of pale olivaceous, capsular material. *Conidiophores* simple, erect, emerging from hyphae, wall thick and smooth, dark olivaceous brown, aseptate or septate, slightly tapering towards the apex. *Conidiogenous cells* terminal, subhyaline to brown, with scattered conidiogenous loci, flat or slightly protuberant, slightly darkened. *Conidia* solitary, pale olivaceous, thin-walled, smooth, obovate to obconical, hila slightly darkened.

Type species: *Pachyramichloridium pini* (de Hoog & Rahman) C. Nakash., Videira & Crous.

Pachyramichloridium pini (de Hoog & Rahman) C. Nakash., Videira & Crous, **comb. nov.** MycoBank MB822769.
Basionym: *Ramichloridium pini* de Hoog & Rahman, Trans. Brit. Mycol. Soc. 81: 485. 1983.

Description in vitro (adapted from Hoog *et al.* 1983): *Hyphae* dimorphic, hyaline to pale olivaceous 0.5–3 µm wide, olivaceous to dark brown, thick-walled, 2–4 µm wide, verrucose, often with irregular clumps of pale olivaceous, capsular material. *Conidiophores* simple, erect, emerging from hyphae, wall thick and smooth, dark olivaceous brown, 60 × 2–3 µm, slightly tapering towards the rounded apex, aseptate or up to 5-septate. *Conidiogenous cells* terminal on conidiophore, with scattered conidiogenous loci, flat or slightly protuberant, subhyaline to brown, up to 1 µm wide. *Conidia* solitary, pale olivaceous, thin wall, mostly smooth, obovate to obconical, 3–8 × 2–3 µm, truncate base, hila slightly darkened.

Material examined: **UK**, Scotland, Old Aberdeen, branch of *Pinus contorta*, unknown date and coll., isol. M.A. Rahman, dep. 1982 (**holotype** CBS 461.82 = MUCL 28942).

Notes: The type species of *Ramichloridium*, *Ramichloridium apiculatum*, clusters in a sister clade to *Dissoconium* (*Dissoconiaceae*) (Arzanlou *et al.* 2007; present study Fig. 1, clade 95; Fig.4, clade 31). Other ramichloridium-like species cluster within the *Zasmidium* complex (Fig. 1, clade 69; Fig. 4, clade 1). The present species forms a single-strain lineage closely related to *Ruptoseptoria* (Fig. 1, clade 81; Fig. 4, clade 14). Morphological evaluation of the strain

CBS 461.82 is impossible since it was sterile (Arzanlou *et al.* 2007; this study). According to the original description (Hoog *et al.* 1983), this species has simple conidiophores, plurigenous conidiogenous cells with flat to prominent conidiogenous scars, producing hyaline obovoid, aseptate conidia. See also notes on *Chuppomyces handelii*.

Clade 83: *Exosporium*

Exosporium Link, Mag. Ges. Naturf. Freunde, Berlin 3(1–2): 9. 1809.
Synonyms: *Cephaloedium* Kunze, Consp. Regni Veget. (Leipzig): 4. 1828.
Cuspidosporium Cif., Sydowia 9: 303. 1955.

Description (from Ellis 1961): *Colonies* discrete and punctiform or effuse, hairy, brown to black. *Mycelium* immersed. *Stroma* usually present, often very well-developed. *Setae* and hyphopodia absent. *Conidiophores* macronematous, mononematous, often caespitose, straight or flexuous, unbranched, or very rarely branched, mid to dark brown or olivaceous brown, smooth or verruculose. *Conidiogenous cells* polytretic, integrated, terminal, becoming intercalary, sympodial, cylindrical, or clavate, cicatrized, conidiogenous loci (scars) often dark and prominent. *Conidia* usually solitary, short catenate in one species, acropleurogenous, simple, mostly obclavate, pale to dark brown or olivaceous brown, smooth, verrucose or echinulate, distoseptate, generally with a thick, dark hilum at the base.

Type species: *Exosporium tiliae* Link.

Exosporium livistonae Crous & Summerell, Persoonia 27: 145. 2011.

Description and illustration: Crous *et al.* (2011a).

Materials examined: **Australia**, Northern Territory, Litchfield National Park, on leaves of *Livistona benthamii*, 25 Apr. 2011, P.W. Crous & B.A. Summerell (**holotype** CBS H-20763, ex-type culture CBS 131313 = CPC 19357).

Note: See notes under *Exosporium livistonicola*.

Exosporium livistonicola U. Braun, Videira & Crous, **nom. nov.** MB822834.
Replaced synonym: *Distocercospora livistonae* U. Braun & C.F. Hill, Fungal Diversity 22: 23. 2006.

Description and illustration: Braun *et al.* (2006).

Materials examined: **Japan**, Yonagunijima Is., *Livistona chinensis*, 27 Feb. 2003, T. Kobayashi & Y. Ono, culture MUCC 190; Hahajima Is., on *Livistona chinensis* var. *boninensis*, 17 Mar. 2003, T. Kobayashi & Y. Ono, culture MUCC 194. **New Zealand**, Auckland, Manurewa, Auckland Regional Botanic Gardens, Hill Road, on *Livistona chinensis*, 10 Sep. 2005, C.F. Hill 1247 (**holotype** of *Distocercospora livistonae*, HAL 1875 F).

Notes: In this study, the type species of the genus *Distocercospora*, *Distocercospora pachyderma*, formed an independent clade within *Mycosphaerellaceae* (Fig. 1, clade 31; Fig.

2, clade 27). Sequences retrieved from cultures of *Distocercospora livistonae*, isolated from *Livistona chinensis* and originating from Japan, clustered together with the sequences obtained from the ex-type culture of *Exosporium livistonae* (Fig. 1, clade 72; Fig. 4, clade 29). The type species of *Distocercospora livistonae* was described from a different country (New Zealand) but the same host (*Livistona chinensis*) as the studied material from Japan, which was found to be a good representative of the species. The morphological characters observed for both species, *Exosporium livistonae* and *Distocercospora livistonae*, were similar, though the two species differ in conidial width, and this is also to be seen in the phylogeny, where the two taxa are shown to be congeneric, but not conspecific. A further paper on *Exosporium* species (Nakashima, in prep.) will provide further detail on the genus. Based on the phylogenetic analyses, the position of *Exosporium* varies as there is no strong backbone support (Fig. 1, clade 83; Fig. 4, clade 29). Although it sits in the *Mycosphaerellaceae* in the displayed trees, this position may change when more species are introduced as the current genus occasionally clustered between *Schizothyriaceae* and *Dissononiaceae* in different analyses (data not shown). Furthermore, sequences based on the type species of *Exosporium*, *Exosporium tiliae*, are not yet available. Therefore, the inclusion of *Exosporium livistonae* in *Exosporium* is only tentative until the application of the latter genus based on the phylogeny of its type species will be resolved.

Clade 84: *Paramycosphaerella*

Paramycosphaerella Crous & Jol. Roux, Persoonia 31: 245. 2013.

Description (from Crous *et al.* 2013b): Foliicolous, plant pathogenic. *Ascomata* erumpent, amphigenous, brown, globose, with central ostiole; wall of 2–3 layers of brown *textura angularis*. *Asci* fasciculate, bitunicate with apical chamber, 8-spored, subcylindrical to narrowly ellipsoid. *Ascospores* tri- to multiseriate, thin-walled, guttulate, not to very slightly constricted at septum, obovoid, remaining hyaline.

Type species: *Paramycosphaerella brachystegiae* Crous & Jol. Roux.

Paramycosphaerella brachystegiae Crous & Jol. Roux ('*brachystegia*'), Persoonia 31: 245. 2013.

Description and illustration: Crous *et al.* (2013b).

Materials examined: **Zimbabwe**, Mtau forest reserve, near Mvuma, on leaves of *Brachystegia* sp., 2 Apr. 2012, J. Roux (**holotype** CBS H-21445, ex-type cultures CBS 136436 = CPC 21136); *idem*. culture CPC 21137.

Notes: *Paramycosphaerella* is morphologically mycosphaerella-like, but since *Mycosphaerella* is restricted to *Ramularia* asexual morphs, a new genus was established to accommodate the type species *Paramycosphaerella brachystegiae* (Crous *et al.* 2013b). Two more species, *Paramycosphaerella intermedia* (Dick & Dobbie 2001, as *Mycosphaerella intermedia*) and *Paramycosphaerella marksii* (Carnegie & Keane 1994, as *Mycosphaerella marksii*), were later placed in this genus based on phylogenetic inference (Quaedvlieg *et al.* 2014). In a recent publication (Guatimosim *et al.* 2016), a large group of species was introduced in this genus, mostly

based on phylogenetic inference, including *Paramycosphaerella aerohyalinosporum* (Crous *et al.* 2009d, as *Zasmidium aerohyalinosporium*), *Paramycosphaerella blechni* (Guatimosim *et al.* 2016), *Paramycosphaerella cyatheae* (Guatimosim *et al.* 2016), *Paramycosphaerella dicranopteridis* (Kirschner & Liu 2014, as *Zasmidium dicranopteridis*), *Paramycosphaerella dicranopteridis-flexuosae* (Guatimosim *et al.* 2016), *Paramycosphaerella gleicheniae* (Kirschner & Liu 2014, as *Mycosphaerella gleicheniae*), *Paramycosphaerella irregularis* (Cheewangkoon *et al.* 2008, as *Mycosphaerella irregularis*), *Paramycosphaerella madeirensis* (Crous *et al.* 2004b, as *Mycosphaerella madeirae*), *Paramycosphaerella nabiacense* (Crous *et al.* 2009d, as *Zasmidium nabiacense*), *Paramycosphaerella parkii* (Crous *et al.* 1993, Crous & Alfenas 1995, as *Zasmidium parkii*), *Paramycosphaerella pseudomarksii* (Cheewangkoon *et al.* 2008, as *Mycosphaerella pseudomarksii*), *Paramycosphaerella sticheri* (Guatimosim *et al.* 2016) and *Paramycosphaerella vietnamensis* (Burgess *et al.* 2007, as *Mycosphaerella vietnamensis*). Morphologically, the majority of these species are only known from their mycosphaerella-like sexual morphs (*Mycosphaerella gleicheniae*, *Mycosphaerella marksii*, *Mycosphaerella intermedia*, *Mycosphaerella pseudomarksii*, *Paramycosphaerella blechni*, *Paramycosphaerella cyatheae*, *Paramycosphaerella dicranopteridis-flexuosae*, *Paramycosphaerella sticheri*). Most of the remaining species produce a zasmidium-like asexual morph (*Zasmidium aerohyalinosporium*, *Zasmidium dicranopteridis*, *Zasmidium nabiacense*, *Zasmidium parkii*). In two cases, both sexual and asexual morphs are known, namely with "*Mycosphaerella*" *madeirensis* and "*Mycosphaerella*" *vietnamensis*, which have a presumed pseudocercospora-like asexual morph. In a later study (Videira *et al.* 2016), a new phylogenetic analysis based on LSU and *rpb2* placed the strains of *Paramycosphaerella madeirensis* in a sister clade to *Microcyclosporella* and, based on their phylogenetic positon and morphological differences, the genus *Mycosphaerelloides* was erected to accommodate them. In the present study, with the addition of more genera belonging to the *Mycosphaerellaceae*, we observe the previously defined *Paramycosphaerella* clade becoming paraphyletic (Fig. 1, clades 84, 87, 93, 94; Fig. 4, clades 17, 21, 22, 26, 27). Consequently, the phylogenetic position of the species *Paramycosphaerella blechni*, *Paramycosphaerella cyatheae* and *Paramycosphaerella diacranopteridis*, that clustered closely related to *Mycosphaerelloides* (Guatimosim *et al.* 2016, as *Paramycosphaerella madeirensis*) need to be re-evaluated based on the *rpb2* gene. Based on the phylogenetic analyses, *Paramycosphaerella* clusters close to *Brunneosphaerella* in a very heterogeneous clade (Fig. 1, clade 84; Fig. 4, clade 17) suggesting that further analysis is necessary to resolve this group of species.

Paramycosphaerella intermedia (M.A. Dick & K. Dobbie) Quaedvlieg & Crous, Persoonia 33: 23. 2014.
Basionym: *Mycosphaerella intermedia* M.A. Dick & K. Dobbie, New Zealand J. Bot. 39(2): 272. 2001.

Description and illustration: Dick & Dobbie (2001).

Materials examined: **New Zealand**, Bay of Plenty, Rotoehu Forest, Kohekohe Road, on living leaves of *Eucalyptus saligna*, 30 Jun. 1998, L. Renney (**holotype** NZFRI-M 3831, ex-type cultures NZFS 301.10 = CBS 114356 = CMW 7163 = CPC 10902); Waimana Forest, 12 Aug. 1998, K. Dobbie, culture NZFS 301.13 = CBS 114415 = CMW 7164 = CPC 10922.

Note: See notes on *Paramycosphaerella brachystegiae.*

Paramycosphaerella marksii (Carnegie & Keane) Quaedvlieg & Crous, Persoonia 33: 23. 2014.
Basionym: *Mycosphaerella marksii* Carnegie & Keane, Mycol. Res. 98: 414. 1994.

Description and illustration: Carnegie & Keane (1994).

Materials examined: **Australia**, Victoria, Briagolong, on leaves of *Eucalyptus globulus*, 14 Oct. 1994, A. Carnegie, culture CBS 110920 = CPC 935. **South Africa**, Northern Province, Magoebaskloof, Eucalyptus grandis × saligna, Oct. 1994, G. Kemp, cultures CBS 110693 = CPC 823, CBS 110750 = CPC 822 = CMW 14778. **Tanzania**, *Eucalyptus* sp., May 1995, M.J. Wingfield, cultures CBS 110981 = CPC 1073.

Notes: The type species of *Paramycosphaerella marksii*, based on *Mycosphaerella marksii*, was isolated from *Eucalyptus botryoides* from Australia (**holotype** IMI 353731). See notes on *Paramycosphaerella brachystegiae* an also Quaedvlieg *et al.* (2014).

Paramycosphaerella wachendorfiae (Crous) Videira & Crous, **comb. nov.** MycoBank MB822773.
Basionym: *Mycosphaerella wachendorfiae* Crous, Persoonia 26: 129. 2011.

Description and illustration: Crous *et al.* (2011a).

Materials examined: **South Africa**, Western Cape Province, Hermanus, Fernkloof Nature Reserve, S 34°2303800 E 19°1609.700, on leaves of *Wachendorfia thyrsifolia*, 2 May 2010, K.L. Crous & P.W. Crous (**holotype** CBS H-20584, cultures ex-type CBS 129579 = CPC 18338).

Notes: The present strain is phylogenetically closest to the type of *Paramycosphaerella*, *Paramycosphaerella brachystegiae* (Fig. 1, clade 84; Fig. 4, clade 17). The morphological characteristics of the sexual morph are compatible with the genus.

***Paramycosphaerella* sp. A**

Materials examined: **South Africa**, Mpumalanga, on *Musa* cv. Williams, 27 Jul. 2000, K. Surridge, culture CBS 118825 = CMW 10904; *idem*. on *Musa* cv. Grande Naine, 27 Jul. 2000, K. Surridge, culture CBS 118849 = CMW 10902.

Notes: The present strains were originally identified as *Mycosphaerella colombiensis* based on their ITS sequences originally deposited in GenBank (AY217106 and AY217108, respectively). However, *Mycosphaerella colombiensis* was described from *Eucalyptus* in Colombia and is currently a synonym of *Parapallidocercospora colombiensis* (Fig. 1, clade 25; Fig. 2, clade 31). Phylogenetically, both the present strains cluster in *Paramycosphaerella* (Fig. 1, clade 84; Fig. 4, clade 17) and were sterile in culture. It is possible that the wrong cultures were deposited in the CBS culture collection. Therefore, they should be treated as *Paramycosphaerella* sp. until more information becomes available.

***Paramycosphaerella* sp. B**

Materials examined: **USA**, Illinois, Rockford, apple fruit, Sep. 2000, J. Batzer, culture CBS 118968 = CUF2d; New York, Geneva, on apple fruit, 30 Oct. 2005, D. Rosenberger, culture CBS 125300 = NY1 3.2F1c.

Notes: The present strains were initially identified based on morphological characters as *Colletogloeum* sp. and, based on an LSU neighbour-joining phylogeny, they clustered closest to *Mycosphaerella marksii*. They formed a dense, fuliginous mycelial mat with no sclerotium-like bodies, had thick-walled, ovoid to allantoid blastospores that were highly vacuolate, subhyaline, and truncate at the base, measuring 6–19 × 2.5–4.5 µm (strain FG 2.1) or 7–11 × 1–2 µm (strain FG 2.3) on CLA culture media (Batzer *et al.* 2005). This description is very broad and the present strains are now sterile which makes it impossible to draw further conclusions. The correct phylogenetic placement of the genus *Colletogloeum*, based on the type *Colletogloeum dalbergiae* (Pakistan), is unknown, although DNA extracted from a herbarium specimen of *Colletogloeum sissoo* (IMI 119162) (= *Colletogloeum dalbergiae*) suggests *Colletogloeum* to cluster in a sister clade to *Pseudocercospora* (Crous *et al.* 2009e). Based on the phylogenetic analysis in the present study, these present strains cluster within the *Paramycosphaerella* clade (Fig. 1, clade 84; Fig. 4, clade 17), and should be treated as *Paramycosphaerella* sp. until more information is available.

Clade 85: *Pseudopericoniella*

Pseudopericoniella Videira & Crous, **gen. nov.** MycoBank MB822699.

Etymology: From pseudo-, that means resembling but not equalling, and the similarity to the genus *Periconiella*.

Description: *Mycelium* composed of submerged hyaline hyphae, smooth and thin-walled, and aerial hyphae subhyaline, later becoming dark brown, smooth and thick-walled. *Conidiophores* arising from creeping aerial hyphae, erect, dark brown at the base, paler towards the apex, thick-walled, septate, branched in the upper part. *Conidiogenous cells* integrated, terminal and intercalary, subhyaline, later becoming pale brown, cylindrical, proliferating sympodially, forming a short rachis with conidiogenous loci darkened, slightly thickened and protruding. *Conidia* solitary, pale olivaceous, smooth, obovoid, ellipsoidal, pyriform to clavate, cylindrical, base long obconicaly truncate and rounded apex, straight to mildly curved, aseptate or septate, sometimes constricted at the septa, with a hilum slightly thickened and darkened.

Type species: *Pseudopericoniella levispora* (Arzanlou *et al.*) Videira & Crous (≡ *Periconiella levispora* Arzanlou *et al*.).

Pseudopericoniella levispora (Arzanlou *et al.*) Videira & Crous, **comb. nov.** MycoBank MB822780.
Basionym: Periconiella levispora Arzanlou *et al.*, Stud. Mycol. 58: 68. 2007.

Description and illustration: Arzanlou *et al.* (2007).

Materials examined: **Sri Lanka**, Hakgala Botanic Gardens, on dead leaves of *Turpinia pomifera*, Jan. 1973, W. Gams (**holotype** CBS H-15611, culture ex-type CBS 873.73).

Notes: Morphologically, *Pseudopericoniella levispora* is similar to *Periconiella velutina* but can be distinguished by producing darker and longer conidia [(7–)8–9(–11) × (2.5–)3(–4) µm, in *Periconiella velutina*; Arzanlou *et al.* 2007]. Based on the phylogenetic analyses in the present study, the type of *Periconiella*, *Periconiella velutina*, clusters within the *Zasmidium* complex (Fig. 1, clade 69; Fig. 4, clade 1), while *Pseudopericoniella levispora* clusters in a unique position (Fig. 1, clade 85; Fig. 4 clade 22) closely related to *Hyalozasmidium*.

***Pseudopericoniella* sp.**

Material examined: **Netherlands**, Aalsmeer, leaf spot on *Rosa* sp., isol. & dep. J.A. von Arx, 1951, culture CBS 330.51.

Notes: The present strain was previously identified as *Mycosphaerella rosigena*. It is currently sterile and no fungarium material has been preserved. The type specimen of *Mycosphaerella rosigena* (from *Rosa* sp., Louisiana, USA, **holotype** NY) was examined by Aptroot (2006) and combined into *Davidiella* (currently a synonym of *Cladosporium*) based on morphological characters. Based on the phylogenetic analysis, the present strain clusters close to *Pseudopericoniella levispora* (Fig. 1, clade 85; Fig. 4, clade 22), and should be treated as *Pseudopericoniella* sp. until more information becomes available.

Clade 86: *Brunneosphaerella*

Brunneosphaerella Crous, Stud. Mycol. 64: 31. 2009.

Description (from Crous *et al.* 2009c): *Ascomata* amphigenous, immersed to semi-immersed, black, single, gregarious, substomatal, pyriform or globose with a papillate, periphysate ostiole; peridium consisting of three strata of slightly compressed *textura angularis*, an outer stratum of dark brown, thick-walled cells, becoming paler in the central stratum, and hyaline, thin-walled in the inner stratum. *Asci* clavate to cylindro-clavate, often curved, tapering to a pedicel, narrowing slightly to a rounded apex with an indistinct ocular chamber, 8-spored, bitunicate with fissitunicate dehiscence. *Pseudoparaphyses* absent. *Ascospores* biseriate, fusiform, broader at the apical end, initially hyaline and 1-septate, becoming yellow-brown and 3-septate at maturity, slightly constricted at median to supra-median septum.

Type species: *Brunneosphaerella protearum* (Syd. & P. Syd.) Crous (≡ *Leptosphaeria protearum* Syd. & P. Syd.).

Brunneosphaerella protearum (Syd. & P. Syd.) Crous, Stud. Mycol. 64: 31. 2009.
Basionym: *Leptosphaeria protearum* Syd. & P. Syd., Ann. Mycol. 10: 441. 1912.

Description and illustration: Crous *et al.* (2009c).

Material examined: **South Africa**, Western Cape Province, Wellington, on leaves of *Protea lepidocarpodendron* (as *P. melaleuca*), 22 Feb. 1912, E.M. Doidge (**holotype** PREM 2061);

Cape town, Kirstenbosch Botanical Garden, on *Protea* sp., 13 Jan. 2009, P.W. Crous, (**epitype** designated by Crous *et al.* 2011c: CBS H-20335, ex-epitype culture CBS 130597 = CPC 16338); Kirstenbosch Botanical Garden, on leaves of *P. coronata*, 8 May 2010, P.W. Crous, CBS H-20673, culture CPC 18308 = CBS 130598; Harold Porter Botanical Garden, Betties Bay, on leaves of *P. mundii*, 4 May 2010, P.W. Crous, CBS H-20683, culture CPC 18328; Bettys' Bay, leaf litter of *Protea magnifica*, 11 Jul. 2000, S. Marincowitz, PREM 59448; Helderberg Nature Reserve, leaf litter of *Protea laurifolia*, 14 Aug. 2000, S. Marincowitz, PREM 59482; Helderberg Nature Reserve, leaf litter of *Protea obtusifolia*, 14 Aug. 2000, S. Marincowitz, PREM 59495; Jonkershoek Nature Reserve, leaf litter of *Protea nitida*, 6 Jun. 2000, S. Marincowitz, PREM 59442; Jonkershoek Nature Reserve, leaf litter of *Protea repens*, 6 Jun. 2000, S. Marincowitz, PREM 59450; Jonkershoek Nature Reserve, S33°59011.200 E18°57014.700 leaves of *Protea* sp., 1 Apr. 2007, P.W. Crous, CBS H-20330, cultures CPC 13914–13916; Jonkershoek Nature Reserve, S33°59026.100 E18°57059.500 leaves of *P. repens*, 1 Apr. 2007, P.W. Crous, CBS H-20331, cultures CPC 13911–13913; Jonkershoek Nature Reserve, leaves of *Protea* sp., 1 Apr. 2007, P.W. Crous, CBS H-20332, cultures CPC 13908–13910; Jonkershoek Nature Reserve, "Tweede Waterval", leaves of *Protea* sp., 1 Apr. 2007, P.W. Crous, CBS H-20333, cultures CPC 13902–13907; Jonkershoek Nature Reserve, leaves of *P. nitida*, 12 Apr. 2008, L. Mostert, CBS H-20334, cultures CPC 15231–15233; Stellenbosch, J.S. Marais Garden, S33°55059.300 E18°52022.500, on living leaves of *P. magnifica*, 1 Apr. 1998, J.E. Taylor, culture CPC 16849.

Notes: The genus *Brunneosphaerella* was established to accommodate species belonging to the *Leptosphaeria protearum* complex (*Pleosporales*) that clustered within the *Mycosphaerellaceae* (Crous *et al.* 2009c, 2011c). These species were characterised by having bitunicate asci without pseudoparaphyses, brown, 3-septate ascospores, and a coniothyrium-like asexual morph. *Brunneosphaerella protearum* is a major leaf spot and blight pathogen of *Protea* spp. causing severe losses in plantations of South African *Protea* spp. wherever they are cultivated (Crous *et al.* 2009c, 2011c). Morphologically *Brunneosphaerella* is distinct from *Leptosphaeria* in that its ascospores are always brown at maturity and similar to *Phaeophleospora* in that conidiogenous cells are brown and proliferate percurrently. The genus *Brunneosphaerella* currently contains three species that cluster in a well-supported clade (Fig. 1, clade 86; Fig. 4, clade 18) that is closely related to *Neomycosphaerella*.

Clade 87: *Hyalozasmidium*

Hyalozasmidium U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822593.

Etymology: Derived from the hyaline conidia + resembling the genus *Zasmidium.*

Description: *Mycelium* composed of subhyaline to pale brown hyphae, smooth, branched and septate, producing large swollen propagules that occur terminaly or lateraly on hyphal strands. *Conidiophores* medium to dark brown, unbranched, smooth to verruculose, becoming constricted at septa, eventually disarticulating, with each conidiophore giving rise to a single conidium. *Conidiogenous cells* apical and intercalary, mono- or polyblastic, straight, proliferating sympodially, with conidiogenous loci unthickened or slightly thickened, located at shoulders and apex. *Conidia* hyaline, thick-walled, subcylindrical, with multiple transverse septa, developing irregular swellings which can form branches with obtuse ends, body granular, basal cell tapering prominently towards the conidiophore. Differs from the genus *Zasmidium*, by bearing hyaline conidia.

Type species: *Hyalozasmidium aerohyalinosporum* (Crous & Summerell) Videira & Crous (≡ *Zasmidium aerohyalinosporum* Crous & Summerell).

Hyalozasmidium aerohyalinosporum (Crous & Summerell) Videira & Crous, **comb. nov.** MycoBank MB822761.
Basionym: *Zasmidium aerohyalinosporum* Crous & Summerell, Persoonia 23: 144. 2009.
Synonym: *Paramycosphaerella aerohyalinosporum* (Crous & Summerell) Guatimosim *et al.* Persoonia 37: 124. 2016.

Description and illustration: Crous *et al.* (2009d).

Materials examined: **Australia**, New South Wales, Road to Robin Falls, 13°31001.300S, 131°16022.500E, 126 m, on leaves of *Eucalyptus tectifica*, 23 Sep. 2007, coll. B.A. Summerell, isol. P.W. Crous (**holotype** of *Zasmidium aerohyalinosporium* CBS H-20274, culture ex-type CBS 125011 = CPC 14636); *idem*., culture CPC 14637.

Notes: In the phylogenetic analyses, the present species is closely related to *Neomycosphaerella* (Fig. 1, clade 87; Fig. 4, clade 21). See notes in Crous *et al.* (2009d) and also notes on *Paramycosphaerella brachystegiae.*

Hyalozasmidium sideroxyli U. Braun, C. Nakash., Videira & Crous, **sp. nov.** MycoBank MB822713. Fig. 47.

Etymology: Named after the host genus on which it occurs, *Sideroxylon.*

Description in vitro (on SNA; CPC 23462): *Mycelium* composed of hyaline to subhyaline hyphae, smooth, branched and septate, producing large swollen propagules that occur terminally or laterally on hyphal strands, 1.5–3 µm diam. *Conidiophores* micro- or macronematous, hyaline to subhyaline, simple or branched, septate, straight to slightly curved, 12.5–60 × 2.5–5 µm. *Conidiogenous cells* apical and intercalary, mono- or polyblastic, proliferating sympodially, with conidiogenous loci slightly thickened and darkened, located at shoulders and apex, 1.5–2 µm diam. *Conidia* solitary, sometimes bearing conidia by microcyclic conidiation, hyaline,

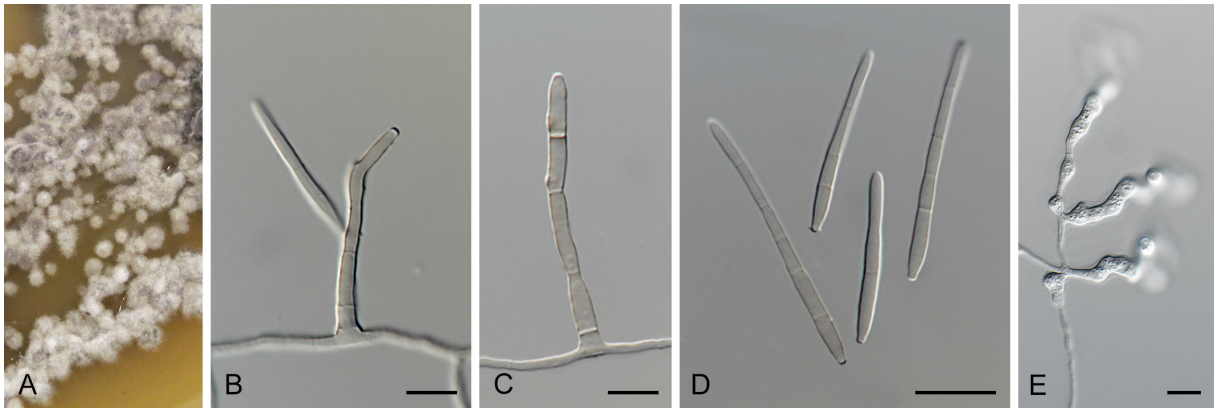


Fig. 47. *Hyalozasmidium sideroxyli* (CPC 23462). A–E. Observations *in vitro*. A. Culture on V8. B, C. Conidiophores and conidiogenous cells. D. Conidia. E. Irregular swollen conidia synanamorph. Scale bars = 10 µm.

smooth to rough, cylindrical to obclavate, straight, base obconically truncate and apex rounded, 20–50 × 2–2.5 µm, 0–4-septate, hila slightly thickened and darkened.

Material examined: **South Africa**, Eastern Cape, Cape St. Francis, on *Sideroxylon inerme*, 8 May 2013, A.R. Wood (**holotype** CBS H-22965, ex-type culture CBS 142191 = CPC 23462).

Notes: Based on the phylogenetic analyses, the present strain clusters within the *Hyalozasmidium* clade (Fig. 1, clade 87; Fig. 4, clade 21). Morphologically, its characteristics are in accordance with the genus description (Fig. 47) and it can be distinguished from *Hyalozasmidium aerohyalinosporium* by having conidiogenous cells that are polyblastic, and longer, less septate conidia.

Clade 88: *Madagascaromyces*

Madagascaromyces U. Braun, C. Nakash., Videira & Crous, **gen. nov.** MycoBank MB822594.

Etymology: Named after the island where the type species was collected, Madagascar.

Description: *Mycelium* composed of pale to medium brown hyphae, septate, branched, smooth, 2–3 µm. *Conidiophores* solitary, medium brown, smooth, subcylindrical, simple or branched, straight to variously curved or geniculate-sinuous. *Conidiogenous cells* terminal and intercalary, proliferating sympodially, with one or multiple conidiogenous loci that are thickened and darkened. *Conidia* solitary, pale brown, smooth, guttulate, subcylindrical when small, narrowly obclavate when larger, apex subobtuse, base long obconically subtruncate, straight to slightly curved, 1- or multiseptate, with hila thickened and darkened, microcyclic conidiation observed in culture. *Spermatogonia* forming on OA. *Spermatia* cylindrical with obtuse ends, smooth, hyaline.

Type species: *Madagascaromyces intermedius* (Crous & M.J. Wingf.) Videira & Crous (≡ *Passalora intermedia* Crous & M.J. Wingf.).

Madagascaromyces intermedius (Crous & M.J. Wingf.) Videira & Crous, **comb. nov.** MycoBank MB822762.
Basionym: *Passalora intermedia* Crous & M.J. Wingf., Persoonia 22: 88. 2009.

Description and illustrations: Crous *et al.* (2009g).

Materials examined: **Madagascar**, Morondavo, on leaf of *Eucalyptus calmadulensis*, Aug. 2007, M.J. Wingfield (**holotype** CBS H-20197, ex-type culture CBS 124154 = CPC 15745); on *E. calmadulensis*, 1 Oct. 2007, M.J. Wingfield, culture CPC 15719.

Notes: The genus *Madagascaromyces* is monotypic and based on *Madagascaromyces intermedius* (syn. *Passalora intermedia*). Morphologically, *Madagascaromyces intermedius* can be considered intermediate between *Pseudocercospora* and *Passalora*, based on the narrowly obclavate conidia with hila that are somewhat thickened and darkened, but not prominently refractive (Crous *et al.* 2009g). Phylogenetically, strains of the present species cluster in a well-supported clade (Fig. 1, clade 88; Fig. 4, clade 19) that is closely related to *Neomycosphaerella*.

Since the species *Madagascaromyces intermedius* is only known from its asexual morph, and the species *Neomycosphaerella pseudopentameridis* is only known by its sexual morph, a direct comparison between both is not possible. Based on a BLAST comparison against the ITS alignment, *Madagascaromyces intermedius* CPC 15745 shares 92 % (450/489) similarity, including 2 % (13/489) gaps, with *Hyalozasmidium sideroxyli* CBS 125011 and 90 % (439/488) similarity, including 3 % (16/488) gaps, with *Neomycosphaerella pseudopentameridis* CBS 136407. Based on a BLAST comparison against the *rpb2* alignment, *Mad. intermedius* CPC 15745 shares 81 % (571/703) similarity with *Pseudopericoniella* sp. CBS 330.51 using megablast search, and 82 % (589/722) with *Neomycosphaerella pseudopentameridis* CBS 136407 using a blastn search. Based on the molecular and morphological differences, we decided to keep the present two taxa in single species genera until more information becomes available.

Clade 89: *Neomycosphaerella*

Neomycosphaerella Crous, Persoonia 31: 195. 2013.

Description (from Crous *et al.* 2013b): Foliicolous, phytopathogenic. *Ascomata* immersed, subepidermal, frequently in a brown stroma, unilocular, in rows of 2–4, globose, with central ostiole; wall of 2–4 layers of brown *textura angularis*. *Asci* fasciculate, stipitate, 8-spored, with minute ocular chamber, obovoid, straight to slightly curved, hyaline. *Ascospores* tri- to multiseriate, hyaline, smooth, granular, medianly 1-septate; ascospores becoming brown and verruculose with age.

Type species: *Neomycosphaerella pseudopentameridis* Crous.

Neomycosphaerella pseudopentameridis Crous, Persoonia 31: 195. 2013.

Description and illustration: Crous *et al.* (2013b).

Material examined: **South Africa**, Western Cape Province, Cape Town, Green Point Park, on leaves of *Pseudopentameris macrantha*, 22 Jul. 2012, P.W. Crous (**holotype** CBS H-21416, ex-type cultures CBS 136407 = CPC 21126); *idem*., culture CPC 21127.

Notes: *Neomycosphaerella* represents a single-strain lineage in the phylogenetic analyses and is closely related to *Brunneosphaerella* (Fig. 1, clade 89; Fig. 4, clade 20). Morphologically, *Neomycosphaerella* is only known by its sexual morph, which is mycosphaerella-like. *Brunneosphaerella* differs from *Neomycosphaerella* by producing pigmented ascospores, 3-septate, and with mucoid caps (Crous *et al.* 2013b).

Clade 90: *Mycosphaerelloides*

Mycosphaerelloides Videira & Crous, Stud. Mycol. 83: 99. 2016.

Description (from Videira *et al.* 2016): *Leaf spots* amphigenous, subcircular, 2–15 mm diam, medium brown, surrounded by a slightly raised, red-purple border. *Ascomata* pseudothecial, predominantly epiphyllous, single, black, immersed, becoming erumpent, globose, up to 120 µm diam; apical ostiole 10–15 µm diam; wall of 2–3 layers of medium brown *textura angularis*.

Asci aparaphysate, fasciculate, bitunicate, subsessile, obovoid to narrowly ellipsoid, straight or slightly incurved, 8-spored, 30–50 × 8–12 µm. *Ascospores* 3- to multiseriate, overlapping, hyaline, guttulate, thin-walled, straight to slightly curved, fusoid-ellipsoid with subobtuse ends, apex frequently acutely rounded, medianly 1-septate, widest in the middle of the apical cell, not constricted at the septum, tapering towards both ends, but more prominently towards the lower end, (9–)10–13(–15) × 2.5–3(–3.5) µm *in vivo*. *Mycelium* internal and external, consisting of smooth, branched, septate, pale to medium brown, 3–6 µm wide hyphae; external mycelium extensive on abaxial leaf surface. *Conidiomata* fasciculate, hypophyllous, medium brown, up to 90 µm wide and 150 µm high. *Conidiophores* arising from superficial mycelium, or aggregated in loose fascicles arising from the upper cells of a brown stroma up to 80 µm wide and 90 µm high; conidiophores pale to medium brown, smooth, unbranched or branched, 1–5-septate, subcylindrical, straight to variously curved, 15–45 × 2.5–4 µm; conidiogenous cells terminal or lateral, unbranched, subcylindrical, pale brown, smooth, proliferating sympodially, or 1–4 times percurrently near apex, 7–15 × 2.5–3 µm; conidiogenous loci inconspicuous. *Conidia* solitary, pale brown, smooth, subcylindrical, but tapering from a subtruncate base towards a subobtuse apex, 3–6- or multiseptate, 35–85 × 2.5–4 µm, hila neither thickened nor darkened-refractive.

Type species: *Mycosphaerelloides madeirae* (Crous & Denman) Videira & Crous (≡ *Mycosphaerella madeirae*).

Mycosphaerelloides madeirae (Crous & Denman) Videira & Crous, Stud. Mycol. 83: 100. 2016.
Basionym: *Mycosphaerella madeirae* Crous & Denman, Stud. Mycol. 50: 204. 2004.
Synonym: *Paramycosphaerella madeirae* (Crous & Denman) Guatimosim *et al.*, Persoonia 37: 127. 2016, as '*madeirensis*'.

Description and illustrations: Crous *et al.* (2004b).

Materials examined: **Portugal**, Madeira, Party Farm, on leaves of *Eucalyptus globulus*, Apr. 2000, S. Denman (**holotype** CBS H-9898, culture ex-type CBS 112895 = CPC 3745 = CMW 14458); *idem*., culture CBS 112301 = CPC 3747. **Netherlands**, Utrecht, Soest, endophytic on green leaves of *Quercus robur*, 2002, G. Verkley, cultures CBS 115936, CBS 116068, CBS 116066.

Notes: *Mycosphaerelloides* is currently a monotypic genus based on *Mycosphaerelloides madeirae*, which has a mycosphaerella-like sexual morph and a presumed pseudocercospora-like asexual morph (Crous *et al.* 2004b, Videira *et al.* 2016). Phylogenetically, the strains of *Mycosphaerelloides madeirae* cluster in a well-supported clade (Fig. 1, clade 90; Fig. 4, clade 24) that is closely related to *Microcyclosporella*. Based on a BLAST comparison against the alignment, *Mycosphaerelloides madeirae* CBS 112895 shares 96 % (467/485) similarity with *Microcyclosporella mali* CBS 126136 based on ITS and shares 88 % (594/674) similarity with *Epicoleosporium ramularioides* CPC 10672 based on *rpb2*.

Clade 91: *Epicoleosporium*

Epicoleosporium Videira & Crous, Stud. Mycol. 83: 100. 2016.

Description (from Videira *et al.* 2016): *Colonies* growing on uredinia of *Coleosporium*, mycophilic. *Mycelium* superficial, consisting of hyaline, septate, thin-walled, smooth hyphae. *Conidiophores* hyaline, loose, straight, subcylindrical, unbranched, septate, thin-walled, smooth. *Conidiogenous cells* hyaline, terminal in the conidiophore, cylindrical-oblong, proliferation sympodial, with conspicuous conidiogenous loci, thickened, darkened and refractive. *Conidia* hyaline, smooth, solitary or in short chains, cylindrical-oblong, clavate, obovate, aseptate, thin-walled, smooth, with hila thickened, darkened and refractive.

Type species: *Epicoleosporium ramularioides* Videira *et al.*

Epicoleosporium ramularioides Videira *et al.*, Stud. Mycol. 83: 100. 2016.

Description and illustrations: Videira *et al.* (2016).

Materials examined: **Republic of Korea**, Pyeongchang, on *Coleosporium phellodendri* on leaves of *Phellodendron amurense*, 4 Sep. 2003, H.D. Shin (**holotype** KUS F19603, isotype CBS H-22542, culture ex-type CBS 141103 = CPC 10672); *idem*., culture CPC 10673.

Notes: The genus *Epicoleosporium* is presently monotypic and is based on *Epicoleosporium ramularioides*, which has a ramularia-like morphology, but is not congeneric with *Ramularia* as currently circumscribed (Videira *et al.* 2016). Based on the phylogenetic analyses in the present study, the representative strains cluster in a well-supported clade (Fig. 1, clade 91; Fig. 4, clade 25) and are closely related to the genus *Mycosphaerelloides*.

Clade 92: *Microcyclosporella*

Microcyclosporella J. Frank *et al.*, Persoonia 24: 101. 2010.

Description (from Frank *et al.* 2010): Hyphomycetous. *Mycelium* consisting of pale brown, smooth to finely verruculose, branched, septate, 2–3.5 µm wide hyphae, at times covered by a mucoid layer, with integrated, lateral, truncate conidiogenous loci. *Conidiophores* mostly reduced to conidiogenous cells. *Conidiogenous cells* integrated, intercalary on hyphae, rarely terminal, cylindrical to doliiform, pale brown, but hyaline if occurring in yeast-like sectors of colonies, smooth, mono- or polyblastic, proliferating sympodially, with inconspicuous, truncate, unthickened, not darkened, pale brown to hyaline loci. *Conidia* solitary, hyaline, smooth, subcylindrical to narrowly obclavate or narrowly fusoid with acutely rounded apex and obconically truncate base, guttulate, 0–6 times transversely septate; microcyclic conidiation common.

Type species: *Microcyclosporella mali* J. Frank *et al.*

Microcyclosporella mali J. Frank *et al.*, Persoonia 24: 101. 2010.

Description and illustration: Frank *et al.* (2010).

Materials examined: **Slovenia**, Senozeti, Dolsko, on fruit surface *Malus domestica*, 7 Aug. 2007, J. Frank (**holotype** CBS H-20413, culture ex-type 300-07 = CBS 126136 = CPC 16184);

Mirna, on *M. domestica* fruit surface, 17 Oct. 2007, J. Frank, culture 174-07 = CPC 16180 = CBS 126132. **USA**, Michigan, Fennville, on *Malus* sp., 1 Sep. 2005, G. Sundin, culture CBS 125653 = RH6 = MI3 20F1a; Ohio, Wooster, on *Malus* sp., 5 Sep. 2005, M. Ellis, culture CBS 125651 = RH1 = OH1 34D2a.

Notes: The genus *Microcyclosporella* is presently monotypic and is based on *Microcyclosporella mali*, a species that is associated with sooty blotch and flyspeck (SBFS) lesions on apples. It has a pseudocercosporella-like morphology but is not congeneric with the type of *Pseudocercosporella*, *Pseudocercosporella bakeri* (Frank *et al.* 2010, Videira *et al.* 2016). Phylogenetically, the present strains clusters in a well-supported clade (Fig. 1, clade 92; Fig. 4, clade 23) that is closely related to *Epicoleosporium ramularioides* and *Mycosphaerella madeirae*.

Clade 93: *Virosphaerella*

Virosphaerella Videira & Crous, **gen. nov.** MycoBank MB822705.

Etymology: The prefix virus- (= slime) for the germinating ascospores enveloped in a slime sheath + *sphaerella* (referring to *Mycosphaerella*).

Description: Phytopathogenic, producing leaf spots or not. *Ascomata* amphigenous or epiphyllous, black, subepidermal to erumpent, ovoid, globose or subglobose, apical ostiole, wall consisting of 2–3 layers of medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, subsessile, subcylindrical to narrowly obovoid, straight to slightly curved, 8-spored. *Ascospores* bi- to tri-seriate, overlapping, hyaline, guttulate, thin-walled, straight to slightly curved, fusoid, fusoid-ellipsoidal with obtuse ends, medianly 1-septate or slightly longer in the basal cell, slightly constricted at septum, widest just above the septum, or in the middle of the apical cell, tapering toward both ends, but with more prominent taper towards lower end, mucilaginous sheath visible around spore. *Ascospore germination* from both ends in two patterns (remaining hyaline): Type I (Crous 1998), growing parallel to the long axis of the spore, with lateral branches parallel or perpendicular to the long axis of spore, irregular in width, constricted at the median septum of the spore, slightly distorting; Type B (Crous 1998), germ tube growing parallel to the long axis of the spore, regular in width, not distorting or becoming constricted at septum. *Spermatogonia*, when present, amphigenous, dark brown, subepidermal to erumpent, globose to subglobose. *Spermatia* hyaline, smooth, rod-shaped, with obtuse ends.

Type species: *Virosphaerella pseudomarksii* (Cheewangkoon *et al.*) Videira & Crous (≡ *Mycosphaerella pseudomarksii* Cheewangkoon *et al.*).

Virosphaerella irregularis (Cheewangkoon *et al.*) Videira & Crous, **comb. nov.** MycoBank MB822803.
Basionym: *Mycosphaerella irregularis* Cheewangkoon *et al.* (as '*irregulari*'), Persoonia 21: 83. 2008.
Synonyms: *Paramycosphaerella irregularis* (Cheewangkoon *et al.*) Guatimosim *et al.*, Persoonia 37: 127. 2016.

Description and illustration: Cheewangkoon *et al.* (2008).

Materials examined: **Thailand**, Udonthani, on living leaves of *Eucalyptus* sp., Jul. 2007, R. Cheewangkoon (**holotype** CBS H-20135, culture ex-type CBS 123242 = CPC 15408); *idem*., cultures CPC 15431, CPC 15432.

Notes: Ascospores of *Virosphaerella irregularis* are similar to *Amycosphaerella africana*, but differ by producing a mucilaginous sheath around the ascospore and by the irregular germ tubes and germination pattern (Cheewangkoon *et al.* 2008). Phylogenetically, the present species clusters in a well-supported clade with *Virosphaerella pseudomarksii* (Fig. 1, clade 93; Fig. 4, clade 26), as previously observed by Cheewangkoon *et al.* (2008) in a phylogeny based only on LSU sequences. Based on a BLAST against the alignment, *Virosphaerella irregularis* CBS 123242 shares 95 % (472/495) similarity on ITS, including 1 % (7/495) gaps, and 85 % (623/734) similarity on *rpb2*, with *Virosphaerella pseudomarksii* CBS 123241.

Virosphaerella pseudomarksii (Cheewangkoon *et al.*) Videira & Crous, **comb. nov.** MycoBank MB822806.
Basionym: *Mycosphaerella pseudomarksii* Cheewangkoon *et al.*, Persoonia 21: 83. 2008.
Synonym: *Paramycosphaerella pseudomarksii* (Cheewangkoon *et al.*) Guatimosim *et al.*, Persoonia 37: 127. 2016.

Description and illustration: Cheewangkoon *et al.* (2008).

Materials examined: **Thailand**, Chiang Mai, Mae Tang, on living leaves of *Eucalyptus* sp., Jun. 2007, R. Cheewangkoon (**holotype** CBS H-20134, ex-type culture CBS 123241 = CPC 15410); *idem*., cultures CPC 15435, CPC 15436.

Notes: *Virosphaerella pseudomarksii* ascospore morphology and ascospore germination patterns are similar to *Paramycosphaerella marksii* (Carnegie & Keane 1994, as *Mycosphaerella marksii*) but differ by producing a visible mucilaginous sheath around the ascospore (Cheewangkoon *et al.* 2008). Phylogenetically, the present species clusters in a well-supported clade based on all three phylogenetic methods employed (Fig. 1, clade 93; Fig. 4, clade 26), and is closely related to *Virosphaerella irregularis*.

Clade 94: *Pseudozasmidium* [and Genus A]

Pseudozasmidium Videira & Crous, **gen. nov.** MycoBank MB822701.

Etymology: Derived from pseudo-, that means resembling but not equalling, and the similar genus, *Zasmidium*.

Description: Phytopathogenic, causing leaf spots. *Pseudothecia* amphigenous, aggregated, black, immersed and becoming erumpent, wall of 2–3 layers of medium brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, narrowly ellipsoid or obclavate to cylindrical, straight or slightly incurved, 8-spored. *Ascospores* bi-seriate to triseriate, overlapping, hyaline, straight to slightly curved, ellipsoid or fusoid-ellipsoid, with obtuse ends, medianly 1-septate, not constricted to slightly constricted at the septum, symmetrical cells or widest at the middle of the apical cell, tapering towards both ends or more prominently towards lower end. *Ascospore* germination parallel to perpendicular to the long axis of the spore. *Mycelium* internal and

external, internal hyphae branched, septate, smooth and hyaline, external hyphae verruculose and pale to medium brown, terminal hyphal ends may develop clusters of globose, multi-celled chlamydospore-like structures. *Conidiophores* pale to medium brown, smooth to verruculose, erect, subcylindrical, straight or curved, branched or unbranched, repeatedly geniculate, septate, sometimes reduced to conidiogenous cells. *Conidiogenous cells* terminal, smooth to verruculose, pale brown to brown, proliferating sympodially, sometimes repeatedly geniculate, with conidiogenous loci thickened and darkened-refractive. *Conidia* single, pale brown to olivaceous brown, smooth to verruculose, obclavate, narrowly obclavate to subcylindrical, obtuse apex and obconically truncate base, straight or curved, 1- to multiseptate, hila thickened and darkened-refractive.

Type species: *Pseudozasmidium parkii* (Crous & Alfenas) Videira & Crous (≡ *Stenella parkii* Crous & Alfenas).

Pseudozasmidium eucalypti (Crous & Summerell) Videira & Crous **comb. nov.** MycoBank MB822783.
Basionym: *Stenella eucalypti* Crous & Summerell, Fungal Diversity 26: 177. 2007.
Synonym: *Zasmidium eucalypti* (Crous & Summerell) Crous & U. Braun, Schlechtendalia 20: 101. 2010.

Description and illustrations: Crous *et al.* (2007c).

Description in vitro (on V8; CPC 13302): *Mycelium* composed of hyaline to subhyaline hyphae, uniform in width, 2–2.5 µm, smooth. *Conidiophores* macronematous, first cell arising from hypha (foot cell) hyaline, following cells pale brown to dark brown, paler towards the apex, cylindrical, simple, rarely branched, straight to geniculate, 20–80 × 5–7.5 µm. *Conidiogenous cells* integrated, terminal, polyblastic, proliferating sympodially, occasionally proliferating percurrently, with rim-like conidiogenous loci, somewhat thickened, darkened and protruding, 2–2.5 µm diam. *Conidia* solitary, hyaline to pale brown, cylindrical to obclavate, obconical truncate at the base and rounded at the apex, 12.5–120 × 3–5 µm, 0–8-septate, hila thickened and darkened, 2–2.5 µm diam.

Materials examined: **Australia**, Queensland, Cairns, Eureka Creek, 48 km from Mareeba, S17°11013.200, E145°02027.400, 468 m, on leaves of *Eucalyptus tereticornis*, 26 Aug. 2006, P.W. Crous (**holotype** CBS H-19830, ex-type culture CBS 121101 = CPC 13302).

Notes: The present species was initially described in *Stenella* (Crous *et al.* 2007c), but was later reallocated to *Zasmidium* (Braun *et al.* 2010a). Its asexual morph is zasmidium-like, with brown and verruculose conidiophores and conidia, with hila thickened, darkened and refractive. However, based on the phylogenetic analysis, it is not part of *Zasmidium* as circumscribed in the present study, but clusters in a poorly resolved clade (Fig. 1, clade 94; Fig. 4, clade 27) that is closely related to *Virosphaerella*. All three phylogenetic methods support the smaller clade including *Pseudozasmidium vietnamense* and *Pseudozasmidium parkii*, but the support for the species *Pseudozasmidium eucalypti* and *Pseudozasmidium nabiacense* is very low. Based on the parsimony analysis, *Pseudozasmidium eucalypti* and *Pseudozasmidium nabiacense* form a basal polytomy closely related to *Pseudozasmidium vietnamense* and *Pseudozasmidium parkii*. Since their morphology is also zasmidium-like, we decided to retain them in the same genus

for now. *Pseudozasmidium eucalypti* is unique among other *Pseudozasmidium* species in its ability to produce clusters of globose chlamydospore-like structures, frequently surrounded by a mucus sheath, at the terminal ends of hyphae.

Pseudozasmidium nabiacense (Crous & Carnegie) Videira & Crous, **comb. nov.** MycoBank MB822784.
Basionym: *Zasmidium nabiacense* Crous & Carnegie, Persoonia 23: 142. 2009.
Synonym: *Paramycosphaerella nabiacensis* (Crous & Carnegie) Guatimosim *et al.*, Persoonia 37: 127. 2016.

Description and illustrations: Crous *et al.* (2009d).

Description in vitro (on V8; CPC 12748): *Mycelium* composed of hyaline to pale olivaceous brown hyphae, verruculose, uniform in width, 2–3 µm. *Conidiophores* micro- to macronematous, pale olivaceous brown, verruculose, simple, straight to geniculate, 25–58 × 3–4 µm. *Conidiogenous cells* integrated, terminal, polyblastic, proliferating sympodially, long-conically truncate at the apex and shoulders, with conidiogenous loci somewhat thickened, darkened and protruding, 1.5–2.5 µm diam. *Conidia* solitary, pale olivaceous brown, verruculose, straight, cylindrical to obclavate, obconically truncate at the base and rounded at the apex, 18–32 × 3–3.5 µm, 0–3-septate, with hila thickened and darkened, 1.5–2.5 µm diam.

Materials examined: **Australia**, New South Wales, Nabiac, on leaves of *Eucalyptus* sp. (red gum), 30 Nov. 2005, A.J. Carnegie (**holotype** CBS H-20273, cultures ex-type CBS 125010 = CPC 12748–CPC 12750).

Notes: *Pseudozasmidium nabiacense* is only known from its asexual morph, which is zasmidium-like. The phylogenetic analyses in the present study showed *Pseudozasmidium nabiacense* clustering in a poorly resolved clade (Fig. 1, clade 94; Fig. 4, clade 27) that is closely related to *Pseudozasmidium parkii*, which agrees with the findings of Crous *et al.* (2009d). See notes on *Pseudozasmidium eucalypti*.

Pseudozasmidium parkii (Crous & Alfenas) Videira & Crous, **comb. nov.** MycoBank MB822785.
Basionym: *Stenella parkii* Crous & Alfenas, Mycologia 87: 121. 1995.
Synonyms: *Zasmidium parkii* (Crous & Alfenas) Crous & U. Braun, Schlechtendalia 20: 102. 2010.
Paramycosphaerella parkii (Crous & Alfenas) Guatimosim *et al.*, Persoonia 37: 127. 2016.
Mycosphaerella parkii Crous *et al.*, Mycol. Res. 97: 582. 1993.

Description and illustrations: Crous *et al.* (1993), Crous & Alfenas (1995).

Materials examined: **Brazil**, Aracruz, Florestal nursery, on living leaves of *Eucalyptus grandis*, 24 Feb. 1990, M.J. Wingfield (**holotype** of *Mycosphaerella parkii*, PREM 50668, ex-type culture CBS 387.92); Rio Grande do Sul, on *Eucalyptus globulus*, 7 Jul. 1993, F.A. Ferreira, PREM 51714, culture CPC 651; São Paulo, on *Eucalyptus saligna*, Apr. 1993, P.W. Crous (**holotype** of *Stenella parkii*, PREM 51713). **Indonesia**, North of Sumatra, on *E. grandis*, 22 Nov. 1993, F.A. Alfenas, PREM 51715.

Notes: *Pseudozasmidium parkii* produces a mycosphaerella-like sexual morph and a zasmidium-like asexual morph, with verruculose hyphae, conidiophores and conidia verruculose and conidiogenous cells with conspicuous, darkened and refractive conidiogenous loci (Crous *et al.* 1993, Crous & Alfenas 1995). Based on the phylogenetic analyses, however, *Pseudozasmidium* clusters apart from the *Zasmidium* clade, as presently defined by the type species *Z. cellare*, in a poorly resolved clade including *Pseudozasmidium vietnamense*, *Pseudozasmidium nabiacense* and *Pseudozasmidium eucalypti* (Fig. 1, clade 94; Fig. 4, clade 27). Based on a BLAST search against the alignment, *Pseudozasmidium parkii* CBS 387.92 shares 99 % (479/485) similarity on ITS with *Pseudozasmidium vietnamense* CBS 119974. Unfortunately, the *rpb2* sequence of *Pseudozasmidium parkii* failed to amplify and is coded as missing data in the alignments, but the next closest strain on ITS is *Virosphaerella irregularis* CBS with only 92 % (455/496) similarity and including 3 % (17/496) gaps. See also notes on *Pseudozasmidium vietnamense* and *Paramycosphaerella brachystegiae.*

Pseudozasmidium vietnamense (Barber & T.I. Burgess) Videira & Crous, **comb. nov.** MycoBank MB822786.
Basionym: *Mycosphaerella vietnamensis* Barber & T. I. Burgess, Fungal Diversity 24: 148. 2007.
Synonym: *Paramycosphaerella vietnamensis* (Barber & T.I. Burgess) Guatimosim *et al.*, Persoonia 37: 128. 2016.

Description and illustration: Burgess *et al.* (2007).

Material examined: **Vietnam**, South East Forestry Institute nursery, on leaves of *Eucalyptus grandis* hybrid, 6 Jul. 2004, coll. T.I. Burgess, isol. P.A. Barber (**holotype** MURU 411, ex-type culture CBS 119974 = CMW 23441 = MUCC 66 = VTN1).

Notes: *Pseudozasmidium vietnamense* was described based on the mycosphaerella-like sexual morph and a presumed pseudocercospora-like asexual morph (Burgess *et al.* 2007). In previous phylogenetic studies, it always clustered close to *Pseudozasmidium parkii* (as *Mycosphaerella parkii*, Burgess *et al.* 2007, Crous *et al.* 2009d). The phylogenetic analyses in the present study agrees with the previous works and this species clusters in a poorly resolved clade of zasmidium-like species (Fig. 1, clade 94; Fig. 4, clade 27). Therefore, the presumed pseudocercospora-like asexual morph should not be considered correct. See also notes on *Pseudozasmidium parkii* and *Paramycosphaerella brachystegiae.*

Genus A

Passalora vaginae (W. Krüger) U. Braun & Crous, in Crous & Braun, CBS Biodiversity Ser.: 417. 2003.
Basionym: *Cercospora vaginae* W. Krüger, Ber. Versuchsstat. Zuckerrohr W.-Java, Kagok-Tegal 1: 64. 1890.
Synonyms: *Mycovellosiella vaginae* (W. Krüger) Deighton, Mycol. Pap. 144: 26. 1979.

Description in vivo (from Braun 2015a): *Spots* mainly on sheaths, sometimes also formed as leaf spots, at first small, subcircular to elliptical, red, margin conspicuous, spots later confluent or increasing to about 15 mm diam, on leaves dark reddish above, indistinct below. *Caespituli* amphigenous, effuse, dark greyish brown, velvety, mostly in the centre of the

lesion. *Mycelium* internal and external; superficial hyphae sparingly branched, septate, pale, thin-walled, smooth. *Stromata* sometimes well-developed, substomatal, 10–75 µm diam, dark brown, but without conidiophore fascicles. *Conidiophores* solitary, arising from superficial hyphae, lateral, at the top of mother cells, occasionally terminal, i.e. at the end of procumbent hyphae, erect to ascending, straight to curved, subcylindrical, conical to geniculate-sinuous, simple or sometimes branched, occasionally entangled, 20–200 × 3–5 µm, 1–5-septate, pale olivaceous brown to darker brown, paler towards the tip, thin-walled, smooth; *conidiogenous cells* integrated, terminal, with conspicuous conidiogenous loci, about 1–1.5 µm diam. *Conidia* solitary, cylindrical or obclavate-cylindrical, straight to somewhat curved, 15–55 × 3–6.5 µm, 0–5-septate, occasionally slightly constricted at the septa, hyaline to olivaceous, thin-walled, smooth, apex obtuse, base short obconically truncate, 1–2 µm wide, somewhat thickened and darkened.

Materials examined: **Taiwan**, on *Saccharum officinarum*, unknown collector and date, dep. T. Miyake, 1934, culture CBS 140.34 = DSM 1148 = IMI 303641.

Notes: *Passalora vaginae* causes a foliar disease of sugarcane (*Sacharum officinarum*) and sorghum (*Sorghum vulgare*) (*Poaceae*) and has a worldwide distribution (Crous & Braun 2003). The strain is presently sterile but clusters as a single-strain lineage in the phylogenetic analysis (Fig. 4, clade 28) that represents a potential new genus. The holotype specimen, on *Saccharum officinarum*, which originates from Java, Indonesia, could not be located, and presently no suitable specimen is available for neotypification (Braun *et al.* 2015a). Therefore, the proposal of a new genus is postponed until suitable material is collected and examined.

CLADES 95–96: *Dissoconiaceae*

Dissoconiaceae Crous & de Hoog, Stud. Mycol. 64: 36. 2009.

Clade 95: *Ramichloridium*

Ramichloridium Stahel ex de Hoog, Stud. Mycol.15: 59. 1977.

Note: See Arzanlou *et al.* (2007).

Clade 96: *Uwebraunia*

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

Note: See Crous & Wingfield (1996), Crous *et al.* (1999) and Li *et al.* (2012).

CLADES 97–100: *Phaeothecoidiellaceae*

Phaeothecoidiellaceae K.D. Hyde & Hongsanan, Mycosphere 8: 140. 2017.

Clade 97: *Exopassalora*

Exopassalora Videira & Crous, **gen. nov.** MycoBank MB822589.

Etymology: Exo- meaning outside, as in outside the family *Mycosphaerellaceae*, where the genus *Passalora* is included.

Description: Foliicolous, phytopathogenic. *Mycelium* composed of brown hyphae, smooth to rough, irregularly branched, septate, with dark brown chlamydospore-like hyphal swellings. *Conidiophores* arising from the mycelium, medium brown, smooth, simple or branched, straight to curved. *Conidiogenous cells* terminal and intercalary, subcylindrical, pale to medium brown, smooth, proliferating sympodially, conidiogenous loci conspicuous, darkened, refractive. *Conidia* catenate, in simple or branched chains, medium brown, smooth, narrowly ellipsoidal, tapering to subtruncate, straight or slightly curved, hila slightly thickened and darkened.

Type species: *Exopassalora zambiae* (Crous & T.A. Cout.) Videira & Crous.

Exopassalora zambiae (Crous & T.A. Cout.) Videira & Crous, **comb. nov.** MycoBank MB822757.
Basionym: *Passalora zambiae* Crous & T.A. Cout., Stud. Mycol. 50: 209. 2004.

Description and illustration: Crous *et al.* (2004b).

Material examined: **Zambia**, on leaves of *Eucalyptus globulus*, 21 Aug. 1995, T. Coutinho (**holotype** CBS H-9895, culture ex-type CBS 112971 = CMW 14782 = CPC 1227); *idem*., cultures CBS 112970 = CPC 1228).

Notes: This species is phylogenetically distant from other *Mycosphaerella* spp. known from *Eucalyptus* (Crous *et al.* 2004b) and clusters in a well-supported clade (Fig. 1, clade 96; Fig. 4, clade 32) within the recently introduced *Phaeothecoidiellaceae* family (Hongsanan *et al*., 2017).

***Exopassalora* sp.**

Material examined: **USA**, Illinois, Chester, on apple fruits, culture CBS 118964 = GTF1a.

Notes: Based on the phylogenetic analyses this strain is closest to *Exopassalora* (Fig. 1, clade 96; Fig. 4, clade 32). The present strain shares 97 % (711/736) similarity on LSU, 88 % (288/326) similarity on ITS and 77 % (537/701) similarity on *rpb2* with *Exopassalora zambiae*. Based on the differences observed between the sequences of the partial genes studied, this can be a new genus. Morphological characters from this strain include mycelium on PDA blackish, brown and convoluted, conidia on CLA dark, catenate, with flattened ends (Batzer *et al.* 2005). Unfortunately, the culture is presently sterile and is tentatively placed in *Exopassalora* until the morphological characters can be observed and properly described.

Clade 98: *Houjia*

Houjia G.Y. Sun & Crous, Persoonia 24: 33. 2010.

Note: See Yang *et al.* (2010).

Clade 99: *Sporidesmajora*

Sporidesmajora Batzer & Crous, Persoonia 24: 35. 2010.

Note: See Yang *et al.* (2010).

Clade 100: *Phaeothecoidiella*

Phaeothecoidiella Batzer & Crous, Persoonia 24: 30. 2010.

Note: See Yang *et al.* (2010).

CLADE 101: *Schizothyriaceae*

Schizothyriaceae Höhn. ex Trotter, Sacc., D. Sacc. & Traverso as "*Schizothyrieae*", in Saccardo, *Syll. fung.* (Abellini) 24(2): 1254. 1928.
Synonym: *Schizothyrieen* Höhn., Ber. Deutsch. Bot. Ges. 35: 417. 1917, nom. inval. (Art. 32.1(b), Art. 18.4).

Clade 101: *Schizothyrium*

Schizothyrium Desm., Ann. Sci. Nat., Bot., Sér. 3, 11: 360. 1849.

Note: See Batzer *et al.* (2008), Schoch *et al.* (2009) and Crous *et al.* (2009c).

CLADES 102–107: *Teratosphaeriaceae*

Teratosphaeriaceae Crous & U. Braun, Stud. Mycol. 58: 8. 2007.

Clade 102: *Teratosphaeria*

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

Note: See Crous *et al.* (2009d) and Quaedvlieg *et al.* (2014).

Clade 103: *Batcheloromyces*

Batcheloromyces Marasas, P.S. van Wyk & Knox-Dav., S. African J. Bot. 41(1): 41. 1975.

Note: See Crous *et al.* (2007a), Crous *et al.* (2008).

Clade 104: *Readeriella*

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

Note: See Crous *et al.* (2009d).

Clade 105: *Stenella*

Stenella Syd., Ann. Mycol. 28(1–2): 205. 1930.

Note: See Quaedvlieg *et al.* (2014).

Clade 106: *Parapenidiella*

Parapenidiella Crous & Summerell, Persoonia 29: 185. 2012.

Note: See Crous *et al.* (2012a).

Clade 107: *Acrodontium*

Acrodontium de Hoog, Stud. Mycol. 1: 23. 1972.

Note: See Videira *et al.* (2016).

CLADE 108: *Cladosporiaceae*

Cladosporiaceae Castell. & R.G. Archibald, Yearbook of Tropical Medicine and Hygiene: 25. 1915.
Synonyms: *Cladosporieae* Mathieu, Flore Générale de Belgique: 2. 1854.
Cladosporieae Sacc., Sylloge Fungorum 4: 341. 1886.
Cladosporiaceae Nann., Repertorio sistematico dei miceti dell' uomo e degli animali 4: 404. 1934.

Clade 108: *Cladosporium*

Cladosporium Link, Mag. Ges. Naturf. Freunde Berlin 7: 37. 1816 ['1815'].

Note: See Bensch *et al.* (2015).

Genera of *Mycosphaerellaceae*

Acervuloseptoria Crous & Jol. Roux.

Note: See treatment in text.

Acrodesmis Syd., Ann. Mycol. 24(5–6): 424. 1926.

Description (adapted from Sydow 1926 and Ellis 1961): *Mycelium* composed of pale brown to olivaceous brown hyphae, branching and anastomosing, smooth, septate. *Stromata* composed of dense and irregular dark brown hyphal cells, semiglobose. *Conidiophores* single or in group, emerging from stromata or from hyphae, erect, straight or flexuous, cylindrical, septate, dark brown, paler towards the tips, densely branched at the apex. *Conidiogenous cells* terminal, hyaline to pale olivaceous brown, polyblastic, with multiple conidiogenous cells. *Conidia* single or in short chains, sometimes branched chains, acropleurogenous, pale olivaceous brown, smooth, cylindrical, elliptical or fusiform, aseptate, with minute hila at the base.

Type species: *Acrodesmis cestri* Syd. [**Costa Rica**, La Caja, pr. San. Jose, on leaves of *Cestrum macrophyllum*, 13 Feb. l925, H. Sydow, Fungi Exot. Exs. 650 (**syntypes** S F12601, S F189761)].

Description and illustration: Ellis (1967, 1971, as *Periconiella cestri*).

Notes: Unconfirmed synonym of *Periconiella.* Two species, *Acrodesmis cestri* and *Acrodesmis secunda*. No cultures available, and its phylogenetic position remains unresolved.

Acrocladium Petr., Sydowia 3(1–6): 263. 1949.

Description (adapted from Petrak 1949): *Mycelium* superficial, composed of olivaceous brown hyphae, branched, septate. *Conidiophores* sparse, brown, long, erect, densely branched at the apex (diverging as in penicillium-like species). *Conidia* greyish to olivaceous brown, aseptate, acrosporogenous, oblong to ellipsoid.

Type species: *Acrocladium andinum* Petr.

Description and illustration: Petrak (1949).

Notes: Unconfirmed synonym of *Periconiella.* Two species, *Acrocladium andinum* and *Acrocladium fragile*. No cultures available, and its phylogenetic position remains unresolved.

Achorodothis Syd., Ann. Mycol. 24: 380. 1926.

Description (adapted from Sydow 1926): *Stromata* mainly intraepidermal, pseudoparenchymatous, dark brown, forming continuous to loose crusts with loculi. *Asci* sparingly developed, clavate to almost ellipsoid, sessile or with short knob-like stalk, wall firm, apically thickened, 8-spored, immersed in a hyaline, viscous, little differentiated to slightly filamentous, paraphysoid mass. *Ascospores* 2- to 3-seriate, hyaline, ellipsoid-ovoid, straight or rarely slightly asymmetric, aseptate, slightly attenuated towards the base, both ends rounded, at the base with a colourless bluntly conoid to capped appendage.

Type species: *Achorodothis poasensis* Syd. [**Costa Rica**, on *Ocotea mollicella* (≡ *Phoebe mollicella*), 15 Jan. 1925 (**syntype** IMI 18604)].

Description (*no illustration*): Sydow (1926).

Note: *Achorodothis* is not known from culture, and its phylogenetic position remains unresolved.

Acrotheca Fuckel, Jahrb. Nassauischen Vereins Naturk.15: 42. 1860.

Type species: *Acrotheca gei* Fuckel [**Austria**, Rhenogovia, on *Geum urbanum*, Fuckel, Fungi Rhen. Exs. 2229, e.g. HAL] = ***Ramularia gei*** (A.G. Eliasson) Lindr.

Description and illustration: Hughes 1951, Braun (1998, as *Ramularia gei*).

Note: *Acrotheca gei* is presently regarded as a species of *Ramularia*, but this conclusion has not been confirmed based on DNA data.

Allantophomoides S.L. Wei & T.Y. Zhang, Mycosystema 22: 9. 2003.

Description (adapted from Wei & Zhang 2003): *Conidiomata* pycnidial, immersed, globose to subglobose, unilocular, sometimes slightly papillate, thin-walled, wall composed by 1-3 cells with pale brown to brown *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* ampulliform to doliiform, hyaline, smooth, covering the entire inside wall, enteroblastic, phialidic with minute collarette. *Conidia* hyaline, guttulate, allantoid to elongate-ellipsoidal, aseptate or septate.

Type species: *Allantophomoides carotae* S.L. Wei & T.Y. Zhang [**China**, Gansu Province, Zhangye, on *Daucus carota* var. *sativa*, 10 Oct. 1995 (**holotype** HSAUP 960001, **isotype** IMI)].

Description and illustration: Wei & Zhang (2003).

Notes: The most closely related genera are *Phoma*, *Coleophoma* and *Allantophomopsis*. Without molecular data the phylogenetic position of this septoria-like genus remains unresolved.

Amycosphaerella Quaedvlieg & Crous

Note: See treatment in text.

Anematidium Gronchi, Boll. Ist. Sieroterap. Milan. 10: 242. 1931.

Description (adapted from Gronchi 1931): *Mycelium* olivaceous, septate, branching. *Conidiophores* absent. *Conidia* catenate, in branched chains, integrated in the mycelium, cylindrical. In solid agar media, colonies olivaceous, coalescent, round, convex, with wrinkled and irregular surface, margin dark. *Hyphae* densely aggregated, olivaceous, branched and septate. In liquid acidic media, *hyphae* within the liquid media, lax, with very long branches, septate, subhyaline to olivaceous. *Conidia* catenate, in branched chains, integrated in the mycelium, cylindrical, branching.

Type species: *Anematidium oxiphilum* Gronchi [**Italy**, Firenze, growing in a N/10 HCL solution in a laboratory].

Description and illustration: Gronchi (1931).

Notes: This genus is insufficiently known, and its status remains unresolved. The author named the genus *Anematidium* after the absence of conidiophores and the type species *Anematidium*

oxiphilum after the fungus affinity to the acidic substrate from which it was isolated, a laboratory solution of N/10 HCL (Gronchi 1931).

Anguillosporella U. Braun, A monograph of *Cercosporella*, *Ramularia* and allied genera (Phytopathogenic Hyphomycetes) 1: 233. 1995.

Description (adapted from Braun 1995): *Mycelium* internal, composed of hyaline hyphae, septate and branched. *Stromata* subcuticular to intraepidermal, often erumpent. *Conidiophores* hyaline, smooth, arising from stromata, macronematous, single or in fascicles, loose or densely aggregated, simple, continuous or septate, straight, subcylindrical to flexuous. *Conidiogenous cells* integrated, terminal, monoblastic, determinate, with conidiogenous loci (scars) more or less truncate, unthickened and not darkened, conidial secession schizolytic. *Conidia* solitary, hyaline, multi-euseptate, scolecosporous, wih apex subacute and base usually with a short appendage.

Type species: *Anguillosporella vermiformis* (Davis) U. Braun [**USA**, Wisconsin, on *Alnus incana* (**lectotype** BPI 442755, see Braun 1995)].

Descriptions and illustrations: Braun (1995), Seifert *et al.* (2011).

Note: The phylogenetic position of *Anguillosporella* remains unresolved.

Annellophora S. Hughes, Trans. Brit. Mycol. Soc. 34: 544. 1952.

Description (adapted from Ellis 1971): *Mycelium* superficial or immersed, composed of subhyaline, brown or olivaceous brown hyphae. *Conidiophores* macronematous, single or in fascicles, brown or dark brown, simple, septate. *Conidiogenous cells* integrated, terminal, monoblastic, proliferating percurrently. *Primary conidia* terminal, cylindrical, obclavate or fusiform, subhyaline to brown, smooth, transversely septate or pseudoseptate. *Secondary conidia* germinating from the apex of primary conidia, one at a time, proliferating percurrently, smaller.

Type species: *Annellophora solani* (Syd.) S. Hughes (≡ *Chaetotrichum solani* Syd. 1927).

Description and illustration: Ellis (1971), Seifert *et al.* (2011); present study (Fig. 48).

Material examined: **Costa Rica**, Los Angeles de San Ramon, on *Solanum erythrotrichum*, 30 Jan. 1925 (**holotype** of *Chaetotrichum solani*, E 00417817).

Notes: The phylogenetic position of *Annellophora* is unknown, and its 11 species are only known by their hyphomycetous sporidesmium-like asexual morph (Seifert *et al.* 2011). Cultures and sequence data are necessary to determine its phylogenetic position.

Annellophragmia Subram., Proc. Indian Acad. Sci., Sect. B, 58: 349. 1963.

Description (adapted from Ellis 1971): *Mycelium* superficial and immersed. *Stroma* erumpent, brown and pseudoparenchymatous. *Conidiophores* macronematous, synnematous, brown,

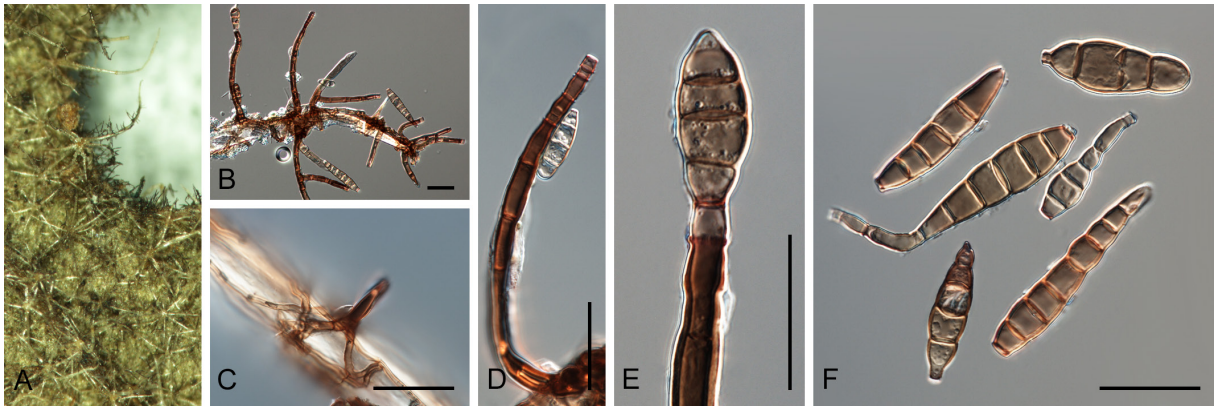


Fig. 48. *Annelophora solani* (E00417817). A–F. Observations *in vivo*. A. Symptoms on host. B, C. Conidiophores erect and developing on the host surface. D. Attachment of the conidiophore to a leaf trichome. E. Conidiogenous cell and conidium. F. Conidia. Scale bars = 10 µm.

smooth, straight, with each individual stipe unbranched, gathered tightly for most of the length and spreading like a hand fan at the apex. *Conidiogenous cells* integrated, terminal and intercalary, cylindrical, proliferating sympodially, polyblastic, conidiogenous loci (scars) large, apical and lateral. *Conidia* solitary, acropleurogenous, pale to dark brown or golden brown, smooth, fusiform to obclavate, truncate at the base, pseudoseptate.

Type species: *Annellophragmia coonoorensis* (Subram.) Subram. (≡ *Arthrobotryum coonoorense* Subram.).

Descriptions and illustrations: Ellis (1971), Seifert *et al.* (2011); present study (Fig. 49).

Materials examined: **India**, Madras, Nilgiris, Coonoor, Simm, on leaves of *Thysanolaena maxima*, 8 Dec. 1953, T.S.S. & C.V. Subramanian (**holotype** of *Arthrobotryum coonoorense* (K(M) 180920); Madhya Pradesh, Balaghat, on *Thysanolaena maxima*, Jan. 1980, S.M. Singh, IMI 245197.

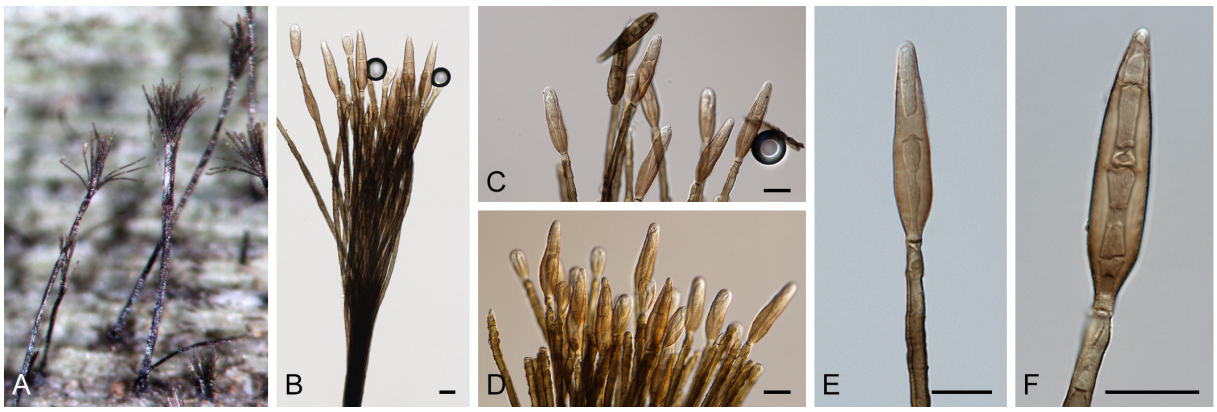


Fig. 49. *Annelophragmia coonoorensis* (IMI 245197). A–F. Observations *in vivo*. A. Conidiophores in compact fascicles, erect and emerging from the host. B. Apical area of the conidiophores, with conidiogenous cells and conidia. C, D. Conidiogenous cells and conidia. E, F. Conidiogenous cell and conidium. Scale bars = 10 µm.

Notes: The phylogenetic position of *Annelophragmia* is unknown and the genus is only known from its hyphomycetous type species, *Annelophragmia coonoorensis* (Kirk *et al.* 2013; genus accepted). Sequence data are necessary to determine its phylogenetic position.

Annellosympodia McTaggart *et al.*, Australas. Pl. Path. 36: 574. 2007.

Description (adapted from McTaggart *et al.* 2007): *Mycelium* immersed. Conidiophores reduced to conidiogenous cells. *Conidiogenous cells* on minute pulvinate sporodochia, macronematous, dark brown, aseptate, verrucose, thick-walled, ampulliform, doliiform or obovoid, mono- or polyblastic, proliferating sympodially (rectilinear), conidiogenous loci ring-like with a central pore, slightly thickened and darkened, apical at first and later displaced laterally. *Conidia* solitary, brown, coarsely verrucose, cylindrical to ellipsoidal, apex rounded, base truncate with a marginal frill and a dark conspicuous hilum, aseptate or septate, sometimes constricted at the septum; secession rhexolytic.

Type species: *Annellosympodia orbiculata* McTaggart *et al.* [**Australia**, Western Australia, on phyllodes of *Acacia* sp. (**holotype** PERTH 03270173)].

Description and illustration: McTaggart *et al.* (2007).

Note: *Annellosympodia* is not known from culture, and hence its phylogenetic position remains unresolved.

Annellosympodiella Crous & Assefa

Note: See treatment in text.

Apseudocercosporella Videira & Crous

Note: See treatment in text.

Asperisporium Maubl.

Note: See treatment in text.

Asteromidium Speg., Ann. Soc. Cient. Argent. 26(1): 66. 1888.

Description (from Quaedvlieg *et al.* 2013, adapted from Sutton 1980): *Mycelium* immersed, branched, septate, hyaline. *Conidiomata* acervular, subcuticular, separate or confluent, pulvinate to doliiform, at the base, composed of hyaline to pale brown, thin-walled *textura angularis* which extends laterally, finally with separate cells dispersed in a mucilaginous matrix to form the overlaying wall; cuticle discoloured and occasionally pseudoparenchymatous, walls adjacent to the upper epidermal wall also discoloured; dehiscence irregular. *Conidiogenous cells* holoblastic, discrete, indeterminate, ± cylindrical, hyaline, smooth, with 1–2 sympodial proliferations, scars unthickened, flat, formed from the basal and lateral walls. *Conidia* cylindrical to fusoid, gently tapered at each end, apex obtuse, base truncate, thin-walled, guttulate to granular, hyaline, 3-septate.

Type species: *Asteromidium imperspicuum* Speg. [**Paraguay**, on leaves of *Sapindaceae*, 1883, ex B. Balansa Pl. du Paraguay No. 4085 (**syntype** K(M) 180228)].

Description and illustration: Quaedvlieg *et al.* (2013).

Note: See Quaedvlieg *et al.* (2013).

Berteromyces Cif., Sydowia 8: 267. 1954.

Description (from Ciferri 1954): Biotrophic, external mycelium lacking, internal mycelium with branched hyphae, hyaline, sparingly developed. *Conidiophores* hyaline or subhyaline, erumpent, with a dense basal stroma, fasciculate, unbranched, erect, distinct. *Conidia* apical, solitary, hyaline, ovoid, at first continuous, later 1-septate.

Type species: *Berteromyces aeneus* Cif. [**Uganda**, Kawanda, on *Senna bicapsularis* (≡ *Cassia bicapsularis*), Jul. 1940, Hansford 2751 (**neotype** designated by Crous & Braun (2003), IMI 8180)] ≡ ***Passalora aenea*** (Cif.) U. Braun & Crous.

Description and illustrations: Ciferri (1954), Deighton (1967, as *Cercosporidium cassiae*).

Notes: This genus is seen as part of the *Passalora* complex, with its type species treated as *Passalora aenea* (Cif.) U. Braun & Crous. The neotype was selected by Crous & Braun (2003) but as no material is available from which DNA can be extracted, its phylogenetic position remains unresolved.

Australosphaerella Videira & Crous

Note: See treatment in text.

Biharia Thirum. & Mishra, Sydowia 7: 79. 1953.

Description (adapted from Thirumalachar & Mishra 1953): *Mycelium* yellowish brown, emerging through stoma and developing a stroma, from which conidiophores arise. *Conidiophores* yellowish brown, smooth, septate, geniculate. *Conidiogenous cell* terminal, polyblastic, proliferating sympodially. *Conidia* single, yellowish brown, obclavate or cylindrical, echinulate or rugose, septate, simple or with protrusions at the region of septa.

Type species: *Biharia vangueriae* Thirum. & Mishra [**India**, Bihar, on *Vangueria spinosa* (**lectotype** designated here IMI 51482, MBT378592)].

Description and illustration: Thirumalachar & Mishra (1953).

Notes: The type species was combined into *Stenella* by Deighton (1979) and later into *Zasmidium* by Kamal (2010). It is regarded as part of the *Zasmidium* complex until sequence data of its type species is available and its phylogenetic position is resolved.

Brunneosphaerella Crous

Note: See treatment in text.

Bryopelta Döbbeler & Poelt, in Döbbeler, Mitt. Bot. Staatssamml. München 14: 126. 1978.

Description (adapted from Döbbeler 1978 and Li *et al.* 2014): *Mycelium* composed of hyaline hyphae, septate, branched within the host cells. *Ascomata* solitary, glabrous, semi-immersed or immersed, globose to subglobose, black, thick-walled, ostiole central, papillate, filled with hyaline to dark brown periphyses. *Peridium* composed of thick-walled hyaline to dark brown cells of *textura angularis* to *textura porrecta*. *Hamathecium* composed of dense, filamentous, hyaline, septate, unbranched, anastomosing pseudoparaphyses. *Asci* 8-spored, bitunicate, fissitunicate, cylindrical to fusiform, obtuse at the tip, slightly widened at base or sometimes with short pedicel, slightly curved. *Ascospores* multiseriate, crowded, ellipsoidal, generally 1-septate, asymmetrical, sometimes 1–3-septate, constricted at septa, with a smooth or rough epispore. *Mycelium* producing black synnemata, with conidiophores directly arising from the basal layers, brown. *Conidia* hyaline, narrow ellipsoid.

Type species: *Bryopelta variabilis* Döbbeler & Poelt [**Sweden**, on *Mylia anomala* (**holotype** GZU 000302175)].

Description and illustration: Li *et al.* (2014).

Notes: The taxonomic history of *Bryopelta* has been discussed in detail by Li *et al.* (2014). *Bryopelta variabilis* is a lichenicolous species with uncertain phylogenetic position due to the lack of sequence data.

Camptomeris Syd., Ann. Mycol. 25: 14. 1927.

Description (adapted from Ellis 1971): *Sporodochia* mostly hypophyllous, pulvinate, punctiform, dark olivaceous brown to black. *Mycelium* immersed. *Stroma* present with one or several swollen cells bearing conidiophores. *Conidiophores* macronematous, often curved inwards, simple, smooth, pale brown to brown. *Conidiogenous cells* integrated, terminal, cylindrical, proliferating sympodially, polyblastic, with prominent conidiogenous loci (scars). *Conidia* solitary, acropleurogenous, pale olivaceous brown or brown, usually verruculose but sometimes smooth, obclavate or oblong, rounded at the ends, aseptate or septate.

Type species: *Camptomeris calliandrae* Syd. [**Costa Rica**, on leaves of *Calliandra houstoniana* var. *calothyrsus* (= *Calliandra similis*), 30 Dec. 1924 (slide ex **type** IMI 7687; fide Hughes 1952)].

Descriptions and illustrations: Ellis (1971), Seifert *et al.* (2011); present study (Fig. 50).

Notes: The phylogenetic position of the genus *Camptomeris* is currently undetermined due to the lack of DNA sequence data from its type species. The cercosporoid nature of the type species suggests an affinity to *Mycosphaerellaceae*. No species of this genus are presently known from culture.

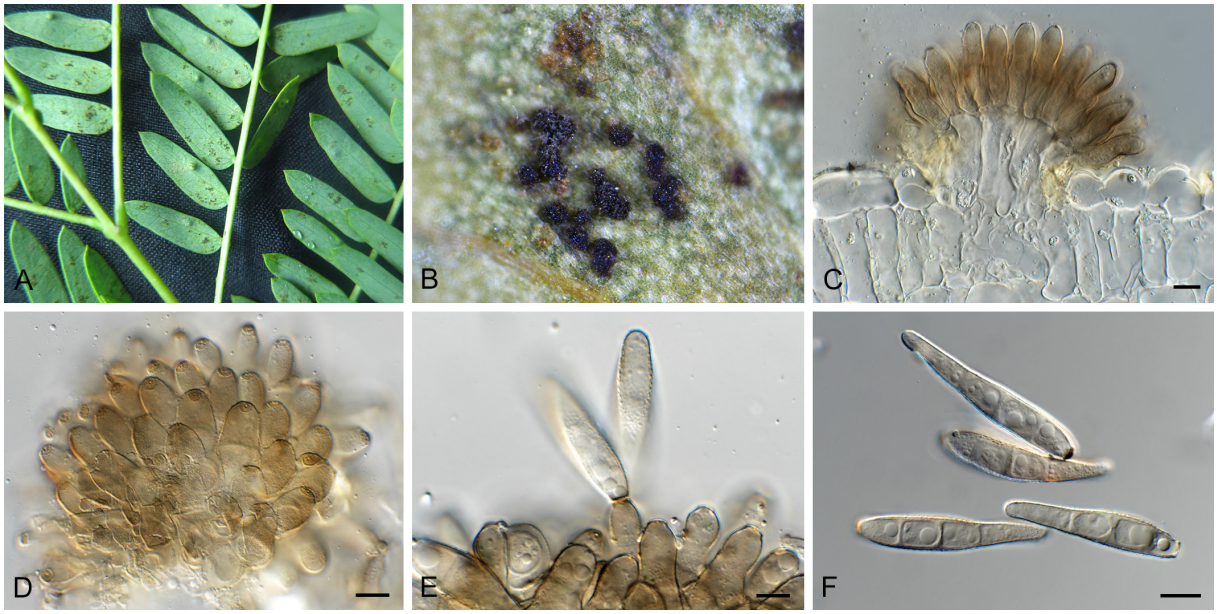


Fig. 50. *Camptomeris leucaenae* (CBS H-22884). A–F. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Conidiophores emerging from the leaf host with conidiogenous cells. D. Apex of the conidiogenous cells with the conidiogenous scar. E. Conidiogenous cells and conidia. F. Conidia. Scale bars = 10 µm.

Camptomeriphila Crous & M.J. Wingf., Persoonia 37: 335. 2016.

Description (from Crous *et al.* 2016a): *Mycelium* consisting of branched, septate, smooth, pale brown hyphae, forming thick-walled, brown, verruculose, intercalary chlamydospores. *Conidiophores* in loose fascicles, erect, branched, flexuous, multi-septate, pale brown, smooth. *Conidiogenous cells* integrated, terminal and lateral, subcylindrical, pale brown, smooth; scars thickened, darkened, refractive. *Conidia* solitary, fusoid-ellipsoid, becoming obclavate when mature, subhyaline to pale brown, smooth, apex subobtuse, *hilum* protruding, truncate, thickened, darkened, refractive.

Type species: *Camptomeriphila leucaenae* Crous & M.J. Wingf.

Description and illustration: Crous *et al.* (2016a).

Materials examined: **Malaysia**, Sabah, growing on *Camptomeris leucaenae*, on leaves of *Leucaena leucocephala*, 29 May 2015, M.J. Wingfield (**holotype** CBS H-22884, culture ex-type CBS 142135 = CPC 27608).

Notes: The present species was observed growing in close association with sporodochia of *Camptomeris leucaenae* (Fig. 50), which causes a leaf spot disease on *Leucaena leucocephala*. Morphologically, it is a passalora-like mycophilic fungus, phylogenetically, it is closely related to species of *Dothistroma* or *Pseudophaeophleospora*, based on LSU (Crous *et al.* 2016a). This strain was not included in the present study.

Caryophylloseptoria Verkley, Quaedvlieg & Crous

Note: See treatment in text.

Catenulocercospora C. Nakash., Videira & Crous

Note: See treatment in text.

Ceratosperma Speg., Physis (Buenos Aires) 4(17): 284. 1918.

Description (adapted from Saccardo & Trotter 1913): *Ascomata* pseudothecial, globose. *Asci* subglobose, 8-spored, stipitate, aparaphysate. *Ascospores* oblong, 2–6-septate, constricted at septa, hyaline to olivaceous, smooth.

Type species: *Ceratosperma theobromae* (Faber) Speg. (≡ *Ceratocarpia theobromae* Faber) [**Cameroon**, on *Theobroma cacao*].

Notes: Very little is known from this genus besides its description. Authentic specimens could not be located and no illustration or recent publication are known. The species needs to be recollected to resolve its phylogenetic position.

Cercocladospora G.P. Agarwal & S.M. Singh, Proc. Natn. Acad. Sci. India, Sect. B, Biol. Sci. 42(4): 439. 1974.

Type species: *Cercocladospora adinae* G.P. Agarwal & S.M. Singh [**India**, on leaves of *Haldina cordifolia* (≡ *Adina cordifolia*) (IMI 148087), fide Deighton 1976a] = ***Pseudocercospora adinicola*** (A.K. Kar & M. Mandal) Deighton.

Notes: Both the generic name, *Cercocladospora*, and the name of the type species, *Cercocladospora adinae*, were not validly published (Art. 40.1, Art. 40.3, Art. 39.1, Melbourne). Since it was morphologicaly identical to *Cercospora adinicola*, Deighton (1976a) synonymised both under *Pseudocercospora adinicola* using the validly published name *Cercospora adinicola* as the basionym. Although *Cercocladospora* is treated as a synonym of *Pseudocercospora*, this conclusion has not been confirmed based on DNA data.

Cercodeuterospora Curzi, Boll. Staz. Patol. Veg. Roma, Ser. 2, 12: 149. 1932.

Type species: *Cercodeuterospora trichophila* Curzi [**Somalia**, on *Cajanus indicus*] = ***Mycovellosiella cajani*** (Henn.) Rangel ex Trotter.

Notes: Although no culture is available, *Cercodeuterospora* is regard as a synonym of *Mycovellosiella cajani* based on morphology. The latter species also occurs on *Cajanus* spp. in Africa. Deighton (1974) did not observe the type material when he proposed the combination *Mycovellosiella cajani* var. *trichophila* for *Cercodeuterospora trichophila*, but a specimen from Kenya (IMI 68281) which he deemed very similar to the material illustrated and described by Curzi. We were unable to trace the location of the Curzi specimen.

Cercoramularia Videira, H.D. Shin, C. Nakash. & Crous

Note: See treatment in text.

Cercoseptoria Petr., Ann. Mycol. 23: 69.1925.

Type species: *Cercoseptoria chamaesyces* (F. Stevens & Dalbey) Petr. (= *Septoriopsis chamaesyces* F. Stevens & Dalbey) [**Puerto Rico**, Rio Piedras, on *Chamaesyce hypericifolia*, F.L. Stevens No. 9445 (**holotype** ILL00011697)] = ***Pseudocercospora chamaesyces*** (F. Stevens & Dalbey) Deighton.

Description and illustration: Stevens & Dalbey (1919, as *Septoriopsis chamaesyces*); Deighton (1976a, as *Cercoseptoria chamaesyces*).

Note: Although *Cercoseptoria* is treated as a synonym of *Pseudocercospora*, this conclusion has not been confirmed based on DNA data.

Cercosphaerella Kleb., Haupt- und Nebenfruchtformen der Askomyzeten: 132. 1918.

Description (based on Klebahn 1918): "*Cercosphaerella*. Konidienform *Cercospora*. Arten: *C. millegrana*; *cerasella*" [*Cercosphaerella*. Conidial form *Cercospora*. Species: *C. millegrana*; *cerasella*].

Type species: *Cercosphaerella millegrana* (Cooke) Kleb. [**Austria**, on leaf litter of *Carpinus betulus* (**holotype** K(M) 56297)].

Description: Saccardo (1882, as *Sphaerella millegrana*), Klebahn (1918).

Notes: Klebahn (1918) introduced *Cercosphaerella* as new genus for *Mycosphaerella* species with asexual morphs belonging to *Cercospora s. lat*. and linked *Cercospora microsora* (≡ *Passalora microsora*) to *Mycosphaerella millegrana*, although Sydow (1940) disagreed, and described the sexual morph of *Passalora microsora* as *Mycosphaerella microsora*. The name *Sphaerella millegrana*, based on a *Mycosphaerella* on leaf litter of *Carpinus betulus*, was misapplied in Klebahn (1918). Klebahn (1918: 132) placed two species in *Cercosphaerella*, viz. *Cercosphaerella millegrana* and *Cercosphaerella cerasella* (Aderh.) Kleb. (≡ *Mycosphaerella cerasella* Aderh.). Clements & Shear (1931) cited *Cercosphaerella* as a subgenus of *Mycosphaerella* and *Mycosphaerella millegrana* as lectotype. However, Klebahn (1918: 131) clearly emphasized that *Septosphaerella*, *Ramularisphaerella*, and *Cercosphaerella* were introduced as separate genera. Therefore, it is concluded that the phylogenetic position of *Cercosphaerella* based on its lectotype species *Cercosphaerella millegrana* remains unresolved pending the availability of phylogenetic analyses, and an epitypification of the latter species. *Cercosphaerella* may be available for some unnamed mycosphaerella-like clades.

Cercosperma G. Arnaud ex B. Sutton & Hodges, Nova Hedwigia 35: 798. 1983 [1981].

Description (from Sutton & Hodges 1981): *Mycelium* mostly superficial, composed of thick-walled, branched, brown, anastomosing, smooth hyphae; hyphopodia and setae absent.

Conidiophores micro- to semi-macronematous, mononematous, erect, pale brown, ofen with a single short lateral branch at base. *Conidiogenous cells* holoblastic, determinate, integrated or discrete, terminal on the main axes or lateral branches, pale brown, smooth, with flattened apex. *Conidia* solitary, dry, acrogenous, straight to curved, tapered towards apex, truncate at base, distoseptate, alternate septa thickened, lumina reduced, smooth, pale brown.

Type species: *Cercosperma arnaudii* B. Sutton & Hodges [**Brazil**, Pará, Monte Dourado, on *Eucalyptus* leaf litter, 20 Jun. 1974, C.S. Hodges, **holotype** IMI 186982i].

Note: When Sutton & Hodges (1983) validated *Cercosperma*, they also pointed out its similarity to *Ceratophorum*, which is another genus that remains phylogenetically unresolved.

Cercospora Fresen. ex Fuckel.

Note: See treatment in text.

Cercosporella Sacc.

Note: See treatment in text.

Cercosporidium Earle

Note: See treatment in text.

Cercosporina Speg., Anal. Mus. Nac. B. Aires, Ser. 3, 13: 424. 1911.

Type species: *Cercosporina asparagicola* Speg. [**Argentina**, La Plata, on *Asparagus officinalis*, Maj. 1906, **holotype** LPS 4966; isotype IMI 247001 (slide)] = ***Cercospora asparagi*** Sacc.

Description and illustration: Chupp (1954, as *Cercospora aparagi*).

Note: *Cercosporina* is currently treated as a synonym of *Cercospora*.

Cercosporiopsis Miura, Flora of Manchuria and East Mongolia. Part III. Cryptogams, fungi: 527. 1928.

Type species: *Cercosporiopsis menispermi* (Ellis & Holw.) Miura (≡ *Cercospora menispermi* Ellis & Holw.) [**USA**, Iowa, Decorah, on *Menispermum canadense*, Jun. 1886 (**holotype** FH-01012294)] = ***Passalora menispermi*** (Ellis & Holw.) U. Braun & Crous.

Description and illustration: Chupp (1954, as *Cercospora menispermi*), Ellis (1976, as *Phaeoisariopsis menispermi*).

Note: The placement of *Cercosporiopsis menispermi* in *Passalora* needs to be confirmed based on DNA data, as this generic name may be available for some of the unnamed passalora-like clades.

Cercostigmina U. Braun, Cryptog. Bot. 4: 107. 1993.

Type species: *Cercostigmina concentrica* (Cooke & Ellis) U. Braun (≡ *Cercospora concentrica* Cooke & Ellis) [**USA**, New Jersey, Gloucester, on *Yucca filamentosa*, 1 Jun. 1874, W.A. Kellerman, no. 2150 (**holotype** NY 00838826; **isotype**: NY 01102862)] = ***Pseudocercospora concentrica*** (Cooke & Ellis) U. Braun & Crous.

Description and illustrations: Braun (1993, as *Cercostigmina concentrica*).

Note: The placement of *Cercostigmina concentrica* in *Pseudocercospora* needs to be confirmed based on DNA data.

Chuppomyces Videira & Crous

Note: See treatment in text.

Ciferriella Petr., Ann. Mycol. 28(5–6): 409. 1930.

Type species: *Ciferriella domingensis* Petr. & Cif. [**Dominican Republic**, on *Vitex umbrosa*, 26 May 1929, coll. R. Ciferri, det. F. Petrak (**holotype** NY 01048475)] = ***Pseudocercospora domingensis*** (Petr. & Cif.) Quaedvl., Verkley & Crous.

Description and illustrations: Quaedvlieg *et al.* (2013).

Note: *Ciferriella* is currently considered a synonym of *Pseudocercospora*, see Quaedvlieg *et al.* (2013).

Cladosporiella Deighton, Mycol. Pap. 101: 34. 1965.

Description (from Braun *et al.* 2013): Morphologically close to *Cladosporium* and mycovellosiella-like *Passalora* species (with superficial hyphae, conidiophores fasciculate or solitary, arising from superficial hyphae, conidiogenous loci conspicuous, thickened and darkened, conidia catenate, pigmented), but the loci and hila are not cladosporium-like (not coronate) and all species assigned to this genus are hyperparasitic.

Type species: *Cladosporiella cercosporicola* Deighton.

Description and illustrations: Braun *et al.* (2013); present study (Fig. 51).

Materials examined: **Malaysia**, Sabah, Tawau, Quoin Hill, on *Passalora koepkei* on *Saccharum officinarum*, 9 May 1964, T.H. Williams (**holotype** IMI 107538b).

Notes: The hyperparasitic habit is the only character to discriminate this genus from *Passalora.* However, as the latter is now a generic complex, we tentatively prefer to maintain *Cladosporiella* as separate genus.

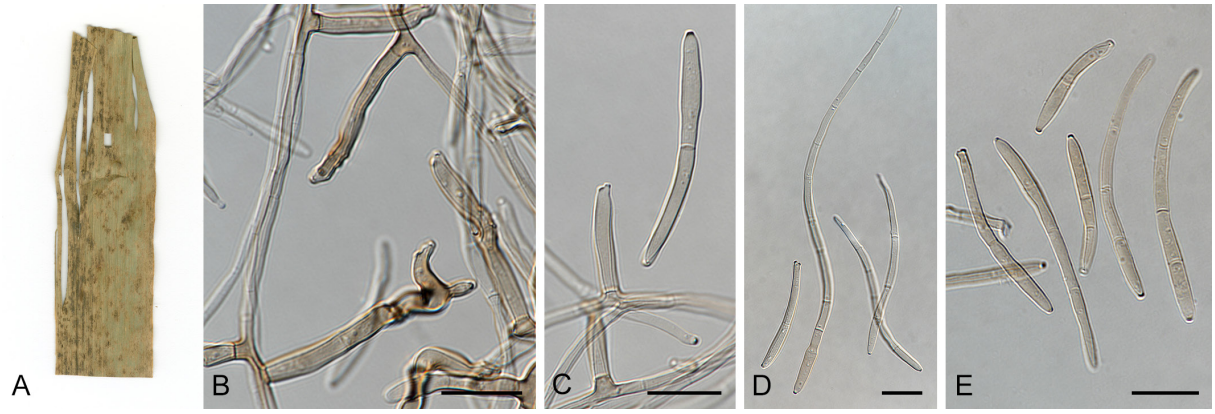


Fig. 51. *Cladosporiella cercosporicola* (IMI 107538). A–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores and conidiogenous cells. C. Conidiophores, conidiogenous cells and conidium. D, E. Catenate and single conidia. Scale bars = 10 µm.

Clarohilum Videira & Crous

Note: See treatment in text.

Clypeispora A.W. Ramaley, Mycotaxon 40: 13. 1991.

Description (from Ramaley 1991): Coelomycetous, phytopathogenic. *Mycelium* immersed, consisting of branched, septate, hyaline hyphae. *Conidiomata* pycnidial, immersed, black to subhyaline, substomatal, unilocular, thin-walled, ostiolate, papillate, exuding translucent conidial cirrhus; wall of hyaline to golden brown cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, discrete, hyaline, golden-brown at base, thin-walled, with thin, thread-like projection giving rise to conidia. *Conidia* hyaline, allantoid, smooth, aseptate, bluntly rounded at both ends, often with irregular apical, and/or basal appendage.

Type species: *Clypeispora angustifoliorum* A.W. Ramaley [**USA**, Colorado, La Plata county, Haflin Creek Trail, on leaves of *Populus angustifolia*, Sep. 1987, A.W. Ramaley, **holotype** BPI 1102631)] = *Mycosphaerella angustifoliorum* A.W. Ramaley [**USA**, Colorado, La Plata county, Durango, Roosa Avenue, on leaves of *Populus angustifolia*, Oct. 1988, A.W. Ramaley (**holotype** BPI 1102629).

Description and illustration: Ramaley (1991).

Note: This species needs to be recollected and its phylogenetic position determined.

Clypeosphaerella Guatimosim, R.W. Barreto & Crous

Note: See treatment in text.

Collarispora Videira & Crous

Note: See treatment in text.

Colletogloeum Petr., Sydowia 7: 368. 1953.

Description (from Sutton 1980): *Mycelium* immersed, branched, septate, hyaline to pale brown. *Conidiomata* acervular, epidermal to subepidermal, separate, occasionally confluent, composed of pale brown to hyaline, thin-walled *textura angularis*. Dehiscence irregular. *Conidiophores* hyaline or very pale brown, sparsely branched, septate, smooth, cylindrical or slightly irregular, formed from the upper cells of the acervulus. *Conidiogenous cells* holoblastic, annellidic, integrated or discrete, indeterminate, cylindrical or doliiform, with several percurrent proliferations. *Conidia* hyaline or pale brown, 0- to multiseptate, straight, curved or irregular, truncate at the base, obtuse at the apex, usually thin-walled, smooth, guttulate or eguttulate.

Type species: *Colletogloeum dalbergiae* (S. Ahmad) Petr. (≡ *Septogloeum dalbergiae* S. Ahmad); = ***Colletogloeum sissoo*** (Syd.) B. Sutton (= *Cercospora sissoo* Syd.) [**Pakistan**, on pods of *Dalbergia sissoo* (presumed slide ex **type** collection IMI 8196; authentic for the name *C. sissoo* IMI 90825, *fide* Sutton 1964)].

Notes: *Colletogloeum* was first described by Petrak (1953) based on *Septogloeum dalbergiae* published earlier in that year. However, *Cercospora sissoo* Syd. (Sydow & Mitter 1933) provides an earlier epithet for the type and a combination was proposed by Sutton (1964) together with an amendment of the genus description to include only fungi with annellate conidiophores. *Colletogloeum* differs from *Ahmadia* only in having epidermal to subepidermal conidiomata as opposed to subcuticular conidiomata. The correct phylogenetic placement of the genus *Colletogloeum* is unknown, though DNA extracted from a fungarium specimen representative of the type species, *C. sissoo* (IMI 119162), showed *Colletogloeum* to be closely related to *Pseudocercospora* (Crous *et al.* 2009e), which fits with its morphology.

Coremiopassalora U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Cucurbitariopsis C. Massal., Mém. Accad. Agricolt. Arti Commerc. Verona, Ser. 3, 65: 133. 1889.

Type species: *Cucurbitariopsis leptospora* C. Massal. [**Italy**, Veneto, Monte Zevola, Passo Ristele, stem of '*Clematidis*? v. *Astragenes*?' (sic. Saccardo, Syll. fung. 10: 396. 1892)] = ***Rhabdospora leptospora*** (C. Massal.) Sacc.

Note: Insufficiently known, seen as synonym of *Rhabdospora* (Saccardo 1892). The type specimen could not be located.

Cyclodothis Syd. & P. Syd., Ann. Mycol. 11: 266. 1913.

Description (adapted from Sydow & Sydow 1913): *Stromata* erumpent through the epidermis, characteristically annular, with numerous densely arranged small perithecioid loculi, wall distinct, dark brown, composed of small cells, ostiolate. *Asci* clavate, 8-spored, ascospores 3- to 4-stichous, indistinctly paraphysate. *Ascospores* oblong cylindrical, colourless, straight, slightly inequilateral, ends obtuse, with a single medial septum.

Type species: *Cyclodothis pulchella* Syd. & P. Syd. [**Philippines**, Mindanao, Todaya, Mt. Apo, on leaf spots of *Piper celtidiforme*, Jul. 1909, A.D.E. Elmer, no. 11163 (**syntypes** BPI 642231, BPI 642230, S F207022, S F207023)].

Notes: The genus has in recent years been treated as synonym of *Mycosphaerella* [*Mycosphaerella pulchella* (Syd. & P. Syd.) Arx]. However, *Cyclodothis* is insufficiently known, and Aptroot (2006) observed the type specimen to only contain a coelomycete.

Cytostagonospora Bubák, Ann. Mycol. 14: 150. 1916.
Synonym: *Cytostaganis* Clem. & Shear, Gen. fung., Edn 2 (Minneapolis): 367. 1931.

Description (from Quaedvlieg *et al.* 2012, adapted from Sutton 1980): *Mycelium* immersed, dark brown, branched, septate. *Conidiomata* pycnidial, amphigenous, separate, globose, dark brown to black, immersed, unilocular, thick-walled, clypeate; walls of dark brown, thick-walled *textura angularis* to *textura globulosa*, becoming hyaline towards the conidiogenous region, extending in the upper part to become a circular clypeus of similar thickness to the wall. Ostiole central, circular, papillate to short rostrate, depressed, situated immersed within the clypeus. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* holoblastic, determinate, discrete, lageniform, hyaline, smooth, formed from the inner cells of the pycnidial wall. *Conidia* hyaline, 0–2-euseptate, not constricted at septa, base truncate, apex obtuse, thin-walled, eguttulate, smooth, filiform, often curved.

Type species: *Cytostagonospora photiniicola* Bubák, [**Italy**, Bozen, Oswald, on *Photinia serrulata*).

Description and illustration: Quaedvlieg *et al.* (2013).

Notes: Arx (1983) treated *Cytostagonospora* as a synonym of *Septoria*, while Sutton (1980) retained it as a separate genus. The genus *Cytostaganis* Clem. & Shear 1931 is based on the same species as *Cytostagonospora*, and is thus a homotypic synonym. The type specimen could not be located.

Davisoniella H.J. Swart, Trans. Brit. Mycol. Soc. 90: 289. 1988.

Description (from Swart 1988): *Conidiomata* in necrotic spots in living leaves, abaxial, single or a few clustered together, stromatic, subepidermal, lifting the epidermis at maturity. *Conidiogenous cells* holoblastic, percurrent, arising from the inner wall of the locules, flask shaped. *Conidia* oval, brown, verruculose, apex rounded, base truncate with a marginal frill.

Type species: *Davisoniella eucalypti* H.J. Swart [**Australia**, Western Australia, Darling Ranges, Mundlimup Block, on leaves of *Eucalyptus marginata*, 24 Nov. 1981, F. Tay (**holotype** DAR 58999)].

Notes: Although Crous *et al.* (2006c) described a sexual morph on the type material as *Mycosphaerella davisoniellae*, the link was never confirmed in culture. However, the morphology of both the sexual and asexual morphs suggests that this taxon would be better accommodated in *Teratosphaeriaceae* (*Teratosphaeria*) than *Mycosphaerellaceae*.

Dearnessia Bubák, Hedwigia 58: 25. 1916.

Description (from Quaedvlieg *et al.* 2013, adapted from Sutton 1980): *Mycelium* hyaline to brown, branched, septate. *Conidiomata* pycnidial, amphigenous, separate, globose, immersed, brown; wall of thin-walled *textura angularis*. *Ostiole* central, circular, papillate. *Setae* ostiolar, approximately straight, unbranched, tapered towards apex, dark brown, smooth, thin-walled, septate. *Conidiogenous cells* holoblastic, determinate, discrete, doliiform to ampulliform, hyaline, smooth and formed from the inner layer of the pycnidial wall. *Conidia* cylindrical to irregular, hyaline, 1–multi-transversely euseptate, rarely with 1–2 longitudinal eusepta, continuous or constricted, often tapered at the apex, base truncate, thin-walled, smooth, guttulate or not.

Type species: *Dearnessia apocyni* Bubák [**Canada**, Ontario, London, on leaves of *Apocynum androsaemifolium*, 11 Aug. 1910, J. Dearness (**holotype** F43227)].

Description and illustration: Quaedvlieg *et al.* (2013).

Notes: The type species needs to be recollected in order to determine the phylogenetic position of this genus. See Quaedvlieg *et al.* (2013).

Deightoniella S. Hughes, Mycol. Pap. 48: 27. 1952.

Description (adapted from Hughes 1952): *Colonies* effuse, grey, brown or black. *Mycelium* immersed, occasionally superficial. *Stroma* absent. *Setae* and *hyphopodia* absent. *Conidiophores* macronematous, mononematous, torsive or flexuous, unbranched brown, smooth, with characteristic swellings along length of conidiophore, due to percurrent rejuvenation, and elongation of conidiophore, producing conidia at higher levels. *Conidiogenous cells* monoblastic, integrated, terminal, percurrent, cylindrical. *Conidia* solitary, acrogenous, obclavate to obpyriform, medium brown, verruculose, transversely 1-septate above the median, with apical cell showing prominent taper towards subobtuse apex; basal scar somewhat darkened and thickened.

Type species: *Deightoniella africana* S. Hughes.

Description and illustrations: Hughes (1952); present study (Fig. 52).

Materials examined: **Ghana**, Hohae (Togoland), on leaves of *Imperata cylindrica* var. *africana*, 28 May, 1949, S.J. Hughes 913 (**holotype** IMI 39675a)]; **Sierra Leone**, Newton (?) colony, on leaves of *Imperata cylindrica* var. *africana*,17 Jan. 1950, T.C. Deighton, M3478A, IMI 41188.

Note: See notes under *Utrechtiana*.

Deightonomyces Videira & Crous

Note: See treatment in text.

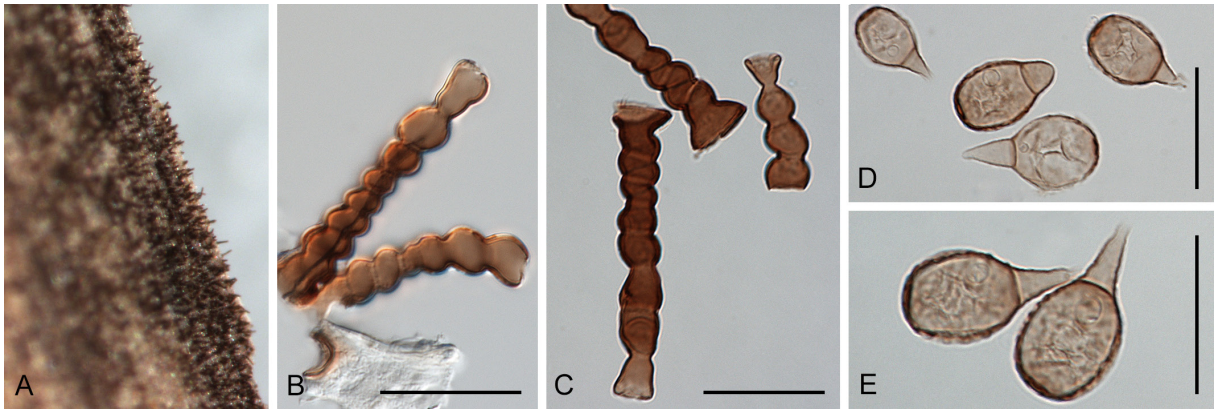


Fig. 52. *Deightoniella africana* (IMI 39675a). A–E. Observations *in vivo*. A. Conidiophores emerging on the leaf surface. B, C. Conidiophores. D, E. Single conidia. Scale bars = 10 µm.

Denticularia Deighton, Trans. Brit. Mycol. Soc. 59: 421. 1972.

Description (from Deighton 1972): Parasitic fungi, causing leaf spots. *Mycelium* immersed. *Conidiophores* arising from stromata, densely crowded, brown, mostly simple, smooth, thin-walled, continuous or few septate, sympodial, polyblastic, denticulate, not cicatrized, the denticles short and subcylindrical with a truncate unthickened apex. *Conidia* pale brown, more or less fusiform, catenulate, with the hila and scars unthickened, thin-walled, smooth or very minutely rough-walled, continuous or 1-septate.

Type species: *Denticularia modesta* (Syd.) Deighton (≡ *Cladosporium modestum* Syd.). [**Sierra Leone**, Kenema (Nougowa), on leaves of *Anthostema senegalense*, 5 Dec. 1938, F.C. Deighton M1681 (**holotype** IMI 7520)].

Description and illustration: Deighton (1972), Ellis (1976); present study (Fig. 53).

Material examined: **Sierra Leone**, Kenema (Nougowa), on *Anthostema senegalense*, 9 Feb. 1956, C.T. Pyne M6473, IMI 62524.

Notes: Cultures of the type species of this genus and results of molecular analyses are necessary to resolve its phylogenetic position and clarify its relation to *Pseudocercospora*. It is still unclear and unproven whether this genus belongs in the *Mycosphaerellaceae*.

Dictyocephala A.G. Medeiros, Publ. Inst. Micol. Recife 372: 13. 1962.

Type species: *Dictyocephala ulmifoliae* (Obreg.-Bot.) A.G. Medeiros (≡ *Cercospora ulmifoliae* Obreg.-Bot.) [Colombia, Quipile, on *Guazuma ulmifolia*, 16 Apr. 1940, R. Obregón-Botero & G.J. Quintana, No. 901] ≡ ***Pseudocercospora ulmifoliae*** (Obreg.-Bot.) U. Braun & Crous.

Descriptions and illustrations: Chupp (1954); Deighton (1976a).

Note: The synonymy with *Pseudocercospora* is based on morphology, and needs to be confirmed based on DNA data. The type specimen could not be located.

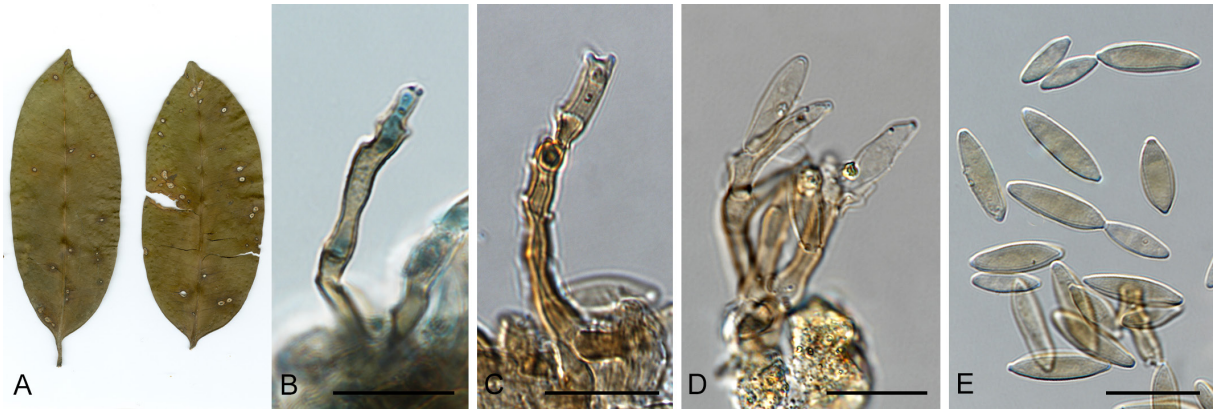


Fig. 53. *Denticularia modesta* (IMI 62524). A–E. Observations in vivo. A. Leaf spot symptoms on the host. B, C. Conidiophores and conidiogenous cells. D. Conidiophores, conidiogenous cells and conidia. E. Catenate and single conidia. Scale bars = 10 μm.

Dictyodesmium S. Hughes, Mycol. Pap. 36: 29. 1951.

Description (from Ellis 1971): *Sporodochia* epiphyllous, erumpent, pulvinate, olivaceous brown. *Mycelium* immersed forming hyphal cushions at the point of origin of the conidiophores but no definite stroma. *Setae* and *hyphopodia* absent. *Conidiophores* mono- and macronematous, caespitose, crowded, straight or flexuous, unbranched, pale brown, smooth. *Conidiogenous cells* monoblastic, integrated, terminal, determinate, cylindrical. *Conidia* solitary, acrogenous, simple, fusiform to obclavate, rostrate, truncate at the base, rather pale olivaceous brown, palest at the ends, smooth, with transverse septa throughout and longitudinal and oblique septa in the central 6–9 cells.

Type species: *Dictyodesmium ulmicola* (Ellis & Kellerm.) S. Hughes (≡ *Ceratophorum ulmicola* Ellis & Kellerm.).

Descriptions and illustrations: Ellis (1971), Seifert *et al.* (2011); present study (Fig. 54).

Materials examined: **USA**, Kansas, on leaves of *Ulmus fulva*, Oct. 1987, W.A. Kellerman 1112 (**holotype** NY 00838655).

Notes: The phylogenetic position of *Dictyodesmium* is unknown and its four species are only known by their hyphomycetous asexual morph (Seifert *et al.* 2011). Sequence data are necessary to determine its phylogenetic position.

Didymaria Corda, Icon. fung. 5: 9. 1842.

Type species: *Didymaria ungeri* Corda [**Switzerland**, on *Ranunculus nemorosus*] = ***Ramularia didyma*** Unger.

Description and illustration: Braun (1998).

Note: See Braun (1998).

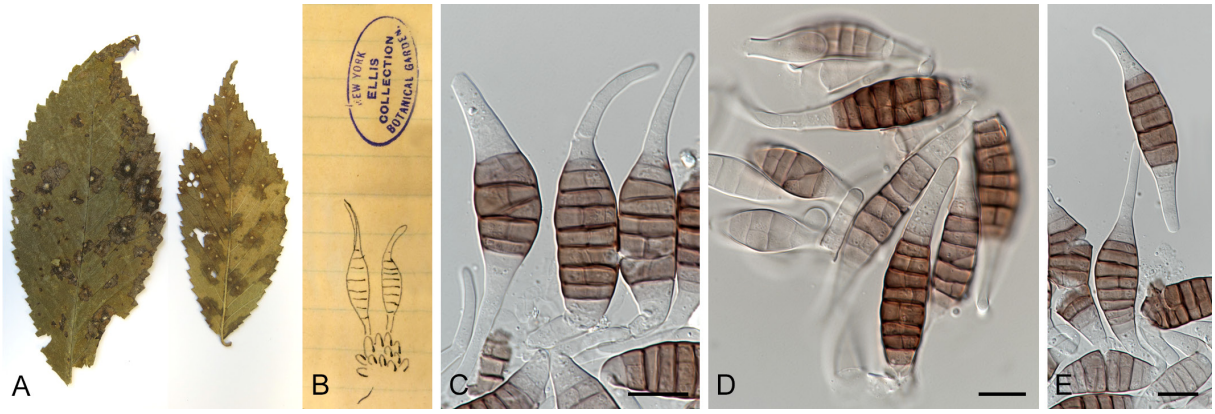


Fig. 54. *Dictyodesmium ulmicola* (NY 00838655). A, C–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores and conidia drawing on the specimen envelope. C–E. Conidia. Scale bars = 10 μm.

Didymellina Höhn., Ann. Mycol. 16: 66. 1918.

Description: *Leaf spots* ellipsoid-lenticular, pale brown with dark brown border. *Ascomata* pseudothecial, black, scattered, subepidermal to erumpent, wall of 2–3 layers of brown *textura angularis*. *Asci* aparaphysate, fasciculate, bitunicate, subsessile, obovoid, straight to slightly curved, 8-spored, with visible apical apiculus. *Ascospores* 3- to multiseriate, hyaline, non-guttulate, thin-walled, straight to slightly curved, fusoid-ellipsoid with obtuse ends, medianly 1-septate, widest in middle of apical cell, not constricted at the septum (but slightly so with age), tapering towards both ends, but slightly more to lower end; ascospores germinating while in ascomata, hyaline, slightly constricted at septum, germinating from both ends with germ tubes parallel to the long axis of the spore, in some cases germinating ascospores becoming 3-septate.

Type species: *Didymellina iridis* (Desm.) Höhn. (≡ *Dothidea iridis* Desm.) [**France**, Trouve a Hermanville, on leaves and capsules of *Iris pseudacorus*, 1847, M. Roberge (**holotype**, PC)].

Notes: *Didymellina iridis* is the type species of the genus *Didymellina*, which Müller & Arx (1962) treated as synonym of *Mycosphaerella*. A short overview of the taxonomic history of this species was presented by (Braun *et al.* 2003a). Ascospores observed in asci were 1-septate, but 3-septate ascospores were observed at the onset of germination. Based on its morphology, it is considered that this represents a separate genus. However, the taxonomic position of this fungus can only be resolved when fresh material has been obtained.

Didymochora Höhn. Hedwigia 60: 172. 1918.

Description (adapted from Höhnel 1918): *Stromata* small, flat, subcuticular, pseudoparenchymatous, carbonaceous, with a vertically arranged successive structure, with a single locus, cover one-layered, irregularly splitting, basal layer pseudoparenchymatous below and palisade-like above. *Conidia* pigmented, 2-celled, solitary, separated from the tips of the internal palisade-like cell layer by a horizontal septum.

Type species: *Didymochora betulina* Höhn. (described as asexual morph of *Euryachroa betulina* (Fr.: Fr.) J. Schröt. ≡ *Atopospora betulina* (Fr.: Fr.) Petr., without any further details, and placed in the *Leptostromaceae*.

Notes: The phylogenetic position of *Didymochora* is unknown and its two species are only known by their stromatic asexual morph. It is currently considered a genus of *incertae sedis* belonging to the *Dothideomycetes* (Wijayawardene *et al.* 2014). Sequence data are necessary to determine its phylogenetic position.

Distocercospora N. Pons & B. Sutton

Note: See treatment in text.

Distocercosporaster Videira, H.D. Shin, C. Nakash. & Crous

Note: See treatment in text.

Distomycovellosiella U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Dothistroma Hulbary

Note: See treatment in text.

Elletevera Deighton, Mycol. Pap. 118: 17. 1969.

Description (from Deighton 1969): *Mycelium* immersed in the host fungus. *Conidiophores* dilute brown, smooth, branched, well developed, fasciculate, thin-walled: conidial scars conspicuous, slightly but distinctly thickened, prominent, aggregated towards the apices of the branchlets of the conidiophores. *Conidia* concolorous with the conidiophores, smooth, thin-walled, mostly cylindric-clavate and 3-septate, sometimes 0–2-septate, the shorter ones very rarely catenulate, sometimes fusoid, rostrate and pluriseptate, with a conspicuous and slightly but distinctly thickened hilum.

Type species: *Elletevera parasitica* (Ellis & Everh.) Deighton (≡ *Pyricularia parasitica* Ellis & Everh.).

Description and illustration: Deighton (1969), Braun *et al.* (2013); present study (Fig. 55).

Material examined: **USA**, Wisconsin, Kenosha Co., on *Phyllachora graminis* on *Elymus virginicus*, 13 Aug. 1893, J.J. Davis 9311, (**holotype** NY 00928212, isotype BPI 420251, slide ex type collection IMI 129275).

Notes: The present genus was introduced by Deighton (1969) to accomodate hyperparasitic cercosporoid hyphomycetes with distinct conidiogenous loci. Upon re-examination of several specimens, Braun *et al*. (2013) considered the conidiogenous loci description to be

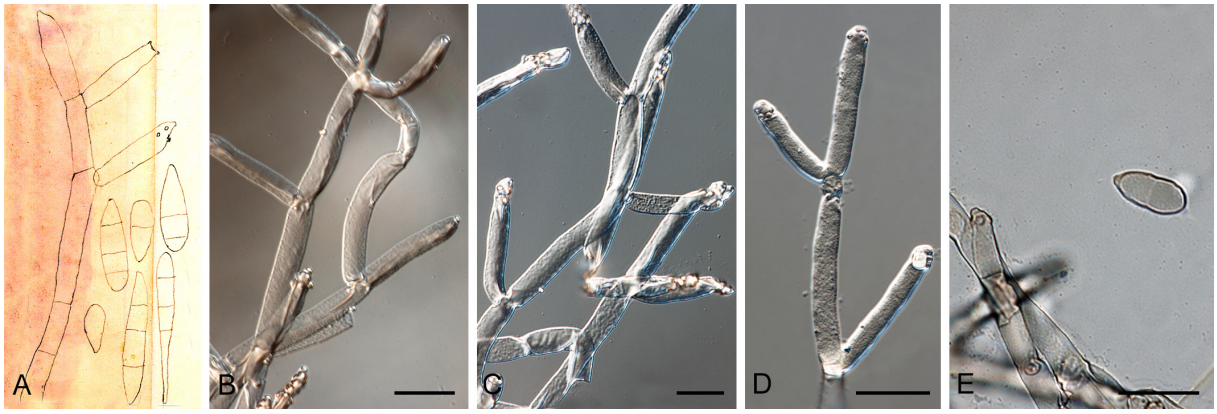


Fig. 55. *Elletevera parasitica* (IMI 127995). A. Drawing in the specimen envelope. B–E. Observations *in vivo*. B–D. Conidiophores and conidiogenous cells. E. Conidiogenous cells and conidium. Scale bars = 10 μm.

misleading and observed that the denticle-like loci are unthickened and undarkened. Due to the morphological characters this genus may be related to *Pseudocercospora* but cultures and sequence data are necessary to determine its phylogenetic position.

Epicoleosporium Videira & Crous

Note: See treatment in text.

Eriocercospora Deighton, Mycol. Pap. 118: 5. 1969.

Description (from Deighton 1969): Hyperparasitic hyphomycetes. *Mycelium* superficial, composed of pale brown, branched, septate, smooth, repent hyphae which bear conidiophores terminally and as lateral branches. *Conidiophores* pale brown, erect simple or branched, smooth, septate, not geniculate at the old conidial scars. *Conidial scars* slightly thickened, slightly prominent, the old ones lying more or less flat against the side of the conidiophore. *Conidia* pale brown, smooth, clavate, fusiform, subcylindric or obclavate, pluriseptate.

Type species: *Eriocercospora balladynae* (Hansf.) Deighton (≡ *Helminthosporium balladynae* Hansf.)

Description and illustration: Deighton (1969), Braun (1995); present study (Fig. 56).

Materials examined: **Uganda**, Entebbe Road, on *Balladynocallia glabra* on *Grumilea succulenta*, Nov. 1943, C.G. Hansford 3264 (**holotype** of *Helminthosporium balladynae*, IMI 562a); Entebbe Road (mile 13), on *Balladyna* sp. on leaves of *Pavetta* sp., Mar. 1940, C.G. Hansford 2609 (**holotype** of *Cercospora balladynae*, IMI 4706c); Entebbe, on *Balladynocallia glabra* on *Pavetta* sp., Dec. 1945, C.E. Hansford 3726, (IMI 5293).

Notes: The present genus was introduced by Deighton (1969) who described the conidiogenous loci as mycovellosiella-like. Upon re-examination of several specimens Crous & Braun (2003) considered the conidiogenous loci description to be misleading and observed that the denticle-

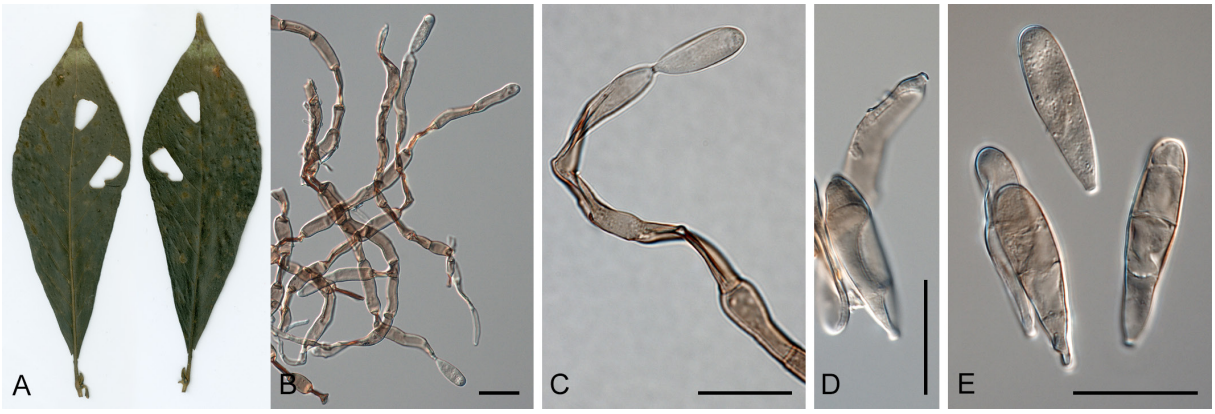


Fig. 56. *Eriocercospora balladynae* (IMI 5293c). A–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores, conidiogenous cells and conidia. C. Partial conidiophore, conidiogenous cells and conidium. D, E. Single conidia. Scale bars = 10 µm.

like loci are neither thickened nor conspicuously darkened. Due to morphological characters this genus may be related to *Pseudocercospora* but sequence data are necessary to determine its phylogenetic position.

Eriocercosporella Rak. Kumar, A.N. Rai & Kamal ex U. Braun, A monograph of *Cercosporella*, *Ramularia* and allied genera (Phytopathogenic Hyphomycetes) 2: 398. 1998.

Description (from Braun *et al.* 2013): Foliicolous hyphomycetes, associated with leaf spots. *Mycelium* internal and external, superficial hyphae emerging through stomata, branched, pigmented, septate, thin-walled, smooth. *Stromata* lacking. *Conidiophores* macronematous, mononematous, *in vivo* solitary, arising from superficial hyphae, lateral, simple, occasionally branched, pigmented, septate, thick-walled, smooth; *conidiogenous cells* integrated, terminal, uni- to multilocal, sympodially or occasionally percurrently proliferating, loci truncate, flat, broad, neither thickened nor darkened, conidiogenesis thalloblastic, i.e. at first blastic, then thallic (base of conidia ± agreeing in width with the diameter of the broad conidiogenous loci). *Conidia* solitary, cylindrical to subclavate, occasionally disarticulating, plurieuseptate, occasionally with 1–2 additional distosepta, thick-walled, brown, smooth, not attenuated at the base, *hila* truncate, broad, width ± agreeing with the diameter of the conidiogenous loci, neither thickened nor darkened, conidial secession schizolytic.

Type species: *Eriocercosporella indica* R. Kumar, A.N. Rai & Kamal ex U. Braun

Description and illustration: Braun (1998), Braun *et al.* (2013); present study (Fig. 57).

Materials examined: **India**, Uttar Pradesh, Pithoragarh, on *Marsdenia roylei*, 1985, Kumar (**holotype** IMI 302747).

Note: Due to its morphological characters this genus may be related to either *Pseudocercospora* or *Sporidesmium*, but sequence data are necessary to determine its phylogenetic position.

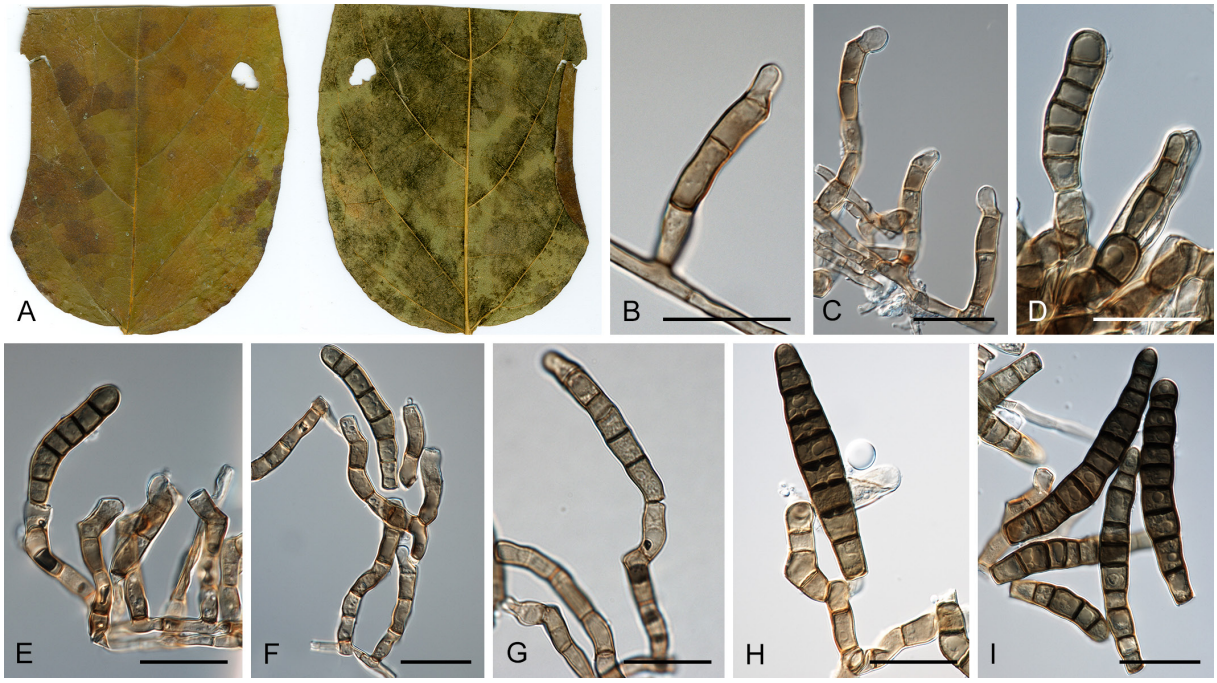


Fig. 57. *Eriocercosporella indica* (IMI 302747). A–I. Observations *in vivo*. A. Leaf spot symptoms on the host. B, C. Conidiophores. D. Conidiogenous cells proliferating percurrently and conidia. E–H. Conidiophores and conidia. I. Conidia. Scale bars = 10 µm.

Euryachora Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 220. 1870 (1869–1870).

Description (from Fuckel 1869): *Ascomata* pseudothecial. *Asci* obovoid, sessile, 8-spored. *Ascospores* obovoid, hyaline, 1-septate.

Type species: *Euryachora sedi* (Link) Fuckel [as '*sebi*'] (≡ *Leptostroma sedi* Link) (**Austria**, on *Sedum maximum*).

Note: The present genus is based on *Euryachora sedi* which is only known by the mycosphaerella-like sexual morph. It is currently considered to belong to *Mycosphaerellaceae* (Lumbsch & Huhndorf 2010) but the type specimen could not be located and no DNA sequence data are available to determine its phylogenetic position.

Exopassalora Videira & Crous

Notes: See treatment in text.

Exosporium Link

Note: See treatment in text.

Exutisphaerella Videira & Crous

Note: See treatment in text.

Filiella Videira & Crous

Note: See treatment in text.

Fulvia Cif.

Note: See treatment in text.

Fusicladiella Höhn., Ber. Deutsch. Bot. Ges. 37: 155. 1919.

Description (from Ellis 1971): *Colonies* suborbicular or angular. *Mycelium* immersed. *Stroma* sometimes present in the host cuticle. *Setae* and *hyphopodia* absent. *Conidiophores* macronematous, mononematous, crowded, unbranched, at first erect, straight or slightly curved, cylindrical, almost colourless, later strongly curved, brown or olivaceous brown, pale and thin-walled on one side, dark and thick-walled on the other, the curvature always taking place towards the thin-walled side, smooth or sometimes finely verruculose near the apex. *Conidiogenous cells* monoblastic, integrated, terminal, determinate, cylindrical, cicatrized, the single apical scar broad and flat. *Conidia solitary*, dry, aerogenous, straight or slightly curved, often cylindrical, rounded at the apex, truncate with a thin scar at the base, but sometimes clavate, ellipsoidal or obclavate, colourless to pale olive, smooth to finely verruculose, almost always 1-septate, rarely 2-septate.

Type species: *Fusicladiella aronici* (Sacc.) Höhn. (≡ *Fusicladium aronici* Sacc.) = ***Fusicladiella melaena*** (Fuckel) S. Hughes) [**syntypes**, **Italy**, Vette di Feltre, on *Doronicum grandiflorum* (= *Aronicum scorpioides*), Aug. 1879, G. Bizzozero (BPI 423776, PAD); Mt. Baldo, Valle delle Pietre, on *D. glaciale* (= *Aronicum doronicum*), V. de Cesati, Rabenh., Fungi Eur. 2339 (numerous fungaria including HAL)].

Descriptions and illustrations: Hughes (1952), Deighton & Pirozynski (1965), Ellis (1971), Arx (1983); present study (Fig. 58).

Materials examined: **Switzerland**, Graubünden, Fimbertal, Silvretta, on leaf of *Doronicum grandiflorum*, 5 Aug. 1967, J. Poelt & M. Steiner, Reliquiae Petrakianae no. 2565 (IMI 371583). **Russia**, Moskovsky, St Petersburg, on leaves of *Carduus crispus*, 2007, V. Melnik. Exsicc. Mycoth. Petropol. 90, UPS:BOT:F-144284.

Notes: *Fusicladiella* is based on *Fusicladiella aronici*, which is only known by its hyphomycetous asexual morph. The phylogenetic position of this genus remains obscure due to absence of DNA data.

Fusoidiella Videira & Crous

Note: See treatment in text.

Gillotia Sacc. & Trotter, Syll. Fung. 22: 253. 1913.

Description (Saccardo & Trotter 1913): *Ascomata* erumpent to superficial, subglobose. *Asci* saccate, subclavate, aparaphysate, stipitate, 8-spored. *Ascospores* oblong, 3-septate, straight to slightly curved, hyaline, becoming olivaceous brown.

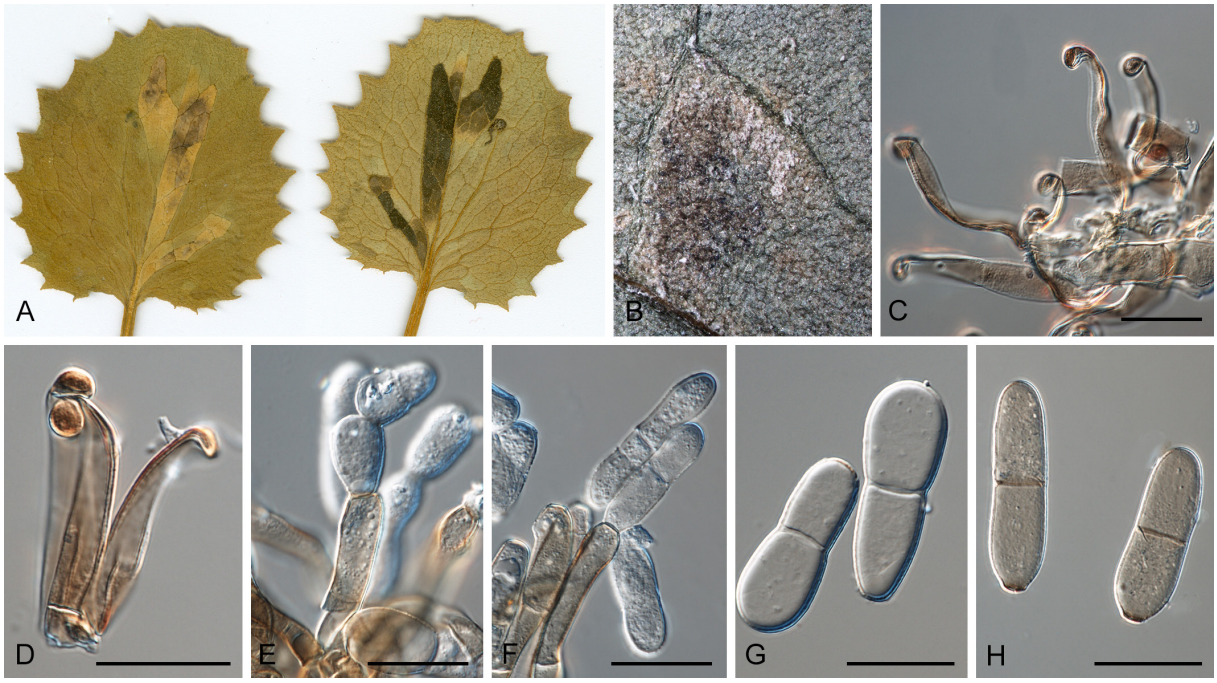


Fig. 58. *Fusicladiella aronici* (IMI 371583). A–H. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C. Conidiophores. D. Partial conidiophore and conidiogenous cell. E, F. Conidiogenous cells and conidia. G, H. Conidia. Scale bars = 10 µm.

Type species: *Gillotia orbicularis* (Syd. & P. Syd.) Sacc. & Trotter (≡ *Diplotheca orbicularis* Syd. & P. Syd.) [**Brazil**, São Paulo, Campinas, on *Cactus* sp., Oct. 1896, F. Noack (**holotype** S F9063).

Notes: *Gillotia* is based on *Gillotia orbicularis*, which is mostly known by its sexual morph. The presence of an asteromella-like asexual morph is indicated by Hyde *et al.* (2010). The fact that this species produces 3-septate ascospores that become olivaceous brown is suggesting it should not belong in the *Mycosphaerellaceae*. However, DNA is not available and hence its phylogenetic position remains obscure.

Gloeocercospora D.C. Bain & Edgerton ex Deighton, Trans. Brit. Mycol. Soc. 57: 358. 1971.

Description (from Deighton 1971): *Mycelium* internal, composed of septate, branched hyphae. *Stroma* small or absent. *Conidiomata* sporodochial, suprastomatal, originating from hyphae which emerge through stomata, pulvinate, composed of more or less hyaline, repeatedly branched hyphae with short cells of which the terminal cells act as conidiogenous cells; conidiogenous loci terminal, minute, unthickened. *Conidia* hyaline, filiform, straight to curved, multi-septate, smooth, in mucoid mass.

Type species: *Gloeocercospora sorghi* D.C. Bain & Edgerton ex Deighton [**USA**, Louisiana, on *Sorghum vulgaris*, Aug. 1943, D.C. Bain (**holotype** BPI 433333)].

Notes: *Gloeocercospora* was considered a synonym of *Microdochium* based on morphological characters (Braun 1995). The ITS sequence of CBS 131812 (unpublished, India, on *Sorghum*

vulgare, Nov. 1971, G.S. Rawla, culture CBS 131812 = IMI 165194) is identical to that of *Gloeocercospora sorghi* NBRC 7430, currently available in GenBank (ITS and partial LSU: accession LC063852). More data are necessary to resolve the phylogenetic position of this pathogen.

Gomphinaria Preuss, Linnaea 24: 130. 1851.

Description (adapted from Preuss 1851 and Saccardo 1886, as *Acrotheca amoena*): *Caespituli* effuse, brown. *Conidiophores* erect, subulate, simple, below densely septate and brown, above subhyaline, transparent and aseptate. *Conidia* terminal, subapically formed, oblong, hyaline, aseptate, base acute or subapiculate, hila hyaline.

Type species: *Gomphinaria amoena* Preuss [**Germany**, on *Alnus glutinosa* (**holotype** in B)].

Description and illustration: Preuss (1851).

Note: Arzanlou *et al.* (2007) examined the holotype of *Gomphinaria amoena* Preuss (B), and concluded that without fresh collections, it would not be possible to ascertain the phylogenetic position of this ramichloridium-like hyphomycete.

Graminopassalora U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Haplodothis Höhn., Sitzungsber. Akad. Wiss. Wien, Math.- Naturwiss. Kl., Abt. 1120: 423 (45 repr.). 1911.

Type species: *Haplodothis singularis* (Henn.) Höhn. (≡ *Lizonia singularis* Henn.) [**Australia**, Western Australia, on *Leucopogon hispidus*, L. Diels, No. 3055] = ***Mycosphaerella singularis*** (Henn.) Arx.

Notes: The genus *Haplodothis* is based on *Haplodothis singularis*, which is currently considered a synonym of *Mycosphaerella singularis*. The type specimen could not be located. Fresh collections and DNA sequence data are necessary to determine if *Haplodothis* is a real synonym of *Mycosphaerella*, which is now treated as *Ramularia* (Videira *et al.* 2015a, b, 2016).

Haplographium Berk. & Broome, Ann. Mag. Nat. Hist., Ser. 3, 3: 360 (1859).

Type species: Haplographium delicatum Berk. & Broome = ***Dematioscypha dematiicola*** (Berk. & Broome) Svrček 1977

Description and illustration: Ellis (1971), Seifert *et al.* (2011).

Notes: The genus *Haplographium* is based on *H. delicatum*, a hyphomycetous species with a link to the sexual morph *Hyaloscypha dematiicola* (Berk. & Broome) Nannf. (Ellis 1971), which is a current synonym of *Dematioscypha dematiicola* (Berk. & Broome) Svrček. The recent work of Han *et al.* (2014) places a representative strain of *Dematioscypha dematiicola*

(TNS-F17834) in the *Leotiomycetes* (*Helotiales*). The work of Crous *et al.* (2009a) summarizes the taxonomic history of *Lauriomyces* and *Haplographium* and shows that the available strains of *Haplographium catenulatum* (CBS 196.73, CBS 482.67, CBS 739.68) cluster in *Hyaloscyphaceae* (*Leotiomycetes*) and apart from the available strains of *Lauriomyces bellulus* (CBS 517.93) and *Lauriomyces heliocephalus* (CBS 112054), which are considered to be *incertae sedis*.

Hawksworthiana U. Braun, Int. J. Mycol. Lichenol. 3: 276. 1988.

Description (from Videira *et al.* 2016): Lichenicolous, forming gall-like deformations. *Mycelium* consisting of hyaline, septate, sparsely branched, thin-walled hyphae. *Conidiophores* reduced to the conidiogenous cells, erumpent, usually ampulliform but sometimes subcylindrical, aseptate, hyaline, thin-walled, mono- or polyblastic, sympodial, conidiogenous loci conspicuous, thickened and darkened. *Conidia* formed singly, acrogenous, oblong-clavate to subcylindrical, hyaline, thin-walled, smooth, aseptate or 1-septate, hilum conspicuous, thickened and darkened.

Type species: *Hawksworthiana peltigericola* (D. Hawksw.) U. Braun (≡ *Ramularia peltigericola* D. Hawskw.) [**UK**, Scotland, Isle of Mull, Killiemore, on thallus of *Peltigera polydactylon*, 16 Jun. 1979, Clark (**holotype** IMI 239715a).

Description and illustration: Braun *et al.* (1998), Videira *et al.* (2016).

Notes: *Hawksworthiana* differs from *Ramularia* by its lichenicolous habit and some morphological features. Although fresh material has been available, all attempts to grow this fungus in culture have thus far been unsuccessful and no sequence data are available.

Helicomina L.S. Olive, Mycologia 40: 16. 1948.

Type species: *Helicomina caperoniae* L.S. Olive [**USA**, Louisiana, Baton Rouge, on *Caperonia castaneifolia*, 2 Oct. 1946, Q.L. Holdman (**holotype** BPI 447607)] = ***Pseudocercospora caperoniae*** (L.S. Olive) Deighton.

Descriptions and illustrations: Olive (1948), Ellis (1971), Deighton (1976a).

Notes: This genus is currently considered a synonym of *Pseudocercospora* based on its morphological characters (Crous *et al.* 2013a). However, the type species needs to be recollected to confirm the generic synonymy based on DNA data.

Hoornsmania Crous, Fungal Planet 11: 1. 2007.

Description (from Crous 2007): Hyphomycetes. *Conidiophores* solitary, brown, arising from superficial hyphae, septate. *Conidiogenous cells* brown, smooth to finely verruculose, elongate-ellipsoid to fusoid, with 1–2 truncate loci, somewhat thickened and darkened, but not prominently refractive. *Conidia* brown, smooth to finely verruculose, broadly ellipsoidal to somewhat fusoidal, occurring in branched, acropetal chains; scars somewhat darkened, thickened, but not refractive; hyperparasitic on *Neonectria ditissima*.

Type species: *Hoornsmania pyrina* Crous [**Netherlands**, Utrecht Prov., Bilthoven, on perithecia of *Neonectria ditissima* on twigs of *Pyrus malus*, Jan. 2005, P.W. Crous (**holotype** CBS H-19769)].

Description and illustration: Crous (2007).

Note: All attempts to cultivate this species, or isolate DNA from freshly collected material, have thus far been unsuccessful.

Hyalodictys Subram., Proc. Indian Acad. Sci., Pl. Sci.: 8. 1962.

Type species: *Hyalodictys degenerans* (Syd. & P. Syd.) Subram. (≡ *Clasterosporium degenerans* Syd. & P. Syd.) = ***Miuraea degenerans*** (Syd. & P. Syd.) Hara.

Description and illustration: Braun (1995, as *Miuraea degenerans*).

Notes: The genus *Hyalodyctis*, based on *Hyalodyctis degenerans*, is currently considered a synonym of *Miuraea* based on morphological characters. See treatment of *Miuraea* in text and Braun (1995).

Hyalocercosporidium Videira & Crous

Note: See treatment in text.

Hyalodothis Pat. & Har., Bull. Soc. Mycol. France 9: 210. 1893.

Description (adapted from Saccardo 1895): Glumicolous. *Stromata* superficial, encrusting ovaria and fruits, black, effuse-pulvinate, coriaceous-horny or subcarbonaceous, sclerotiform, with numerous immersed little loci. *Asci* 8-spored. *Ascospores* oblong, aseptate, hyaline.

Type species: *Hyalodothis clavus* Pat. & Har. [**Democratic Republic of the Congo**, on culms of *Poaceae*].

Descriptions and illustrations: Arnold (1967), Patouillard & Hariot (1893).

Notes: Arnold (1967) found that the type specimen contained two distinct species of fungi that were used to generate the description of *Hyalodothis*, and thus recommended that the genus be considered a *nomen confusum*, which is currently not part of the ICN. Hence, a lectotypification confining this name to one of the included elements is necessary to clarify the identity of this genus. According to Arnold (1967) the type specimen is part of Patouillard collection (no.597) in FH, but it could not be traced using the online catalog.

Hyalozasmidium U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Isariella Henn., Hedwigia 48: 19. 1908.

Description (adapted from Hennings 1908): "*Sporodochia*" (fascicles/coremia) parasitic, superficial, fasciculate-fasciate, waxy, composed of hyaline, septate, loosely united, converging "hyphae" (conidiophores). *Conidia* ellipsoid, aseptate, hyaline.

Type species: *Isariella auerswaldiae* Henn. [**Brazil**, São Paulo, Horto Botanico, on stromata of *Auerswaldia puttemansia* on leaves of *Lauraceae*, 1902, Puttemans, No. 571 (**holotype** S F40445)]

Description and illustrations: Hennings (1908), Seifert *et al.* (2011).

Notes: The phylogenetic position of *Isariella* is unknown and its two species are only known by their hyphomycetous asexual morph (Seifert *et al.* 2011). Sequence data are necessary to determine its phylogenetic position.

Isariopsella Höhn., in Weese, Mitt. Bot. Inst. Tech. Hochsch. Wien 6: 68. 1929.

Type species: *Isariopsella vossiana* (Thüm.) Höhn. (≡ *Ramularia vossiana* Thüm.) [**Slovenia**, Ljubljana (Laibach), on *Cirsium oleraceum*, Oct. 1879, W. Voss, Thüm., Mycoth. Univ. 1769 (**lectotype** HAL)] = ***Phacellium vossianum*** (Thüm.) U. Braun.

Description and illustration: Braun (1998, as *Phacellium vossianum*).

Notes: *Isariopsella* is currently considered a synonym of *Phacellium*. If *Phacellium* is synonymous with *Ramularia* as is expected, the older name *Ramularia vossiana* will be used for this species. Sequence data are necessary to confirm this hypothesis.

Isariopsis Fresen., Beitr. Mykol. 3: 87. 1863.

Type species: *Isariopsis pusilla* Fresen. [**Germany**, on *Cerastium holosteoides*] = ***Phacellium alborosellum*** (Desm.) U. Braun.

Description and illustration: Braun (1998, as *Phacellium alborosellum*).

Notes: *Isariopsis* is currently considered a synonym of *Phacellium*. If *Phacellium* is synonymous with *Ramularia* as is expected, the name *Ramularia alborosella* (Desm.) Gjaerum would be available for the type species of *Isariopsis* as well as *Phacellium* (see Braun 1998). Sequence data are necessary to confirm this hypothesis.

Jaczewskiella Murashk., Mater. Mikol. Fitopatol. Rossii 5(2): 5. 1926.

Description (adopted from Shkarupa 1992 and Mel'nik & Popushoj 1992): Saprobic. *Conidiomata* stromatic, cupulate, with a more or less well-developed stalk, sometimes sessile, large, scattered, composed of light brown to brown prismatic or oblong cells, darker and thick-walled towards the periphery. *Conidiophores* lacking. *Conidiogenous cells* lining the whole inner surface of the conidiomata, holoblastic, annellidic, indeterminate, discrete, cylindrical,

thin-walled, smooth, light brown, with a single percurrent proliferation, margin uneven, fimbriate. *Conidia* solitary, clavate, obclavate, broad ellipsoid, smooth, with transverse and oblique to vertical septa, constricted at transverse septa, light brown, transparent.

Type species: *Jaczewskiella altajensis* Murashk. [**Russia**, Altai, valley of the river Dzhelo, 2200 m alt, on dead branches of *Comarum salessowianum*, 19 July 1925, S. Antonov (**holotype** LEP)].

Description and illustration: Shkarupa (1992).

Notes: *Jaczewskiella* is a coelomycetous genus that was considered a synonym of *Stigmina* by Sutton (1977). Shkarupa (1992) and Braun & Mel'nik (1996) considered *Jaczewskiella* to be an independent genus based on cupulate conidiomata and brown phragmo- to dictyoconidia. This genus is insufficiently known, and will have to be recollected and sequenced in order to determine its true status.

Janetia M.B. Ellis, More Dematiaceous Hyphomycetes (Kew): 33. 1976.

Description (from Ellis 1976): *Colonies* effuse, thin, dark blackish brown. *Mycelium* superficial composed of a network of branched and anastomosing septate, olivaceous or dark brown, smooth hyphae. *Stroma* none; *setae* and *hyphopodia* absent. Conidiophores micronematous, mononematous. *Conidiogenous cells* integrated, mostly intercalary, polyblastic, denticulate; denticles large, flat-topped. *Conidia* solitary, dry, obclavate, multiseptate, brown, smooth.

Type species: *Janetia euphorbiae* M.B. Ellis [**Tanzania**, Ukiriguru Hill, on *Euphorbia tirucalli*, 13 Nov. 1972, D.L. Ebbels (**holotype** IMI 163941)].

Description and illustration: Ellis (1976), Seifert *et al.* (2011).

Notes: The genus *Janetia* is characterised by the production of polyblastic, pigmented and denticulate conidiogenous cells that give rise to phragmosporous, disto- or eu-septate conidia. The LSU sequences of two recently described species, *Janetia wilsonii* and *Janetia dimorphandrae-mollis*, place the genus in the *Mycosphaerellaceae*, in close association with species of the *Zasmidium* complex (Silva *et al.* 2016). However, until sequences from the type species *Janetia euphorbia* are obtained, the phylogenetic placement of this genus in the *Mycosphaerelaceae* is only tentative.

Jahniella Petr., Ann Mycol. 18(4/6): 123. 1921. 1920.

Description (from Quaedvlieg *et al.* 2013, adapted from Sutton 1980): *Mycelium* branched, immersed, septate, brown. *Conidiomata* pycnidial, superficial on epidermis, immersed, separate, globose, papillate, dark brown, thick-walled, sclerenchymatic; wall consisting of an outer layer of dark brown, thick-walled *textura angularis*, a middle layer of 8 cells thick, of hyaline to pale brown, thickwalled cells, and an inner layer of thin-walled, hyaline, irregular cells. *Ostiole* single, circular, with a distinct channel and hyaline periphysoid cells. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous* cells holoblastic, determinate, discrete, hyaline, ampulliform, lining the wall of the pycnidium. *Conidia* straight or slightly

curved, hyaline, thin-walled, smooth, 3–4-euseptate, eguttulate, truncate at the base, slightly tapered to the apex.

Type species: *Jahniella bohemica* Petr., [**Czech Republic**, Bohemia, on stems of S*crophularia nodosa*, 18 Mar. 1916, J. Jahn (**isotype** K(M) 180917 (slides) ex BPI).

Description and illustration: Quaedvlieg *et al.* (2013).

Notes: The type species needs to be recollected in order to determine the phylogenetic position of the genus. See Quaedvlieg *et al.* (2013).

Laocoön J.C. David, Mycol. Pap. 172: 116. 1997.

Description (from David 1997): Hyphomycetous, phytopathogenic. *Mycelium* superficial, hyphae creeping, septate, branched, pigmented, smooth. *Conidiophores* arising from creeping hyphae, macronematous, mononematous, simple, rarely branched, straight to flexuous, septate, densely verruculose, not spirally twisted. *Conidiogenous cells* integrated, terminal, multilocal, sympodial; conidiogenous loci broad, aggregated, cercospora-like, thickened and darkened, flattened with a rough surface, raised at the edge and with a conspicuous central dome. *Conidia* solitary, consisting of only one filament, transversely euseptate, pustulate, not proliferating, thin-walled, pigmented; conidial secession schizolytic.

Type species: *Laocoön paradoxus* (Syd. & P. Syd.) J.C. David (≡ *Heterosporium paradoxum* Syd. & P. Syd.).

Descriptions and illustrations: David (1997), Braun (1998), Seifert *et al.* (2011); present work (Fig. 59).

Materials examined: **Colombia**, Antioquia, Guaca, on *Calea glomerata*, 12 Sep. 1910, E. Mayor 346 (**holotype** S F40564, isotype IMI 375866).

Note: *Laocoön* is a hyphomycetous genus that includes a single species thus far only known from the type locality (Seifert *et al.* 2011). Sequence data are necessary to determine its phylogenetic position.

Lecanosticta Syd.

Notes: See treatment in text.

Lecanostictopsis B. Sutton & Crous, Mycol. Res. 101: 215. 1997.

Description (from Sutton & Crous 1997): *Mycelium* immersed, intercellular, branched, septate, dark to reddish brown. *Conidiomata* epidermal to subepidermal, erumpent, eustromatic, acervular to sporodochial, composed of thick-walled, dark to reddish brown *textura angularis*. *Conidiophores* dark to reddish brown, coarsely verrucose, cylindrical, unbranched, septate, formed from the upper cells of the conidiomata. *Conidiogenous cells* integrated, dark to reddish brown, coarsely verrucose to tuberculate, cylindrical, with several percurrent enteroblastic

Fig. 59. *Laocoön paradoxus* (IMI 375866). A–D. Observations *in vivo*. A. Leaf spot symptoms on the host. B–D. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

proliferations. *Conidia* holoblastic, dark to reddish brown, coarsely verrucose to tuberculate, with 0- to several eusepta, straight to curved, obtuse or acute at apex, truncate at base, cylindrical to fusiform. *Conidiogenesis*: a succession of conidia is formed by holoblastic conidial ontogeny, delimitation by a transverse septum, schizolytic secession, replacement wall building apex leading to enteroblastic percurrent conidiogenous cell proliferation followed by holoblastic conidial ontogeny, with successive conidia seceding at progressively higher levels.

Type species: *Lecanostictopsis kamatii* (Ullasa) B. Sutton & Crous (≡ *Stigmina kamatii* Ullasa) [**India**, Mysore State, Bettigeri, on leaves of *Syzygium aromaticum* (**type** IMI 147817)].

Descriptions and illustrations: Sutton & Crous (1997), Seifert *et al.* (2011).

Notes: All attempts to culture species of *Lecanostictopsis* have thus far proven unsuccessful, even from freshly collected material, therefore its phylogenetic position remains unknown. The taxonomic history of this genus is detailed by Sutton & Crous (1997).

Lembosiopsis Theiss., Ann. Mycol. 15: 422. 1918.

Description (from Hongsanan *et al.* 2014): *Ascomata* solitary to clustered, subcuticular, circular, slightly irregular from above, black, shiny, with a central rounded ostiole. *Hamathecium* lacking pseudoparaphyses. *Asci* 8-spored, bitunicate, obclavate, tapering towards the apex, apedicellate or with short pedicel, apically rounded with a small ocular chamber. *Ascospores* 2–3-seriate in the ascus, narrowly ovoid, tapering from the apex to the base, 1-septate slightly above the centre, slightly constricted at the septum, hyaline, surrounded by thin gelatinous sheath, smooth-walled.

Type species: *Lembosiopsis andromedae* (Tracy & Earle) Theiss. (= *Lembosia andromedae* Tracy & Earle) [**USA**, Mississippi, Biloxi, on leaves of *Andromeda nitida*, 26 May 1895, S.M. Tracy and F.S Earle 4005 (**holotype** BPI 647155]

Description and illustration: Hongsanan *et al.* (2014).

Notes: Based on the literature, Lumbsch & Huhndorf (2010) place *Lembosiopsis* in *Asterinaceae*, but in a recent review of *Asterinales* Hongsanan *et al.* (2014) transferred the genus to the *Mycosphaerellaceae* based on morphological characters (subcuticular ascomata with a rounded central ostiole, without pseudoparaphyses, and procuding obclavate asci). The phylogenetic placement of this genus is uncertain as DNA sequence data are not available.

Lophiosphaerella Hara, Byogaichu-Hoten (Manual of Pests and Diseases): 778. 1948.

Description (from Li *et al.* 2014): Parasitic on terrestrial plants, forming conspicuous small, rounded, pale grey leaf spots on both sides of the leaf. *Ascomata* solitary, scattered, gregarious or confluent, globose or subglobose, semi-immersed or immersed, ostiolate. *Ostiole* centrally located. *Peridium* composed of brown to black, thick-walled cells arranged as *textura angularis*. *Pseudoparaphyses* absent. *Asci* 8-spored, bitunicate, fissitunicate, clavate, oblong or elongate, with an ocular chamber. *Ascospores* multi-seriate or crowded, irregularly arranged in the asci, oblong to fusiform or clavate, 1-septate, slightly constricted at the septum, hyaline, smooth-walled.

Type species: *Lophiosphaerella euryae* (Syd. & P. Syd.) Hara (≡ *Aulographum euryae* Syd. & P. Syd.) [**Japan**, Tokyo, on *Eurya chinensis*, Jun. 1899, M. Shirai (**syntypes** S F12246, S F171544)].

Description and illustration: Li *et al.* (2014).

Notes: *Lophiosphaerella* was considered *incertae sedis* by Lumbsch & Huhndorf (2010) but was transferred to *Mycosphaerellaceae* by Li *et al.* (2014) based on morphological characters. This genus is insufficiently known, and the type species needs to be recollected and subjected to molecular analysis.

Marcosia Syd. & P. Syd., Ann. Mycol.14: 96. 1916.

Type species: *Marcosia ulei* Syd. & P. Syd. [**Brazil**, Brazilia, on leaves of *Cynometra bauhiniifolia*] ≡ ***Stigmina ulei*** (Syd. & P. Syd.) B. Sutton.

Description: Sydow & Sydow (1916).

Notes: *Marcosia* is based on *Marcosia ulei* and is considered a synonym of *Stigmina ulei.* The genus *Stigmina* is currently considered a synonym of *Pseudocercospora* (Crous *et al.* 2013a). However, since no molecular data are available for this species, the current name remains in *Stigmina*.

Madagascaromyces U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Megaloseptoria Naumov, Bolêz. Rast. 14: 144. 1925.

Description (from Quaedvlieg *et al.* 2013, adapted from Sutton 1980): *Mycelium* immersed, branched, septate, brown. *Conidiomata* pycnidial, separate, globose, slightly papillate, dark

brown to black, superficial, sessile, often aggregated in groups, unilocular, thick-walled; wall of several cell layers of brown *textura angularis*, more darkly pigmented on the outside. *Ostiole* single, circular. *Conidiophores* hyaline, branched, septate (mainly at the base), smooth, straight or irregular, formed from the inner cells of the pycnidial wall. *Conidiogenous cells* enteroblastic, determinate, discrete or integrated, doliiform, ampulliform or irregularly cylindrical, hyaline, smooth, collarette evident, channel wide, periclinal thickening present. *Conidia* hyaline to pale brown with several transverse eusepta, continuous, tapered near the obtuse apex and truncate base, thin-walled, smooth, cylindrical, straight or slightly curved, often with 2 guttules in each cell.

Type species: *Megaloseptoria mirabilis* Naumov [**Russia**, on *Picea pungens*].

Description and illustration: Quaedvlieg *et al.* (2013)

Notes: A specimen of *Megaloseptoria mirabilis* collected by Naomov in Russia was located in BPI (BPI 389179), but was not observed. See also Quaedvlieg *et al.* (2013).

Melanodothis R.H. Arnold, Canad. J. Bot. 49: 2188. 1972 (1971).

Description (adapted from Arnold 1971): *Ascostromata* arising from a hypostroma formed within the ovary and perigynum, black, subglobose, multilocular, wall composed of a *textura angularis* with pseudoparenchymatic cells. *Locules* in a single layer beneath the surface of the stroma, each with an ostiole. *Microconidial locules* are formed in the early stages of ascostromata. *Microconidia* (spermatia) narrowly oblong, hyaline, formed on short projections on the hyaline cells lining the microconidial cavity. *Asci* oblong to rarely oblong-pyriform, aparaphysate, sessile, 8 spored, arising from a basal cushion of pseudoparenchymatic cells. *Ascospores* hyaline, one celled, thick-walled, narrowly ellipsoidal, with ends sometimes narrowly and abruptly tapered. *Conidiophores* indeterminate. *Conidiogenous* cells holoblastic. *Macroconidia* ramularia-like, hyaline, smooth, catenulate, branched or unbranched, cylindrical, aseptate or 1 septate, with a disc-like hilum at each end. *Blastoconidia* formed singly at the apex of hyphae in the periphery of the colony or on the long cylindrical conidia as secondary conidia, one celled, hyaline, smooth, ovoid.

Type species: *Melanodothis caricis* R.H. Arnold [Canada, on flowers of *Carex aquatilis* var. *dives* (= *C. sitchensis*), (**holotype** DAOM 116433, ex-type culture CBS 860.72 = ATCC 24309)].

Description and illustration: Arnold (1971).

Notes: The ex-type culture of *Melanodothis caricis* clusters in *Cladosporiaceae*, suggesting that *Melanodothis* is an older name for *Davidiella*. However, the name presently being used for this genus is that of the asexual morph, *Cladosporium* (Bensch *et al.* 2012). Arnold (1971) reported the presence of an ascostroma with pseudothecial locules and this could be consistent with the variation observed in *Davidiella* (see Schubert *et al.* 2007). Furthermore, he also reported ramularia-like conidia, which could be *Cladosporium*, which at times mutates, and produces hyaline conidia with darkened hila only. Furthermore, the relation of this species to the North American *Ramularia caricis* U. Braun (Braun 1998) has to be proven.

Microcyclosporella Jana Frank, Schroers & Crous

Note: See treatment in text.

Microcyclus Sacc. *et al.*, Ann. Mycol. 2: 165. 1904.

Description (from Monkai *et al.* 2013): Biotrophic on leaves and stems. *Ascostromata* pulvinate, irregularly shaped, developing from central basal hypostroma, superficial, multilocular, composed of *textura angularis*, thick-walled, reddish brown. *Ostiole* papillate, periphysate. *Asci* 8-spored, thick-walled, bitunicate, fissitunicate, cylindrical to clavate, with an ocular chamber, with a long pedicel. *Ascospores* 1–3-seriate, 1-septate, obovoid, upper cell shorter and wider than lower, not or slightly constricted at the septum, smooth wall, granular, hyaline.

Type species: *Microcyclus angolensis* Sacc. *et al.* [**Angola**, on living leaves of *Millettia thonningii*, Welwitsch (**holotype** S F8592, isotype S F8593)].

Notes: Monkai *et al.* (2013) placed the genus in *Mycosphaerellaceae*, and even though molecular data are lacking, this assumption seems likely. The genus *Microcyclus* includes an important pathogen on *Hevea*, *Microcyclus ulei*, that was recently recollected and transferred to *Pseudocercospora* based on morphological and molecular data (Hora Júnior *et al.* 2014).

Micronectriella Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Cl., Abt. 1, 115: 1194. 1906.

Type species: *Micronectriella pterocarpi* (Racib.) Höhn. (≡ *Micronectria pterocarpi* Racib.) [**Indonesia**, Java, on leaves of *Pterocarpus indicus*] = ***Sphaerulina pterocarpi*** (Racib.) Arx & E. Müll.

Description and illustration: Arx & Müller (1975).

Notes: The genus *Sphaerulina* was recently shown to be distinct from others in the *Mycosphaerellaceae* (Quaedvlieg *et al.* 2013), but fresh collections are required to determine the phylogenetic position of *Micronectriella*. The type specimen could not be located.

Micronematomyces U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Miuraea Hara

Note: See treatment in text.

Mycodiella Crous

Note: See treatment in text.

Mycoporis Clem., The Genera of Fungi: 50, 173. 1909.

Description (from Thambugala *et al.* 2014): Parasitic on leaves. *Ascomata* appearing as black spots on the host surface, gregarious, scattered, superficial, very easily removed from the host surface, globose, uniloculate, ostiolate. *Peridium* one-layered, composed of dark to brown cells of *textura angularis*. *Haemathecium* lacking pseudoparaphyses. *Asci* eight-spored, bitunicate, broadly cylindrical to fusiform, sessile, with a large ocular chamber. *Ascospores* overlapping, uniseriate at the apex to tri-seriate near the base, hyaline, 5-septate, strongly constricted at the primary septum, broadly fusiform to cylindrical with broadly rounded ends.

Type species: *Mycoporis perexigua* (Müll. Arg.) Clem. (≡ *Mycoporellum perexiguum* Müll. Arg.) [**Australia**, Queensland, Brisbane, Bailey, on bark (**holotype** G 00110864)].

Description and illustration: Thambugala *et al.* (2014).

Notes: Thambugala *et al.* (2014) allocated the genus to *Mycosphaerellaceae* based on its ascomatal morphology. Since there are no available DNA sequences the phylogenetic position of *Mycoporis* remains unresolved.

Mycosphaerelloides Videira & Crous

Note: See treatment in text.

Mycovellosiella Rangel

Note: See treatment in text.

Neoceratosperma Crous & Cheew.

Note: See treatment in text.

Neocercospora M. Bakhshi, Arzanlou, Babai-ahari & Crous

Note: See treatment in text.

Neocercosporidium Videira & Crous

Note: See treatment in text.

Neodeightoniella Crous & W.J. Swart

Note: See treatment in text.

Neomycosphaerella Crous

Note: See treatment in text.

Neoovularia U. Braun, Nova Hedwigia 54: 473. 1992.

Description (from Videira *et al.* 2016, adapted from Braun 1998): Phytopathogenic, causing leaf spots. *Caespituli* amphigenous, whitish to pink or ochraceous. *Mycelium* consisting of hyaline to faintly pigmented, septate, branched, thin-walled hyphae forming well-developed stromata. *Conidiophores* arising from stromata, emerging through stomata or erumpent through the cuticle, often forming sporodochia, subcylindrical, subclavate, simple, thin-walled, smooth, hyaline or lightly pigmented, continuous or septate. *Conidiogenous cells* integrated, terminal, straight to moderately geniculate-sinuous, polyblastic and sympodial, conidiogenous loci numerous, conspicuous, bulging, papilla-like, but not thickened and darkened, at most slightly refractive. *Conidia* formed singly, subglobose, obovoid, ellipsoid, aseptate, hyaline to faintly pigmented, thin-walled, smooth to verruculose, basal *hilum* not thickened or darkened; conidial secession schizolytic.

Type species: *Neoovularia nomuriana* (Sacc.) U. Braun (≡ *Tuberculina nomuriana* Sacc.) [**Japan**, Kikotaro, on *Astragalus sinicus*, 1903, Nomura (**holotype** PAD)].

Descriptions and illustrations: Braun (1998), Videira *et al.* (2016).

Notes: The phylogenetic position of *Neoovularia* remains unresolved since no DNA from the type species is available. See treatment in Braun (1998) and Videira *et al.* (2016).

Neopenidiella Quaedvlieg & Crous

Note: See treatment in text.

Neophloeospora Videira & Crous

Note: See treatment in text.

Neopseudocercospora Crous

Note: See treatment in text.

Neopseudocercosporella Videira & Crous

Note: See treatment in text and Videira *et al.* (2016).

Neoramularia U. Braun, Nova Hedwigia 53: 291. 1991.

Description (from Videira *et al.* 2016, adapted from Braun 1998): Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline or subhyaline, septate, branched, thin-walled hyphae forming stromata or not. *Conidiophores* macronematous, usually in large fascicles, sometimes forming sporodochial and basistromatic conidiomata, emerging through stomata or erumpent through the cuticle, straight, subcylindrical to geniculate-sinuous, simple, hyaline or faintly pigmented, continuous or septate, thin-walled, smooth or occasionally rough. *Conidiogenous cells* integrated, terminal, polyblastic, percurrent and sympodial, conidiogenous loci inconspicuous,

not thickened or darkened. *Conidia* solitary or catenate, ellipsoid-ovoid, subcylindrical or fusoid, hyaline or slightly pigmented, aseptate to 3-septate, thin-walled, smooth or almost so, *hila* unthickened and hyaline, conidial secession schizolytic.

Type species: *Neoramularia eurotiae* (Gamalizk.) U. Braun (≡ *Ramularia eurotiae* Gamalizk.) [**Kyrgyzstan**, Central Tien-Shan, on *Krascheninnikovia ceratoides*, 5 Jun. 1958, Gamalitzkaya (**holotype** LE 41968] = ***Neoramularia kochiae*** (Woron.) U. Braun (Azerbeijan, on *Kochia* sp.).

Description and illustration: Braun (1991), Videira *et al.* (2016).

Notes: *Neoramularia* is ramularia-like but differs in having unthickened and not darkened conidiogenous loci and conidial hila, i.e. characteristic *Ramularia* loci and hila are lacking. Cultures from fresh specimens must be obtained in order to determine the phylogenetic position of this genus based on DNA sequences. See treatment in Videira *et al.* (2016).

Neoseptoria Quaedvlieg, Verkley & Crous

Note: See treatment in text.

Nothopassalora U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Nothopericoniella Videira & Crous

Note: See treatment in text.

Nothophaeocryptopus Videira, C. Nakash., U. Braun, Crous

Note: See treatment in text.

Oedothea Syd., Ann. Mycol. 28: 202. 1930.

Description (adapted from Sydow 1930): *Stromata* on leaf veins, forming small gall-like swellings, subepidermal, erumpent through longitudinal fissures, exposed surface dull black-brown, finely pulverulent to floccose by abundant superficial conidia, intramatrical stromata composed of brown hypertrophic cells of the host tissue, interrupted by small to larger cavities, and sparingly developed filamentous, hyaline hyphae. *Conidia* in small to larger aggregations, broad ovate, ellipsoid to subglobose, with a single median septum, barely constricted, dark brown but transparent.

Type species: *Oedothea vismiae* Syd.

Description and illustrations: Sydow (1930), Seifert *et al.* (2011); present study (Fig. 60).

Materials examined: **Venezuela**, Los Naranjos pr. Puerto la Cruz, on leaves of *Vismia hamanii*, 7 Jan. 1928, H. Sydow 183 (**holotype** S F42267).

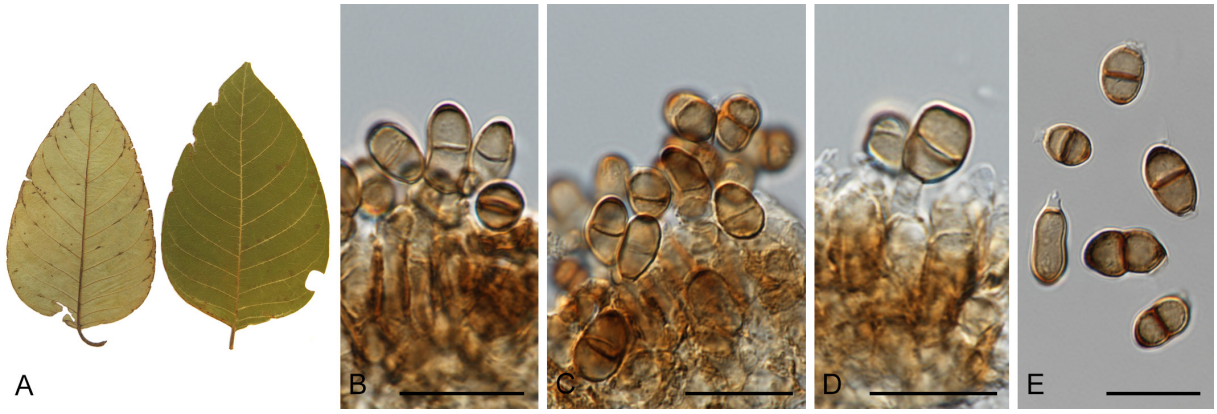


Fig. 60. *Oedothea vismiae* (NY 00945740). A–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B–D. Conidiophores and conidia. E. Conidia. Scale bars = 10 µm.

Notes: The phylogenetic position of *Oedothea* is unknown and only its hyphomycetous asexual morph is known (Seifert *et al.* 2011). Sequence data are necessary to determine its phylogenetic position.

Ophiocarpella Theiss. & Syd., Ann. Mycol. 13: 644. 1915.

Description (adapted from Theiss & Sydow 1915): Like *Montagnella*, but paraphyses lacking, ascospores colourless, filiform, septate. *Stromata* hypophyllous, black, irregular, with dense protuberant loculi, half immersed in the host tissue, connected by vertical hyphal strands, apex free, protuberant through the epidermis. *Hyphae* greyish brown, with swollen cells, several layers around the loculi forming a kind of wall, dense between loculi, sparingly developed below, loculi globose, non-ostiolate. *Asci* fasciculate, paraphyses lacking, 8-spored. *Ascospores* polystichous, colourless, filiform, with a distinct median septum, possibly with several septa when mature.

Type species: *Ophiocarpella tarda* (Harkn.) Theiss. & Syd. (≡ *Ophiodothis tarda* Harkn.) (**USA**, California, San Francisco, on fruit of *Rhus diversiloba*, H.W. Harkness (**holotype** BPI 798419)]) ≡ *Sphaerulina tarda* (Harkn.) M.E. Barr.

Description (*no illustration*): Theissen & Sydow (1915).

Notes: Based on morphology, *Ophiocarpella* was considered as a synonym of *Sphaerulina*. Fresh collections are required to determine the phylogenetic position of *Ophiocarpella tarda.*

Ophiocladium Cavara, Z. Pflanzenkrankh. 3: 26. 1893.

Type species: *Ophiocladium hordei* Cavara [Cavara, Z. Pflanzenkrankh. 3: Plate (Tab.) I, Fig. 9, 1893 (**lectotype** designated by Braun 2017)] [**Austria**, Reichersberg am Inn, on *Hordeum vulgare* (**epitype** designated by Braun 2017, CBS H-22641, culture ex-epitype CBS 101180)] ≡ ***Ramularia collo-cygni*** B. Sutton & J.M. Waller.

Description and illustration: See Braun (1998, as *Ramularia collo-cygni*).

Notes: See treatment in Videira *et al.* (2016) as *Ramularia collo-cygni*. The typification of the type species has recently been clarified by Braun (2017).

Oreophylla Cif., Sydowia 8: 253. 1954.

Description (adapted from Ciferi 1954): Biotrophic. *Mycelium* internal, superficial hyphae lacking. *Conidiophores* in fascicles, arising from an immersed pseudostromatic base, erect, brown, unbranched, straight to tortuose, septate. *Conidia* solitary, acrogenous, cylindrical-attenuated, transversely pluriseptate, straight to curved, hyaline.

Type species: *Oreophylla angelae-mariae* Cif. (as '*angelaemariae*') [**Dominican Republic**, Hato del Yaque, on leaves of *Gliricidia sepium*] = *Passalora gliricidiasis* (Gonz. Frag. & Cif.) R.F. Castañeda & U. Braun.

Descriptions and illustrations: Ciferri (1954), Ellis (1976, as *Cercosporidium gliricidiasis*).

Notes: Deighton (in Ellis 1976) considered *Oreophylla angelaemariae* a synonym of *Sirosporium gliricidiae* (Syd.) Deighton (≡ *Passalora gliricidiae* (Syd.) U. Braun & Crous), but Braun *et al.* (1999) stated that this species has to be reduced to synonymy with *Passalora gliricidiasis*. *Oreophylla* was treated as synonym of *Passalora s. lat.* by Crous & Braun (2003), but as DNA of *Passalora gliricidiasis* (= *Oreophylla angelae-mariae*) is not available, the phylogenetic position of *Oreophylla* remains unresolved.

Ormathodium Syd., Ann. Mycol. 26: 138. 1928.

Description (adapted from Sydow 1928): *Leaf spots* lacking. *Caespituli* hypophyllous, regularly spread, loose to dense, mostly on tips of stellate hairs, rarely on the epidermis. *Conidiomata* superficial, 30–130 µm diam, globose to hemispherical, more rarely irregular, with a basal dense plectenchymatous stroma composed of yellow to olivaceous brown hyphae, equipped with short protuberant free ends [conidiophores] giving rise to simple or dichotomously branched conidial chains. *Conidia* oblong, often almost cylindrical, more rarely fusiform, olivaceous brown, transversely 1–2-septate, not or only slightly constricted at the septa.

Type species: *Ormathodium styracis* Syd. [**Costa Rica**, San José, Rio Torres, on leaves of *Styrax argenteus*].

Description (no illustration): Sydow (1928).

Notes: The genus *Ormathodium* was considered a synonym of *Mycovellosiella* by Muntañola (1960), and subsequently placed in synonymy of *Passalora* by Crous & Braun (2003). Unfortunatelly, the type material of this genus has not been preserved (Crous & Braun 2003), and this synonymy remains unconfirmed.

Ovosphaerella Laib., Centralbl. Bakteriol., 2. Abth., 55: 293. 1922.

Description (based on Laibach 1922): Introduced for a mycosphaerella-like sexual morph with an *Ovularia* asexual morph.

Type species: *Ovosphaerella lapathi* Laib. [Germany, on *Rumex* sp.) ≡ ***Mycosphaerella lapathi*** (Laib.) Petr.

Description: Arx (1983, as *Mycosphaerella lapathi*).

Notes: Laibach (1922) introduced *Ovosphaerella* as genus for the mycosphaerella-like sexual stage of *Ovularia obliqua* (current name *Ramularia rubella*, see Braun 1998). *Ramularia obovata*, another synonym of *Ramularia rubella*, was linked to *Mycosphaerella lapathi* by Arx (1983). The type material of *Ovosphaerella lapathi* is probably missing (Aptroot 2006). Fresh collections are required to confirm this relationship, and clarify the phylogenetic position of *Ovosphaerella*. In case that the connection between these sexual and asexual morphs on *Rumex* were correct, *Ovosphaerella* would be a synonym of *Ramularia*.

Ovularia Sacc., Michelia 2(no. 6): 17. 1880.

Type species: *Ovularia obovata* (Fuckel) Sacc. (≡ *Ramularia obovata* Fuckel) [**Germany**, Erbach, on *Rumex crispus*, Fuckel, Fungi Rhen. Exs. 1635 (**lectotype** HAL)] = ***Ramularia rubella*** (Bonord.) Nannf.

Description: Braun (1998, as *Ramularia rubella*).

Note: See Videira *et al.* (2016) for neotypification details of *Ramularia rubella*.

Pachyramichloridium Videira & Crous

Note: See treatment in text.

Pallidocercospora Crous

Note: See treatment in text.

Pantospora Cif.

Note: See treatment in text.

Paracercospora Deighton

Note: See treatment in text.

Paracercosporidium Videira & Crous

Note: See treatment in text.

Paramycosphaerella Crous & Jol. Roux

Note: See treatment in text.

Paramycovellosiella Videira, H.D. Shin & Crous

Note: See treatment in text.

Parapallidocercospora Videira, Crous, U. Braun, C. Nakash.

Note: See treatment in text.

Parastenella J.C. David, Mycol. Res. 95: 124. 1991.

Description (from Braun *et al.* 2013): Dematiaceous hyphomycete genus resembling *Zasmidium* (*in vivo* with superficial mycelium, hyphae, conidiophores and solitary conidia pigmented, distinctly verruculose to verrucose), but the conidiogenous cells are terminal and intercalary, denticulate, with lateral short peglike protuberances, conidiogenous loci inconspicuous, neither thickened nor darkened.

Type species: *Parastenella magnoliae* (Weedon) J.C. David (≡ *Heterosporium magnolia* Weedon) [**USA**, Florida, St. Petersburg, on leaves of *Magnolia grandiflora*, 15 Feb. 1923, A.J. Weedon (**holotype** ILL 6019, isotypes BPI 443255, 443261, 443270, 443274, K(M), MICH 15715)].

Illustration: Braun *et al.* (1995).

Notes: The phylogenetic position of this genus is unknown; it should be recollected to resolve this uncertainty. See also notes under *Zasmidium gupoyu* in text.

Passalora Fr.

Note: See treatment in text.

Periconia Tode, Fung mecklenb. sel. (Lüneburg) 2: 2. 1791.

Description (adapted from Ellis 1971): *Colonies* effuse, occasionally small and compact, grey, brown, olivaceous brown or black, hairy. *Mycelium* mostly immersed but sometimes partly superficial. *Stroma* frequently present, mid to dark brown, pseudoparenchymatous. *Setae* and *hyphopodia* absent. *Conidiophores* micro- and macronematous, mononematous, with a stipe and spherical head, branches present or absent, stipe straight or flexuous, rarely torsive, pale to dark brown or black, smooth or rarely verrucose, apex sometimes sterile and setiform. *Conidiogenous* cells mono- or polyblastic, discrete on stipe and branches, determinate, ellipsoidal, spherical or subspherical. *Conidia* catenate, often in branched chains, usually spherical or subspherical, occasionally ellipsoidal, oblong or broadly cylindrical, pale to dark brown, verruculose or echinulate, aseptate.

Type species: *Periconia lichenoides* Tode.

Descriptions and illustrations: Mason & Ellis (1953), Ellis (1971), Seifert *et al.* (2011).

Notes: *Periconia* is currently the type genus of the *Periconiaceae* (Tanaka *et al.* 2015). The type species is not known from any recent collections and the original material is presumably lost (Ellis 1971, Tanaka *et al.* 2015). The type species needs to be recollected to determine the phylogenetic position.

Periconiella Sacc.

Note: See treatment in text.

Phacellium Bonord.

Note: See treatment in text.

Phaeocercospora Crous

Note: See treatment in text.

Phaeoisariopsis Ferraris, Ann. Mycol. 7: 280. 1909.

Type species: *Phaeoisariopsis griseola* (Sacc.) Ferraris (≡ *Isariopsis griseola* Sacc.) [**Italy**, Selva, on *Phaseolus vulgaris*, Aug. 1877, Saccardo, Mycotheca Veneta 1247 (**lectotype** designated here, HAL, MBT378593] ≡ ***Pseudocercospora griseola*** (Sacc.) Crous & U. Braun [**Tanzania**, on *Phaseolus vulgaris*, F.S. Ngulu & C. Mushi (**epitype** designated here CBS H-19683, MBT378594, culture ex-epitype CBS 119906 = CPC 10468)].

Description and illustration: Crous *et al.* (2006a), Seifert *et al.* (2011).

Notes: The present genus has been determined as a synonym of *Pseudocercospora* by the phylogenetic placement of the type species *Phaeoisariopsis griseola* (Crous *et al.* 2006a). The epitype designated by Crous *et al.* (2006a) did not cite a lectotype, and thus this matter is addressed here.

Phaeophleospora Rangel

Note: See treatment in text.

Phaeophloeosporella Crous & B. Sutton, S. Afr. J. Bot. 63: 281. 1997.

Description (from Crous & Sutton 1997): Associatted with leaf spots. *Mycelium* immersed, consisting of smooth, hyaline to olivaceous, branched, septate hyphae. *Conidiomata* amphigenous, separate, palle yellow to light brown, acervular, subepidermal, base consisting of olivaceous cells of *textura angularis*. *Conidiophores* pale olivaceous, smooth, simple or branched at the base, septate, cylindrical, erect, formed from the upper cells of the conidioma. *Conidiogenous cells* integrated, terminal, smooth, pale olivaceous, cylindrical, straight to geniculate-sinuous with a subtruncate apex, proliferating sympodially and holoblastically. *Conidia* holoblastic, pale olivaceous, smooth, subcylindrical, straight to gently curved, obtuse at apex, and subtruncate at base, guttulate, euseptate, with inconspicuous hila.

Type species: *Phaeophloeosporella ekebergiae* (Syd. & P. Syd.) Crous & B. Sutton (≡ *Cercosporella ekebergiae* Syd. & P. Syd.) [**South Africa**, KwaZulu-Natal, Verulam, on leaves of *Ekebergia* sp., 1913, J.B. Pole Evans 6799 (**holotype** S F37999)].

Description and illustration: Crous & Sutton (1997).

Note: This species needs to be recollected to resolve its phylogenetic position.

Phaeoramularia Munt.-Cvetk.

Note: See treatment in text.

Pharcidia Körb., Parerga lichenol. (Breslau) 5: 469. 1865.

Type species: *Pharcidia congesta* Körb. [**Europe**, on thallus of *Lecanora subfusca*, (**holotype** in L, fide Santesson (1960)] ≡ ***Stigmidium congestum*** (Koerb.) Triebel.

Note: See Triebel *et al.* (1991).

Phloeospora Wallr.

Note: See treatment in text.

Phlyctaeniella Petr., Ann. Mycol. 20(5/6): 323. 1922.

Description (from Quaedvlieg *et al.* 2013): *Mycelium* immersed, branched, septate, hyaline. *Conidiomata* eustromatic, separate, immersed, pale brown, globose, unilocular, scarcely erumpent; side wall and base of several cell layers of hyaline, thin-walled *textura angularis*, above of larger pale brown tissue. *Ostiole* indistinct, and dehiscence by rupture of the upper wall. *Conidiophores* hyaline, smooth, septate, irregularly branched, especially at the base, formed from the inner cells of the stroma wall. *Conidiogenous cells* phialidic, integrated or discrete, determinate, hyaline, markedly tapered at the apices, smooth, with apical or lateral apertures, collarette minute, with periclinal thickening; only rarely becoming percurrent. *Conidia* hyaline, smooth, thinwalled, irregularly guttulate, filiform, straight, curved or irregular, multiseptate (Sutton 1980).

Type species: *Phlyctaeniella polonica* Petr. [**Austria**, on *Aruncus dioicus* (= *A. silvestris*)].

Description and illustration: Quaedvlieg *et al.* (2013).

Notes: The type specimen of the present species could not be traced. The phylogenetic position of this genus remains unresolved until fresh specimens are collected.

Placocrea Syd., Ann. Mycol. 37: 380. 1939.

Description (from Sydow 1939): *Ascomata* aggregated in stroma, immersed, globose to ovoid, with papillate ostiole. *Asci* clavate to cylindrical-clavate, 8-spored. *Ascospores* biseriate,

oblongclavate to fusoid, medianly 1-septate, constricted at septum, hyaline, pseudoparaphyses present.

Type species: *Placocrea pulchella* Syd. [**Equador**, Prov. Pichincha, Mindo, on leaves of *Sarcorhachis sydowii*, 1937, H. Sydow 252 and 284 (**syntypes**, NY 01102921, NY 01102922, RMS0017369, S F44505; S F44506; BPI 631051 and Syd., Fungi Exot. Exs. 1200, e.g. S F8589].

Notes: This genus is insufficiently known, and needs to be recollected to resolve its phylogenetic position. Lumbsch & Huhndorf (2010) tentatively place this genus in *Mycosphaerellaceae* based on its morphological characters.

Pleopassalora Videira & Crous

Note: See treatment in text.

Pleuropassalora U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Pleurovularia R. Kirschner & U. Braun, Mycoscience 43: 16. 2002.

Description (from Kirschner *et al.* 2002): Phytoparasitic, conidiophores macronematous, mononematous, hyaline, simple or sparsely branched, verruculose at least in the distal part, emerging mainly through the outer wall of epidermal cells of the host, conidiogenous cells intercalary and terminal with slightly thickened, pigmented scars, mono- or polyblastic, producing hyaline conidia with vacuole.

Type species: *Pleurovularia polliniae* (Henn.) R. Kirschner & U. Braun (≡ *Ovularia polliniae* Henn.).

Description and illustration: Kirschner *et al.* (2002), Seifert *et al.* (2011), present study (Fig. 61).

Materials examined: **Japan**, Prov. Tosa, Katakasa-mura, on *Pollinia imberbis*, Jun. 1901, T. Yoshinaga No. 25 (**holotype** S F43065).

Notes: The phylogenetic position of *Pleurovularia* is unknown and only the hyphomycetous asexual morph is known. It is necessary to recollect the type species and obtain cultures to determine the phylogenetic position of *Pleurovularia*.

Pluripassalora Videira & Crous

Note: See treatment in text.

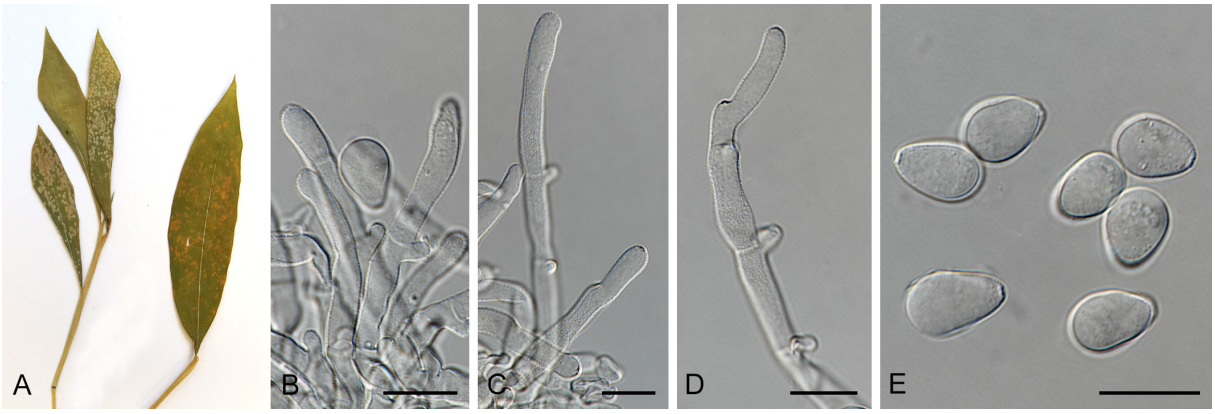


Fig. 61. *Pleurovularia polliniae* (S F43065). A–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores, conidiogenous cells and conidium. C, D. Conidiophores and conidiogenous cells. E. Conidia. Scale bars = 10 µm.

Polyphialoseptoria Quaedvlieg, R.W. Barreto, Verkley & Crous

Note: See treatment in text.

Polysporella Woron., Izv. Kavkazsk. Muz. 10: 7. 1916.

Description: *Ascomata* pseudothecial, scattered, immersed, later erumpent through the epidermis, flattened, 120–150 µm diam, 75–90 µm high, parenchyma composed of polygonal cells, 12–15 µm diam. *Asci* oval, apex thickened, sessile, 60–67 × 30–32 µm, aparaphysate, 24–27(–32?)-spored. *Ascospores* 1-celled, at first hyaline, late slightly brown, oblong-ovate, aggregated, 20–22 × 7–8 µm.

Type species: *Polysporella woronowii* Woron. [**Turkey** (locality historically situated in Russia), eastern Anatolia, Province Kars, Kavgızman ('district Kaghyzman, Novo-Nikolaevka'), on stems of *Dianthus crinitus*, 7 Jun. 1913, G. Woronow (**type** TBIP)].

Description and illustration: Woronichin (1916: 7, fig. 3).

Notes: This genus is insufficiently known, and needs to be recollected to resolve its phylogenetic position. The allocation of *Polysporella* to *Mycosphaerelaceae* dates back to Lumbsch & Huhndorf (2007: 79, no 4542), with reference to 'O. Eriksson, in litt.' However, the position of this genus and its assignment to *Mycosphaerelaceae* are quite unclear and unproven, which was also confirned by T. Lumbsch and O. Eriksson (pers. comm.). The locality of the holotype was historically located in the Russian Province Kars (Karsskaya Oblast), district Kagizman (Kaghyzman), which nowadays belongs to Turkey (southeast Anatolia, Province Kars, Kavğzman). The continued existence and possible current Turkish name of the settlement 'Novo-Nikolaevka' could not be clarified.

Polythrincium Kunze, in Kunze & Schmidt, Mykologische Hefte (Leipzig) 1: 13. 1817.
Synonym: *Cymadothea* F.A. Wolf, Mycologia 27: 71. 1935.

Description (from Ellis 1971): Colonies punctiform or effuse, olivaceous brown. *Mycelium* immersed. *Stroma* pseudoparenchymatous, brown to black. *Setae* and *hyphopodia* absent. *Conidiophores* macronematous, mononematous, caespitose, unbranched or with several branches arising at one point, the upper part curved and often thickened on the side away from the curvature, undulate, often torsive, mid pale brown, smooth. *Conidiogenous cells* polyblastic, integrated, terminal, sympodial, cylindrical, undulate, cicatrized; scars large, flat, unilateral. *Conidia* solitary, acropleurogenous, simple, cuneiform or pyriform, hyaline to pale brown, smooth or verruculose, 1-septate.

Type species: *Polythrincium trifolii* Kunze [**Germany**, on leaves of *Trifolium pratense*].

Descriptions and illustrations: Sivanesan (1984), Ellis (1971), Simon *et al.* (2009).

Notes: This species is an obligate biotroph, and does not grow in culture. The phylogenetic link between the sexual morph, *Cymadothea trifolii*, and *Polythrincium trifolii* was confirmed by Simon *et al.* (2009). In addition, Simon *et al.* (2009) determined the phylogenetic position of the genus as belonging in *Mycosphaerellaceae* by extracting DNA directly from lesion caused by the pathogen on *Trifolium repens* collected in Germany (CBS H-20110).

Prathigada Subram., J. Madras Univ. 26: 366. 1956.

Type species: *Prathigada cratevae* (Syd.) Subram. (≡ *Napicladium cratevae* Syd.) ≡ ***Pseudocercospora cratevicola*** C. Nakash. & U. Braun.

Description and illustration: Braun *et al.* (2013), present study (Fig. 62).

Materials examined: **India**, Madras, Coimbatore, Government Farm, on *Crateva religiosa*, 5 Feb. 1912, W. McRae 9 (**holotype** S F42112); Calcuta, on *Crateva nurvala*, 30 May 1978, J.B. Ray PCC2700 Dep. Botany Presidency College (IMI 234117). **Myanmar**, Tutkon, on *Crateva religiosa*, 20 Nov. 1973, Mya Tharng (IMI 182578). **Japan**, on *Crataeva falcata*, 18 Sep. 1998, S. Uematsu & C. Nakashima, culture MUCC 1088.

Notes: Braun *et al.* (2013) examined type material of this species and compared it with conspecific Japanese collections on *Crateva formosensis*. The morphological characteristics are quite uniform among the observed specimens (Fig. 62). Sequences retrieved from Japanese cultures (MUCC 1088, Table 1, Fig. 1) clusted within the big *Pseudocercospora* clade close to *Pseudocercospora fijiensis*. Thus, *Prathigada* was reduced to synonymy with *Pseudocercospora* (Braun *et al.* 2013).

Protostegia Cooke, Grevillea 9(49): 19. 1880.

Description (from Crous *et al.* 2015a): *Conidiomata* immersed, becoming somewhat erumpent, solitary, exuding a mucoid conidial cirrhus, pale brown, splitting the leaf surface, with central ostiole; wall of brown *textura intricata*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* hyaline, smooth, lining the inner cavity, lageniform to subcylindrical, proliferating percurrently at apex. *Conidia* hyaline, smooth, scolecosporous, euseptate.

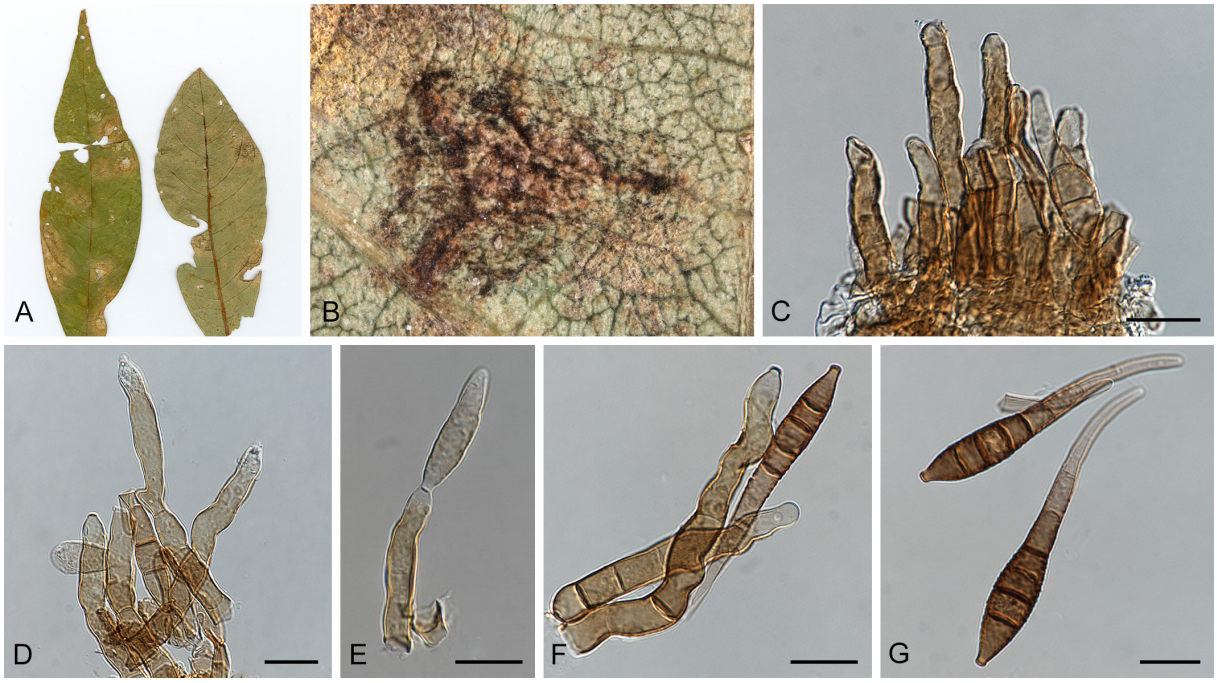


Fig. 62. *Prathigada crataevae* (IMI 234117 and IMI 182578). A–G. Observations *in vivo*. A, B. Leaf spot symptoms on the host. C, D, F. Conidiophores, conidiogenous cells and conidia. E. Conidiogenous cell and conidium. G. Conidia. Scale bars = 10 µm.

Type species: *Protostegia eucleae* Kalchbr. & Cooke [**South Africa**, on *Euclea undulata*, (**epitype** designated by Crous *et al.* 2015a: PREM 60879, culture ex-epitype CPC 23549 = CBS 137232)].

Description and illustration: Crous *et al.* (2015a).

Notes: *Protostegia* is a coelomycetous genus only known from its asexual morph and was recently epitypified (Crous *et al.* 2015a). Based on the epitype, the phylogenetic position of this genus is close to *Cytostagonospora martiniana* (Crous *et al.* 2015a).

Pseudocercospora Speg.

Note: See treatment in text.

Pseudocercosporella Deighton

Note: See treatment in text.

Pseudocercosporidium Deighton

Description (from Braun *et al.* 2013): Foliicolous, plant pathogenic, leaf spotting hyphomycetes, teleomorph unknown. *Mycelium* internal. *Stromata* lacking. *Conidiophores in vivo* solitary or in small loose fascicles (groups) emerging through stomata, laxly erect, macronematous, frequently branched, septate, pigmented (very pale brown), thin-walled, smooth; *conidiogenous cells*

integrated, terminal, intercalary or pleurogenous (as lateral branchlets), sympodial, polyblastic, conidiogenous loci conspicuous, protruding, convex (papilla-like), but wall of the loci neither thickened nor darkened, only somewhat refractive. *Conidia* solitary, didymo- to scolecosporous, pigmented (deeper in pigmentation than the conidiophores), thin-walled, smooth or almost so, hila neither thickened nor darkened.

Type species: *Pseudocercosporidium venezuelanum* (Syd.) Deighton.

Description and illustration: Ellis (1971), Crous & Braun (2003), Seifert *et al.* (2011), Braun *et al.* (2013), present study (Fig. 63).

Material examined: **Venezuela**, Aragua, between La Victoria and Guacamaya, on *Cordia heterophylla*, 3 Jan. 1928, H. Sydow No. 381 (**holotype** S F38692).

Notes: The phylogenetic position of *Pseudocercosporidium venezuelanum* is unknown due to the absence of DNA sequence data. Morphologically, *Pseudocercosporidium* resembles *Passalora*, but differs in the structure of the conidiogenous loci that are not thickened or darkened (Braun 2013).

Pseudodidymaria U. Braun, Cryptog. Bot. 4: 110. 1993.

Description (from Videira *et al.* 2016, adapted from Braun 1998): Phytopathogenic, causing leaf spots. *Mycelium* consisting of hyaline or faintly pigmented, septate, thin-walled and branched hyphae, forming well developed stromata. *Conidiomata* basistromatic and sporodochial.

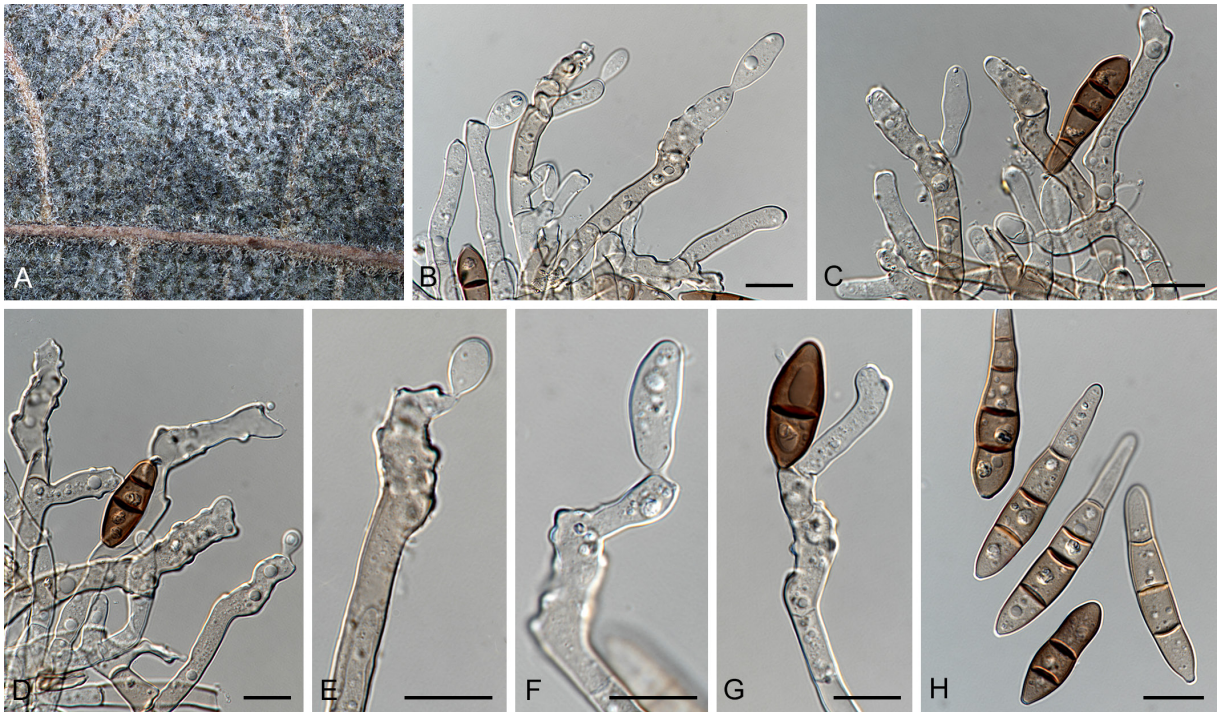


Fig. 63. *Pseudocercosporidium venezuelanum* (S F38692). A–H. Observations *in vivo*. A. Leaf spot symptoms on the host. B–D. Conidiophores, conidiogenous cells and conidia. E–G. Conidiogenous cells and conidia. H. Conidia. Scale bars = 10 µm.

Conidiophores arranged in palisade-like fascicles, subcylindrical, subclavate, straight to flexuous, sinuous, rarely septate, hyaline to faintly pigmented, thin-walled, smooth, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, terminal, polyblastic, sympodial, conidiogenous loci bulging, unthickened or with a thickened rim, not darkened but refractive. *Conidia* formed singly, ellipsoid-obovoid, subclavate, aseptate to 2-septate, base rounded to broadly truncate, hyaline to faintly pigmented, thin-walled, smooth to verruculose, hilum unthickened, not darkened but refractive, conidial secession schizolytic.

Type species: *Pseudodidymaria wyethiae* (Ellis & Everh.) U. Braun (≡ *Marssonina wyethiae* Ellis & Everh.) [**USA**, California, Sonoma, on *Wyethia glabra*, 25 May 1894, Blasdale (**lectotype** NY 01087025; isolectotypes Ellis & Everh., Fungi Columb. 589 and Ellis & Everh., N. Amer. Fungi 3184)].

Descriptions and illustrations: Braun (1998), Videira *et al.* (2016).

Notes: *Pseudodidymaria* is tentatively maintained as a separate genus. Molecular data are required to fully resolve its phylogenetic position.

Pseudophaeoramularia U. Braun, Trudy Bot. Inst. im. V.L. Komarova 20: 18. 1997.

Type species: *Pseudophaeoramularia geranii* (W.B. Cooke & C.G. Shaw) U. Braun (≡ *Cercosporella geranii* W.B. Cooke & C.G. Shaw) [**USA**, Washington State, Whiteman Co., on *Geranium viscosissimum*, 20 Jul. 1948, Shaw & Coheen (**holotype** WSP 19945)] ≡ ***Pseudocercospora geranii*** (W.B. Cooke & C.G. Shaw) U. Braun.

Description and illustration: Braun & Mel'nik (1997).

Notes: Braun & Mel'nik (1997) introduced *Pseudophaeoramularia* as intermediate between *Pseudocercospora* and *Phaeoramularia*. Although the genus has since been treated as synonymous with *Pseudocercospora* (Crous *et al.* 2001b, Crous *et al.* 2013a), phylogenetic proof from the type species is still lacking to confirm this synonymy.

Pseudopericoniella Videira & Crous

Note: See treatment in text.

Pseudophaeophleospora U. Braun, C. Nakash., Videira & Crous

Note: See treatment in text.

Pseudopuccinia Höhn., Mitt. Bot. Inst. Techn. Hochsch. Wien 2: 41. 1925.

Description (adapted from Ellis 1976): *Stromata* present. *Conidiophores* with anellations. *Conidia* pale to brown, verrucose, ellipsoid-obovoid with 1–2 transverse septa and occasionally an oblique septum.

Type species: *Pseudopuccinia thermopsidis* (Harkn.) Höhn. [as '*thermopsis*'] (≡ *Stigmina thermopsidis* Harkn.) [**USA**, California, on *Thermopsis californica*].

Description and illustration: Ellis (1976, as *Stigmina thermopsidis*).

Notes: *Pseudopuccinia* was considered to be a synonym of *Stigmina* (Seifert *et al.* 2011). Based on DNA sequence comparisons, the genus *Stigmina* was treated as synonym of *Pseudocercospora* (Braun & Crous 2006, Crous *et al.* 2013a). However, the phylogenetic position of *Pseudopuccinia*, a stigmina-like genus, is unknown, pending fresh collections and molecular analyses.

Pseudostigmidium Etayo, Biblioth. Lichenol. 98: 193. 2008.

Description (Etayo & Sancho 2008): Lichenicolous. *Ascomata* perithecioid, black, subconical or subglobose, immersed to semiimmersed, protruding, periphyses abundant, paraphyses lacking, gelatinuous hymenial mass I+, KI+ red to violaceous. *Asci* bitunicate, fissitunicate, clavate, broad obovoid to saccate, apically thickened, with an ocular chamber, wall I+, KI+ red to violaceous, 8-spored. *Ascospores* ellipsoid, ellipsoid-ovoid, fusiform, (0–)1–3-septate, colourless, sometimes becoming somewhat pigmented with age.

Type species: *Pseudostigmidium nephromiarium* (Linds.) Etayo. (≡ *Microthelia nephromiaria* Linds.) [**Chile**, Cape Horn, Hermit Island, on thalus and apothecia of *Nephromium cellulosum*, Antartic expedition 1839-43, Dr. Hooker.]

Description and illustrations: Etayo & Sancho (2008).

Notes: *Pseudostigmidium* includes lichenicolous species that are only known by their sexual morph. Hyde *et al.* (2013) accepted this genus in *Mycosphaerellaceae*, but it needs to be recollected before its phylogenetic position can be resolved.

Pseudovularia Speg., Anales Mus. Nac. Hist. Nat. Buenos Aires, Ser. 3, 13: 418. 1911.

Type species: *Pseudovularia trifolii* Speg. [**Argentina**, Lezama, on *Trifolium pratense*, 2 Nov. 1904, Spegazzini (**holotype** LPS 12946)] = ***Ramularia sphaeroidea*** Sacc. [**Germany**, Berlin, Spandau, on *Lotus uliginosus*, Jul. 1875, Magnus (**type** PAD)].

Descriptions and illustrations: Spegazzini (1910), Deighton (1972).

Notes: *Pseudovularia* is considered a synonym of *Ramularia* based on morphological characteristics and *Pseudovularia trifolii* is currently a synonym of *Ramularia sphaeroidea* (Braun 1998, Videira *et al.* 2016). However, no material originating from the type of *Pseudovularia trifolii* has thus far been obtained for further DNA studies.

Pseudozasmidium Videira & Crous

Note: See treatment in text.

Quasiphloeospora B. Sutton *et al.*, Mycol. Res. 100: 979. 1996.

Description (from Sutton *et al.* 1996): Foliicolous, associated with lesions. *Mycelium* internal, brown, branched, septate. *Conidiomata* separate, acervular to sporodochial, epidermal to subepidermal, composed of brown *textura angularis* at the base, and *textura prismatica* above. *Conidiophores* brown, verruculose, irregularly branched at the base, septate, cylindrical, formed from the upper cells of the conidiomata. *Conidiogenous cells* integrated, terminal or lateral, smooth or verruculose, brown, cylindrical, straight, proliferating percurrently and enteroblastically to form annellations or sympodially and holoblastically; conidiogenous loci dark and thickened. *Conidia* holoblastic, pale brown, smooth, cylindrical, septate, obtuse at the apex and truncate at the base; basal scar dark and thickened.

Type species: *Quasiphloeospora saximontanensis* (Deighton) B. Sutton *et al.* (≡ *Cercospora saximontanensis* Deighton) [**USA**, Wyoming, Grand Tehon National Park, on leaves of *Ribes viscosissimum*, 16 Aug. 1937, W.G. & R. Solheim & H.F. House 5369, Solh., Mycofl. Saximon. Exs. 1191 (**holotype** IMI 98069, isotypes Solh., Mycofl. Saximon. Exs. 1191, e.g. BPI 762561, PUL 25574).

Descriptions and illustrations: Sutton *et al.* (1996), Seifert *et al.* (2011).

Notes: *Quasiphloeospora* is a cercosporoid genus with intricate morphology and complex morphological relations to several other genera, including *Cercospora*, *Passalora* and *Pseudocercospora* (Crous & Braun 2003), but due to very pale, almost hyaline structures, it is also similar to *Pseudocercosporella*. Sutton *et al.* (1996) classified the conidiomata as acervuli, although they may better be referred to as sporodochia. The particular characters of *Quasiphloeospora saximontanensis*, above all the structure of the conidiogenous loci, are intermediate between the three similar genera cited above. A clear affiliation to one of these genera, just based on morphology, is not possible. It is also possible that this species is unrelated to any of the cercosporoid genera. Affinity and position of *Quasiphloeospora* can only be proven by means of results of molecular sequence analyses, which are, however, not yet available.

Ragnhildiana Solheim

Note: See treatment in text.

Ramularia Unger

Note: See treatment in text.

Ramichloridium Stahel ex de Hoog

Note: See treatment in text under *Zasmidium*.

Ramulariopsis Speg.

Note: See treatment in text.

Ramularisphaerella Kleb., Haupt- und Nebenfruchtformen der Ascomyzeten (Leipzig) 1: 131. 1918.

Description (from Klebahn 1918): "*Ramularisphaerella*. Konidienform *Ramularia*. Arten: *R. hieracii*, *fragariae*, *punctiformis*, *maculiformis*, *tussilaginis*" [*Ramularisphaerella*. Conidial form *Ramularia*. Species: *R. hieracii*, *fragariae*, *punctiformis*, *maculiformis*, *tussilaginis*].

Type species: *Ramularisphaerella hieracii* (Sacc. & Briard) Kleb. (≡ *Sphaerella nebulosa* var. *hieracii* Sacc. & Briard, ≡ *Mycosphaerella hieracii* (Sacc. & Briard) Jaap) [**France**, on *Hieracium* sp.].

Description and illustration: Sivanesan (1984, as *Mycosphaerella hieracii* and *Ramularia hieracii*), Braun (1998, as *Ramularia hieracii*).

Notes: Klebahn (1918) introduced *Ramularisphaerella* as new genus for a mycosphaerella-like sexual morph on *Hieracium* that he considered to be linked to *Ramularia* on hawkweed. The type specimen could not be located (Aptroot 2006), and the status of this genus remains unclear due to the absence of DNA sequence data. Jaap (1908) considered this species to be the sexual morph of *Ramularia hieracii* (Bäumler) Jaap. Klebahn (1918) has proved the connection between the ascus and conidial state. In case that this connection was correct, *Ramularisphaerella* would be a synonym of *Ramularia*.

Ramulispora Miura

Note: See treatment in text.

Rasutoria M.E. Barr, Mycotaxon 29: 501. 1987.

Description (from Barr 1987): *Ascomata* pseudothecial, globose, superficial, densely clustered on mycelium on the undersides of leaves, dark brown, with numerous hyphal appendages, brown, obtuse, septate ot not. *Asci* saccate, bitunicate, oblong, paraphysate. *Ascospores* hyaline to pale brown, obovoid, 1-septate.

Type species: *Rasutoria abietis* (Dearn.) M.E. Barr (≡ *Dimerosporium abietis* Dearn.) [**USA**, Washington, on needles of *Abies amabilis* (**holotype** BPI 691065)].

Illustration: Farr (1963).

Notes: A very similar description was also presented by Dearness (1926), as *Dimerosporium abietis*. See treatment in text under *Zasmidium cellare*.

Rhabdospora (Durieu & Mont.) Sacc., Syll. fung. (Abellini) 3: 578. 1884.

Description (adapted from Saccardo 1884): *Pycnidia* (perithecia) subcuticular-erumpent, globose-depressed, papillate, solid, soon subhysterioid, black or brown, usually neither on spots nor on leaves. *Spores* [conidia] bacilliform or filiform, pluriguttulate or pluriseptate, hyaline. 'Basidia' diverse or lacking. Differs from *Septoria* like *Phoma* from *Phyllosticta*.

Type species: *Rhabdospora oleandri* (Durieu & Mont.) Sacc. (≡ *Septoria oleandri* Durieu & Mont.) [Algeria, on *Nerium oleander*].

Description and illustration: Bory de St.-Vincent & Durieu de Maisonneuve (1849).

Notes: *Rhabdospora* is a poorly known genus from which many species are currently placed in *Septoria*. The type species needs to be recollected in order to resolve its phylogenetic position (Quaedvlieg *et al.* 2013). The type specimen could not be located.

Rhachisphaerella Videira & Crous

Note: See treatment in text.

Rhopaloconidium Petr., Sydowia 6: 300. 1952.

Type species: *Rhopaloconidium asiminae* (Ellis & Morgan) Petr. (≡ *Phloeospora asiminae* Ellis & Morgan) [**USA**, Ohio, Preston, on *Asimina triloba*, H.P. Morgan 463 (**holotype** NY 01097272)] ≡ ***Pseudocercospora asiminae*** (Ellis & Morgan) U. Braun & Crous.

Description and illustration: Braun (1995, as *Miuraea asiminae*).

Notes: Braun & Crous (2008) proposed the combination of *Phloeospora asiminae* into *Pseudocercospora*. Sequence data authentic for the type species of this genus are necessary to confirm the synonymy of *Rhopaloconidium* and *Pseudocercospora.*

Rosisphaerella Videira & Crous

Note: See treatment in text.

Rosenscheldiella Theiss. & Syd., Ann. Mycol. 13: 645. 1915.

Description (adapted from Sultan *et al.* 2011): *Ascomata* globose, dark-walled. *Pseudothecia* develop on stromatic pads of globose cells with thick, dark walls that form amongst thick-walled, multi-lobed hairs on lower surface of leaves. *Hamathecium* lacking. *Asci* fissitunicate, cylindrical, 8-spored. *Ascospores* cylindrical, tapering slightly to rounded ends, 1 median septum, slightly constricted at septum, hyaline.

Type species: *Rosenscheldiella styracis* (Henn.) Theiss. & Syd. (≡ *Naemacyclus styracis* Henn.) [Brazil, São Paulo, Morro pelado, on *Styrax* sp.].

Descriptions and illustrations: Sultan *et al.* (2011).

Notes: The type species *Rosenscheldiella styracis* is only known from its sexual morph. The genus *Rosenscheldiella* is currently accepted in the *Mycosphaerellaceae* (Wijayawardene *et al.* 2014) but recollection of the type species is necessary to determine its true phylogenetic position. Two species for which there are cultures available, *Rosenscheldiella brachyglottidis*

and *Rosenscheldiella korthalsellae*, cluster in the *Mycosphaerellaceae* and are closely related to *Pseudocercospora* and *Amycosphaerella*, respectively (Sultan *et al.* 2011).

Ruptoseptoria Quaedvlieg, Verkley & Crous

Note: See treatment in text.

Scirrhia Nitschke ex Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 220. 1870 (1869–1870).

Description (from Sivanesan 1984): *Stromata* subepidermal to erumpent, elongated, depressed globose, rounded, unilocular or with locules in many rows, opening by an apical pore. The stromatic wall is composed of vertically-orientated rows of brown to reddish brown cells *of textura globosa* or *angularis* and *textura prismatica* between locules; the outermost layers composed of black to dark brown cells and the cells of the inner layers brown to hyaline. *Asci* oblong or clavate, 8-spored, stalked, arising from compressed hyaline tissue at the base of the locule. *Ascospores* biseriate overlapping in the ascus, hyaline or yellowish, elliptic or obovoid, septate near the middle, not or slightly constricted at the septum, straight or often inequilateral, smooth, sometimes guttulate. *Interthecial tissue* compressed between asci and intact over the asci.

Type species: *Scirrhia rimosa* (Alb. & Schwein.) Fuckel (≡ *Sphaeria rimosa* Alb. & Schwein.) [**Germany**, Lusatia (Lausitz), on stems of *Phragmites australis*].

Notes: *Scirrhia rimosa* is presently not known from available collections. *Scirrhia aspidiorum* (CBS 204.66) clusters in the *Didymellaceae*, while *Scirrhia brasiliensis* (CBS 128762) clusters in *Mycosphaerellaceae* (Crous *et al.* 2011b). The status of purported synonyms of *Scirrhia*, namely *Scirrhodothis*, *Scirrhophragma* and *Metameris* also remains unresolved.

Scolecostigmina U. Braun

Note: See treatment in text.

Semipseudocercospora J.M. Yen, Mycotaxon 17: 361. 1983.

Description (from Braun *et al.* 2013): Morphologically close to *Pseudocercospora* (leaf spotting hyphomycetes with unthickened, not darkened conidiogenous loci and hila), but the conidiogenous cells are not geniculate, i.e. not distinctly sympodially proliferating, the conidiogenous loci are distinctly denticle-like, and the solitary conidia are didymo- to phragmosporous, i.e. not scolecosporous.

Type species: *Semipseudocercospora peristrophes-acuminatae* (J.M. Yen) J.M. Yen (≡ *Cercospora peristrophes-acuminatae* J.M. Yen).

Description and illustrations: Yen (1983), Seifert *et al.* (2011), present study (Fig. 64).

Materials examined: **Singapore**, Katung, on *Peristropha acuminata*, 20 Apr. 1964, Sun No. 20 (**holotype** PC; isotype IMI 122324).

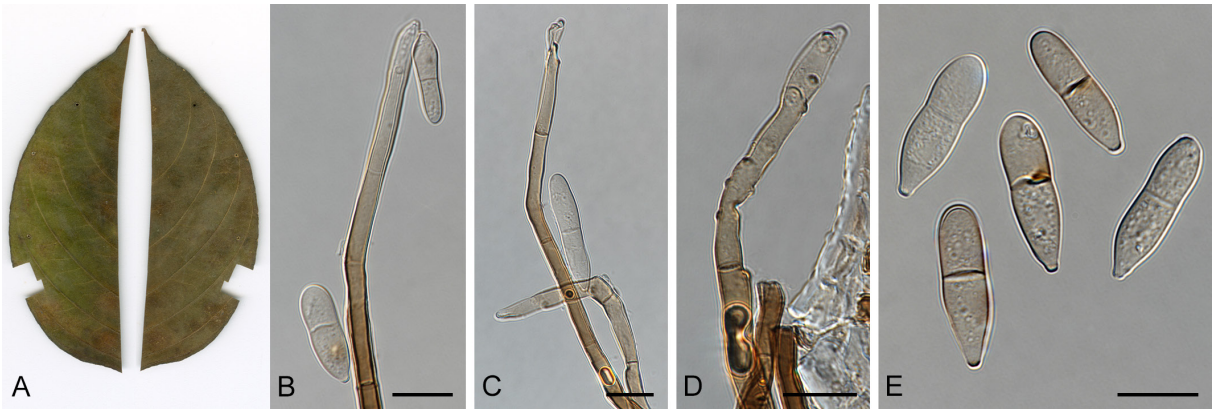


Fig. 64. *Semipseudocercospora peristrophes-acuminatae* (IMI 122324). A–E. Observations *in vivo*. A. Leaf spot symptoms on the host. B–D. Partial conidiophore, conidiogenous cells and conidia. E. Single conidia. Scale bars = 10 μm.

Notes: The phylogenetic position of the type species of this genus and its relation to the *Mycosphaerellaceae* as well as to the genus *Pseudocercospora* are still unknown and unproven. Therefore, *Semipseudocercospora* is tentatively maintained as a separate cercosporoid genus.

Septocylindrium Bonord. ex Sacc., Michelia 2: 15. 1880.

Type species: *Septocylindrium bonordenii* Sacc., *nom. illegit*., Art. 52.1 [**Italy**, Padova, on *Galanthus nivalis*, Apr. 1876, Sacc., Mycoth. Ven. 1050 (**neotype** HAL)] = ***Ramularia septata*** (Bonord.) Bubák.

Description and illustration: Braun (1998, as *Ramularia septata*).

Notes: *Septocylindrium* is currently accepted as a synonym of *Ramularia* (Braun 1998, Videira *et al.* 2016). However, no DNA sequences are available of the type species and that assumption, therefore needs to be re-evaluated.

Septocyta Petr., Ann. Mycol. 25(3/4): 330. 1927.

Description (from Quaedvlieg *et al.* 2013, adapted from Sutton 1980): *Mycelium* immersed, branched, septate, hyaline to pale brown. *Conidiomata* eustromatic, immersed, separate, erumpent, dark brown to black, finally opening widely, unilocular, multilocular or convoluted, thick-walled; wall of pale brown, thin-walled *textura angularis* except in the dehiscent region which is darker brown and more thick-walled. *Ostiole* absent, dehiscence by breakdown of the upper wall. *Conidiogenous cells* are holoblastic, sympodial with 1–3 apical, scarcely protruding, unthickened denticles, indeterminate, discrete, ampulliform to lageniform, hyaline, smooth, formed from the inner cells of the locular walls. *Conidia* hyaline, 1–3 euseptate, smooth, straight or slightly curved, acicular, apex obtuse, base truncate, often with minute guttules associated with septa.

Type species: *Septocyta ramealis* (Roberge ex Desm.) Petr. (≡ *Septoria ramealis* Roberge ex Desm.) [**Europe**, on stems of *Rubus* spp.]

Description and illustration: Quaedvlieg *et al.* (2013).

Notes: The type specimen could not be traced. See Quaedvlieg *et al.* (2013).

Septopatella Petr., Ann. Mycol. 23(1/2): 128. 1925.

Description (from Quaedvlieg *et al.* 2013, adapted from Dyko & Sutton 1979 and Sutton 1980): *Mycelium* immersed, branched, septate, hyaline to subhyaline. *Conidiomata* superficial, often subtended by a superficial, pale brown, septate, branched mycelium, pulvinate, separate to occasionally aggregated, dark brown to black, finally opening widely, cupulate; basal wall of small-celled, brown, thin-walled *textura angularis*, becoming *textura porrecta* as it merges into the periclinal walls; a hypostroma attaches the conidioma to the substrate; *Ostiole* absent. *Conidiophores hyaline*, septate, branched at the base, thin-walled, cylindrical, formed from the gelatinized basal wall of the conidioma. *Conidiogenous cells* holoblastic, sympodial, integrated, indeterminate, cylindrical, hyaline, smooth, produced as 2–3 branches from the apex of the conidiophores. *Conidia hyaline*, 3–4-euseptate, thin-walled, smooth, minutely guttulate, straight or curved, occasionally irregularly filiform (Dyko & Sutton 1979, Sutton 1980).

Type species: *Septopatella septata* (Jaap) Petr. (≡ *Pseudocenangium septatum* Jaap) [**Austria**, *Pinus montana*, 31 Jul. 1907, O. Jaap (**holotype** BPI 393484; **isotype** IMI 225733, slide)].

Description and illustration: Quaedvlieg *et al.* (2013)

Notes: The present species needs to be recollected and its phylogenetic position determined. The holotype specimen could not be traced. See Quaedvlieg *et al.* (2013).

Septoria Sacc.

Note: See treatment in text.

Septoriopsis Gonz. Frag. & M.J. Paúl, Bol. Real Soc. Esp. Hist. Nat. 15: 127. 1915.

Description (adapted from Saccardo *et al.* 1931): *Pycnidia* on leaf spots, superficial, membraneous-carbonaceous, usually caespitose, globose to conoid. *Spores* [conidia] bacilliform, hyaline, usually 1-septate, formed at the apex of filiform conidiophores.

Type species: *Septoriopsis citri* Gonz. Frag. [**Spain**, Sevilla, Huevar, on *Citrus vulgaris*, M. de Paul].

Description and illustration: González Fragoso (1915).

Note: Seen as synonym of *Septoria*, though fresh collections are required to resolve its phylogenetic position.

Septorisphaerella Kleb., Haupt- und Nebenfruchtformen der Ascomyzeten (Leipzig) 1: 131. 1918.

Description (from Klebahn 1918): "*Septorisphaerella*. Konidien- form *Septoria* oder *Phloeospora*. Arten: *S. hippocastani*, *populi*, *ribis*, *sentina*, *ulmi*, *aegopodii*, *exitialis*, *jaczewskii*, *lathyri*, *nigerristigma*" [*Ramularisphaerella*. Conidial form *Septoria* or *Phloeospora*. Species: *S. hippocastani*, *populi*, *ribis*, *sentina*, *ulmi*, *aegopodii*, *exitialis*, *jaczewskii*, *lathyri*, *nigerristigma*].

Type species: *Septorisphaerella hippocastani* (Jaap) Kleb. (≡ *Sphaerella maculiformis* var. *hippocastani* Jaap), [**Germany**, Brandenburg, Prignitz, Triglitz, on *Aesculus hippocastanum*, Mar. 1910, O. Jaap, Fungi Sel. Exs. 423 (**syntypes** Jaap, Fungi Sel. Exs. 423, e.g. B, HAL, L)] = *Mycosphaerella hippocastani* Jaap.

Description and illustration: Klebahn (1918).

Notes: Klebahn (1918) introduced *Septorisphaerella* as genus for sexual mycosphaerella-like morphs associated with septoria-like asexual morphs. *Septorisphaerella hippocastani*, the type species, was linked to a *Septoria* on *Aesculus* which was nomenclaturally discussed in detail, with the conclusion to refer to it as '*Septoria aesculicola* (Fr.) Fuckel' (including *Septorisphaerella hippocastani* Berk. & Broome, see Klebahn 1918: 45). Fresh material of the type species needs to be recollected to resolve the phylogenetic position of this genus, above all since *Septoria s. lat.* has recently been split into several genera (see Verkeley *et al.* 2013).

Sirosporium Bubák & Serebrian., Hedwigia 52: 273. 1912.

Description (from Braun *et al.* 2013): Leaf spotting dematiaceous hyphomycetes with internal and external mycelium, superficial hyphae giving rise to solitary conidiophores, lateral and terminal, conidiophores may also be formed in fascicles, conspicuous conidiogenous loci and hila, thickened and darkened, conidia solitary, size, shape and septation variable, but the conidia are relatively thick-walled and at least partly dictyosporous.

Type species: *Sirosporium antenniforme* (Berk. & M.A. Curtis) Bubák & Serebrian.

Descriptions and illustrations: Ellis (1971), Seifert *et al.* (2011); present study (Fig. 65).

Materials examined: **USA**, Alabama, on leaves of *Celtis* (microscope slide **ex-type** of *Macrosporium antenniforme*, IMI 1253).

Notes: The genus *Sirosporium* is passalora-like in morphology, but until the type species *S. antenniforme* has been recollected and its phylogenetic position resolved, its status remains unresolved. *Sirosporium* has been tentatively treated as a separate genus confined to species with thick-walled dictyosporous conidia (Braun 1995, Crous & Braun 2003, Braun *et al.* 2013). The two *Sirosporium* species included in this study cluster within the *Mycosphaerellaceae* but in separate clades, *Sirosporium celtidis* (Fig. 1, clade 39; Fig. 3, clade 4) and *Sirosporium diffusum* (Fig. 1; clade 60; Fig. 3, clade 24, as *Ragnhildiana diffusa*).

Sonderhenia H.J. Swart & J. Walker

Note: See treatment in text.

Fig. 65. *Sirosporium antenniforme* (IMI 1253). A–F. Observations *in vivo*. A, B. Conidiophores emerging from the host leaf. C–F. Conidia. Scale bars = 10 µm.

Sphaerellothecium Zopf, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 70: 184. 1897.

Description (adapted from Roux & Triebel 1994 and Knudsen *et al.* 2009): Lichenicolous, usually distinguished by the formation of a superficial reticulum of dark hyphae occurring on the thallus and apothecia of the host. *Ascomata* perithecioid, black, immersed to superficial, ostiolate, wall pigmented, hamathecium of unbranched periphyses, but often rudimentary, with colourless interascal filaments (paraphysoids). *Asci* bitunicate, fissitunicate, 8-spored, clavate, ellipsoid-ovoid, obpyriform, saccate to irregular, with distinct ocular chamber. *Ascospores* hyaline, sometimes turning brown when mature, 1–3(–5)-septate, smooth-walled.

Type species: *Sphaerellothecium araneosum* (Rehm) Zopf (≡ *Sphaerella araneosa* Rehm) [**Austria**, Tirol, oberhalb der Waldrast (Mattrei), on *Ochrolechia tartarea*, Aug. 1872, Arnold, ex Herb. Rehm. Ascomyc. nr. 133 (syntype S F45258, designated here as **lectotype** MBT378595)].

Description: Vouaux (1913, as *Discothecium araneosum*).

Note: The type species is lichenicholous and, in the absence of DNA, its phylogenetic position remains obscure.

Sphaerulina Sacc.

Note: See treatment in text.

Spilosphaeria Rabenh., Klotzschii Herb. Viv. Mycol., Ed. Nov., Ser. Prima, Cent. 6: no. 559. 1857.

Type species: Not indicated (Rabenhorst assigned eight species to the new genus *Spilosphaeria* in Cent. 6 of this exsiccatum).

Notes: This genus is insufficiently known, but regarded as synonym of *Septoria* based on morphology. The status of *Spilosphaeria* needs to be clarified by lectotypification of the genus and recollection of a lectotype species to determine the phylogenetic position of the genus.

Stenella Syd., Ann. Mycol. 28(1–2): 205. 1930.

Type species: *Stenella araguata* Syd. [**Venezuela**, Aragua, La Victoria, on leaves of *Pithecellobium lanceolatum*, Jan. 1928, H. Sydow (**lectotype**, designated in Crous *et al.* 2007b, IMI 15728a; isolectotypes BPI 443420, 443422, S F64888; syntypes Syd., Fungi Exot. Exs. 883, e.g. CUP, MICH 13093, S F64890, Petr., Mycoth. Gen. 1399, e.g. S F64889)].

Description and illustration: Crous *et al.* (2007b).

Note: Currently assigned to *Teratosphaeriaceae* (Crous *et al.* 2007b, Arzanlou *et al.* 2008, Crous *et al.* 2009d).

Stenospora Deighton, Mycol. Pap. 118: 22. 1969.

Description (from Deighton 1969): *Mycelium* hyperparasitic: hyphae colourless, septate. *Conidiophores* arising as lateral branches of the mycelial hyphae, short, smooth, simple or branched, septate, with conidial scars very slightly but distinctly thickened and refractive and slightly prominent. *Conidia* colourless, acicular, much resembling those of *Cercospora*, smooth, pluriseptate, with a very slightly but distinctly thickened and refractive truncate hilum.

Type species: *Stenospora uredinicola* Deighton [**Sierra Leone**, Bundulai (Loko Masama), on *Puccinia kraussiana* on *Smilax anceps* (= *S. kraussiana*), 26 Nov. 1951, F.C. Deighton M4515 (**holotype** IMI 48655b)].

Description and illustration: Deighton (1969).

Note: *Stenospora* is very similar to *Eriocercospora* but mucedinaceous (hyaline).

Stenellopsis B. Huguenin, Bull. Trimestriel Soc. Mycol. France 81: 695. 1966.

Description (from Ellis 1971): *Colonies* effuse, greyish olive, hairy. *Mycelium* immersed. *Stroma* rudimentary or prosenchymatous, immersed. *Setae* and *hyphopodia* absent. *Conidiophores* macronematous, mononematous, caespitose, unbranched, usually rather short, straight or flexuous, olivaceous, smooth or verruculose. *Conidiogenous cells* polyblastic, integrated, terminal, sympodial, cylindrical, cicatrized; scars broad, flat. *Conidia* solitary, dry, acropleurogenous, simple, cylindrical to obclavate, rounded at the apex, truncate at the base, pale olivaceous brown, verrucose, multiseptate.

Type species: *Stenellopsis fagraeae* Huguenin.

Descriptions and illustrations: Ellis (1971), Seifert *et al.* (2011); present study (Fig. 66).

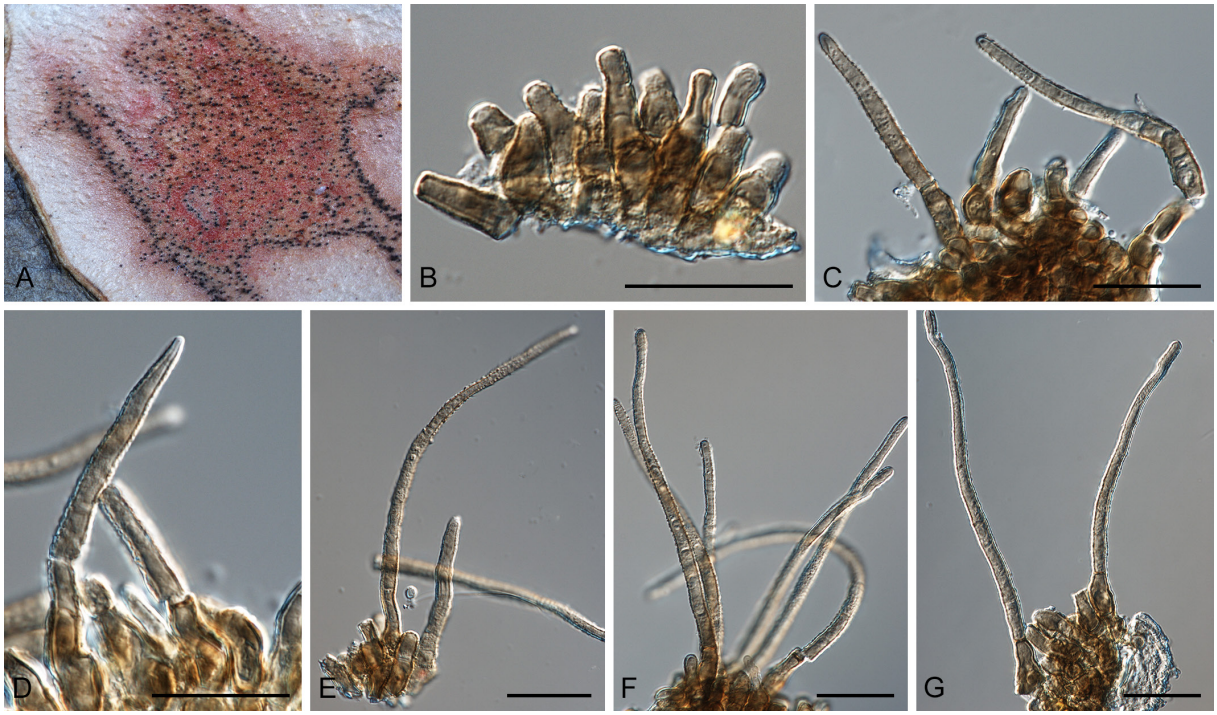


Fig. 66. *Stenellopsis fragariae* (PDD 75945). A–G. Observations *in vivo*. A. Leaf spot symptoms on the host. B. Conidiophores. C–G. Conidiophores, conidiogenous cells and conidia. Scale bars = 10 µm.

Materials examined: **Cook Islands**, Rarotonga, Takitumu Conservation Area, on *Fagraea berteroana*, 14 Jul. 2002, E.H.C. McKenzie EHCM 284 (PDD 75945); Rarotonga, Totokoitu Valley, 19 Oct. 1975, J.M. Dingley (PDD 35381). **New Caledonia**, Rivière de Thi (St. Louis), on *Fagraea berteroana* (= *F. schlechteri*), 24 Nov. 1963, Huguenin, NC 63219 (**holotype** PC).

Notes: *Stenellopsis* is morphologically similar to *Zasmidium*. It has single, conspicuously verrucose conidia with hila that are barely to slightly thickened and somewhat darkened-refractive, but lacks verruculose superficial hyphae (Crous & Braun 2003). The type species needs to be recollected to resolve the phylogenetic position of the genus.

Stictosepta Petr., Sydowia 17: 230. 1964 (1963).

Description (from Quaedvlieg *et al.* 2013, adapted from Sutton 1980): *Mycelium* immersed, branched, septate, hyaline. *Conidiomata* eustromatic, immersed, globose to collabent, papillate, unilocular, often convoluted, hyaline; walls thick, of hyaline, thin-walled *textura intricata*. *Ostiole* central and circular, single, furfuraceous. *Conidiophores* hyaline, septate, branched, anastomosing, formed from the inner cells of the locular wall. *Conidiogenous cells* sympodial or synchronous, integrated, indeterminate, hyaline, thin-walled, with usually two small, unthickened, apical, slightly protuberant conidiogenous loci. *Conidia* solitary, hyaline, thin-walled, smooth, multiseptate, slightly constricted at the septa, each cell medianly guttulate, straight or curved, base truncate, apex obtuse.

Type species: *Stictosepta cupularis* Petr. [**Czech Republic**, Hranice, Ribar, *Fraxinus*, 30 Mar. 1927, F. Petrak (syntype BPI 668877, designated here as **lectotype** MBT378596; syntype IMI 204093 [slide])].

Illustration: Quaedvlieg *et al.* (2013).

Note: This species needs to be recollected to resolve its phylogenetic position.

Stigmidium Trevis., Conspect. Verruc.: 17. 1860.

Description (adapted from Roux & Triebel 1994): *Vegetative hyphae* absent. *Ascomata* perithecioid, black, globose to subglobose, ostiolate, usually half-immersed to sessile. *Ascomatal wall* dark brownish black in upper part, paler brown in middle or lower part. *Periphysoids* originating from the upper wall of the ascomatal cavity, hyaline, branched or not. *Interascal filaments* lacking. *Asci* originating from the lower wall of the ascomatal cavity, fissitunicate, saccate, 8-spored, with ascospores irregularly arranged. *Ascospores* 1-septate, hyaline, but occasionally turning brown when overmature.

Type species: *Stigmidium schaereri* (A. Massal.) Trevis. (≡ *Sphaeria schaereri* A. Massal.) [**Italy**, on thalli of *Solorina* spp.].

Description and illustration: Roux & Triebel (1994).

Notes: The genus *Stigmidium* is distinguished by ascomata with punctiform ostioles with a hamathecium of periphyses, with periphysoids, and hyaline 1-septate ascospores (rarely turning brown in a few species). The type species is lichenicolous and until DNA data have been generated, the phylogenetic position of the genus remains unresolved.

Stigmina Sacc., Michelia 2: 22. 1880.

Type species: *Stigmina platani* (Fuckel) Sacc. (≡ *Stigmella platani* Fuckel) [**Greece**, Attikis, Kifisia, on *Platanus orientalis*, 7 Nov. 1869, Th. de Heldreich (syntype BPI 428005, designated here as **lectotype**, MBT378597] ≡ ***Pseudocercospora platanigena*** Videira & Crous, **nom. nov.** MycoBank MB822835. *Replaced synonym*: *Stigmella platani* Fuckel, in Thümen, Bot. Zeitung (Berlin). 29: 27. 1871, non *Pseudocercospora platani* (J.M. Yen) J.M. Yen, 1979.

Description and illustration: Ellis (1971).

Note: *Stigmina* is a synonym of *Pseudocercospora* (Braun & Crous 2006, Crous *et al.* 2006a) and a new name is herewith introduced for *Stigmina platani*.

Stromatoseptoria Quaedvlieg, Verkley & Crous

Note: See treatment in text.

Sultanimyces Videira & Crous

Note: See treatment in text.

Tandonella S.S. Prasad & R.A.B. Verma, Indian Phytopathol. 23: 112. 1970.

Description (from Sutton & Pascoe 1987): *Mycelium in vivo* immersed and superficial, subhyaline to pigmented, branched, septate, thin-walled. *Stromata* superficial, small, brown, pseudoparenchymatic. *Conidiomata* synnematous, synnemata composed of parallel threads, determinate, solitary or grouped, erect, brown, apically lax, splaying out. *Individual conidiophores* filiform, usualy unbranched, septate, pigmented, smooth to rough-walled; *conidiogenous* cells integrated, terminal or intercalary (conidiogenous region terminal, rarely lateral or extending down the synnemata), proliferation sympodial, geniculate, cicatrized, conidiogenous loci conspicuous, slightly thickened, darkened-refractive, often protuberant. *Conidia* holoblastically formed, catenate, in short simple or branched chains, ellipsoid-ovoid, fusiform, cylindrical, aseptate to euseptate, pigmented, rough-walled, hila somewhat thickened and darkened-refractive.

Type species: *Tandonella ziziphi* S.S. Prasad & R.A.B. Verma [**India**, Bihar, on leaves of *Ziziphus jujuba* (**holotype** IMI 112255c as *Cercospora ziziphi*)] ≡ *Passalora ziziphi* (S.S. Prasad & R.A.B. Verma) U. Braun & Crous.

Description and illustration: Sutton & Pascoe (1987).

Notes: *Tandonella* has currently been treated as a synonym of *Passalora* (Crous & Braun 2003, Braun *et al.* 2013), but the type species *Tandonella ziziphi* is not known from DNA data. Sutton & Pascoe (1987) added *Tandonella oleariae*, re-examined and illustrated holotype material of *Tandonella ziziphi* [IMI 112255c], and published an emended description of the genus *Tandonella*, which is characterised by a combination of synnematous conidiomata and conspicuous conidiogenous loci (thickened and darkened) giving rise to catenate, pigmented conidia (phaeoramularioid). The species *Tandonella cubensis* was described by Castañeda & Kendrick (1990) and the holotype was collected from *Bauhinia divaricata* in Cuba [INIFAT C88/58 (13. IV.1988)]. The strain in this study was collected by the same author from *Bauhinia cuyabensis* in Cuba and was deposited at the CBS [CBS 500.92, INIFAT C92/43-3 (Nov. 1992), CBS H-18755). The morphology of *Tandonella cubensis* varied from *Tandonella ziziphi* mainly in the falcate, lunate or irregular and smooth conidia instead of cylindrical to fusiform and verrucose conidia. Morphologically, *Tandonella cubensis* (CBS 500.92) differs significantly from *Pseudocercospora* spp. by the formation of long synnematous fascicles, dark brown at the base and brown above, brown, polyblastic conidiogenous cells and brown, falcate conidia developing in chains. In all phylogenetic analyses performed in this study, this strain clustered within *Pseudocercospora*.

Tapeinosporium Bonord., Bot. Zeitung (Berlin) 11: 285. 1853.

Description (from Bonorden 1853): Conidial chains multiseptate, arising from aseptate, simple or sometimes branched "stalks" [*conidiophores*]. *Spores* [conidia] ovate, 3-septate, greenish, caespitose conidial chains olivaceous or later black.

Type species: *Tapeinosporium viride* Bonord. [**Germany**, on *Solanum tuberosum* (**lectotype** [iconotype] designated here, MBT378598, Bonorden, Bot. Zeitung (Berlin) 11: Pl. (Tafel) VII, Fig. 6. 1853)] ≡ *Septocylindrium tapeinosporum* (Bonord.) Sacc.

Description and illustration: Bonorden (1853).

Notes: Saccardo (1886) considered *Tapeinosporium* a synonym of *Septocylindrium*, which in turn is considered a synonym of *Ramularia* (Braun 1998, Videira *et al.* 2016), but as emphasized in Braun (1998: 13) *Tapeinosporium*, described from potato tubers, is a doubtful genus of quite unclear affinity. Type material is not preserved, but Bornorden added an illustration to the original description, which is part of the protologue and has to be used for lectotypification. This illustration does not agree with genuine *Ramularia* species and could rather pertain to *Cladosporium* or similar saprobic hyphomycetous genera. New collections from potato tubers are necessary for an epitypification of *Tapeinosporium viride* and corresponding sequence data for a clarification of its phylogenetic affinity.

Trochophora R.T. Moore

Note: See treatment in text.

Utrechtiana Crous & Quaedvlieg, Persoonia 26: 153. 2011.

Description (from Crous *et al.* 2011a): Hyphomycetous, associated with leaf spots. *Mycelium* internal, consisting of septate, smooth, hyaline, branched hyphae. *Conidiophores* solitary, erect, bursting through epidermis, with circular scar where base of conidiophore is attached to immersed hyphal network; conidiophores dark brown, erect, base subglobose, giving rise to a subcylindrical, brown conidiogenous cell that ends in a clavate, bluntly rounded apex, with truncate, flattened scar; sometimes thickened, not darkened, nor refractive. *Conidia* solitary, pale brown, ellipsoid, guttulate to granular, smooth to finely verruculose, 1-septate slightly above the conidial median, thin-walled, apex bluntly to acutely rounded, base obtusely rounded with a flattened, darkened and thickened hilum that has a central pore.

Type species: *Utrechtiana cibiessia* Crous & Quaedvlieg [**Netherlands**, Utrecht, on leaves of *Phragmites australis*, 14 Dec. 2010, W. Quaedvlieg (**holotype** CBS H-20594, cultures ex-type CPC 18917, 18916 = CBS 128780)] = *Utrechtiana roumeguerei* (Cavara) Videira & Crous [**France**, Toulouse, on *Phragmites australis*, undated, coll. C. Roumeguère, Biosi & Cavara, **syntypes** of *Scolicotrichum roumeguerei* Briosi & Cavara, Funghi Parass. Piante Colt. Util. Ess. 112 (**lectotype** in HAL here designated, MBT378701)].

Utrechtiana roumeguerei (Cavara) Videira & Crous, **comb. nov.** MycoBank MB822836.
Basionym: *Scolicotrichum roumeguerei* Cavara (as '*roumegueri*'), in Briosi & Cavara, Funghi Parass. Piante Colt. Util. Ess., Fasc. 5: no. 112. 1890.
Synonyms: *Deightoniella roumeguerei* (Cavara) Constant., Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 86(2): 137. 1983.
Utrechtiana cibiessia Crous & Quaedvl., Persoonia 26: 153. 2011.

Notes: The genus *Utrechtiana* was regarded as synonymous with *Deightoniella* by Seifert *et al.* (2011) based on morphology. The type species, *Utrechtiana cibiessia*, is synonymous with *Deightoniella roumeguerei*, which Klaubauf *et al.* (2014) showed to belong to *Pyriculariaceae*, a family containing numerous cryptic fungal genera on *Poaceae*. An examination of the type species of *Deightoniella*, *Deightoniella africana*, has shown, however, that *Deightoniella*

is also a generic complex in *Pyriculariaceae*, meaning that the generic circumscription provided by Ellis (1976) needs to be emended. *Deightoniella torulosa*, a foliar pathogen of *Musa*, has been shown to be a species of *Corynespora* (Crous *et al.* 2013b). A similar fungus occurring on leaf spots of *Phragmites* in South Africa, was shown to represent a distinct genus, *Neodeightoniella*, which lacks conidiophores with percurrent rejuvenation, has well-developed apical and intercalary conidiogenous loci, and conidia with mucoid caps (Crous *et al.* 2013b). The genus *Deightoniella* (based on *Deightoniella africana*), is distinct from *Utrechtiana*, as the latter lacks torsive to flexuous conidiophores with percurrent rejuvenation and prominent conidiophore swellings. Conidia of *Utrechtiana* are also very pale brown, smooth to finely roughened, with prominent thickened, darkened scars, while those of *Deightoniella* are medium brown, verruculose, and obpyriform with prominent apical taper. Fresh material of *Deightoniella africana* needs to be recollected to facilitate epitypification, and to clarify its phylogenetic relationships.

Uwemyces Hern.-Restr., G.A. Sarria & Crous

Note: See treatment in text.

Verrucisporota D.E. Shaw & Alcorn

Note: See treatment in text under *Zasmidium*.

Virgasporium Cooke, Grevillea 3(28): 182. 1875.

Type species: *Virgasporium maculatum* Cooke [**Jersey** (UK), on leaves of *Reseda* sp.] = ***Cercospora resedae*** Fuckel [**Germany**, on leaves of *Reseda odorata*, Fuckel, Fungi Rhen. Exs. nr. 1632 (**syntype** S F267614)

Description and illustration: Cooke (1875).

Note: *Virgasporium* is currently considered a synonym of *Cercospora* based on morphological characteristics (Braun *et al.* 2013). The type specimen of *Virgasporium maculatum* could not be traced and the species needs to be recollected in order to confirm its phylogenetic position. A tentative clade of *Cercospora* cf. *resedae* is considered in a recent phylogenetic study by Groenewald *et al.* (2013).

Virosphaerella Videira & Crous

Note: See treatment in text.

Walkeromyces Thaung, Trans. Brit. Mycol. Soc. 66: 213. 1976.

Description (from Thaung 1976): Hyphomycetous, foliicolous, phytopathogenic. *Stroma*, setae and hyphopodia absent. *Mycelium* superficial, consisting of brown, branched, septate, creeping hyphae. *Conidiophores* simple or branched, medium brown, arising from superficial mycelium, straight to flexuous, with intergrated terminal conidiogenous cells. *Conidiogenous cells* polyblastic, terminal, sympodial, with thickened, darkened scars. *Conidia* dry, solitary,

acropleurogenous, straight or curved, obclavate or fusiform or short navicular, septate, smooth, brown, with thickened, darkened hilum.

Type species: *Walkeromyces grewiae* Thaung [**Myanmar**, Maymyo, Kyaukchaw, on *Grewia* cf. *macrophylla*, 26 Sep. 1974, M.M. Thaung (**holotype** IMI 188948)].

Description and illustration: Thaung (1976).

Notes: *Walkeromyces* is mycovellosiella-like in morphology, and has been treated as synonym of *Passalora* in the past (Crous & Braun 2003). However, until the type species has been recollected and subjected to molecular comparison, its phylogenetic position remains unknown.

Xenomycosphaerella Quaedvlieg & Crous

Note: See treatment in text.

Xenoramularia Videira, H.D. Shin & Crous

Note: See treatment in text.

Xenosonderhenia Crous

Note: See treatment in text.

Xenosonderhenioides Videira & Crous.

Note: See treatment in text.

Zasmidium Fr.

Note: See treatment in text.

Zymoseptoria Quaedvlieg & Crous

Note: See treatment in text.

DISCUSSION

The *Mycosphaerellaceae* Lindau (1897), based on *Mycosphaerella* Johanson (1884) has an intricate taxonomic history spread over many years and numerous publications. From the traditional morphological approaches, to the more recent phylogenetic and genomics studies, species of *Mycosphaerellaceae* remain as popular among mycologists, due to their morphological diversity, and as infamous among phytopathologists due to the destructive impact some species have on crops that we depend on for food, feed and fuel.

Traditional identification relies on morphological characters in association with the host. The morphology of the sexual morph of *Mycosphaerellaceae* is extremely uniform and descriptions are mainly based on ascospores size, shape and position of the septa (Aptroot 2006). Believing

most species to be host-specific, numerous species were described multiple times under different names only based on the hosts they were isolated from, or their countries of origin. Arx (1949) was the first to compare these morphological descriptions and synonymise many species in the genus, a task later continued by Tomilin (1979). Barr (1972) introduced a system of sections to treat the species which was partially followed and improved upon by Aptroot (2006), who provided the most recent revision of *Mycosphaerella* species based on the study of type material. Many of these specimens contained only immature or over mature material with no ascospores, rendering many species doubtful. As a consequence, only 3000 taxa were estimated to exist in *Mycosphaerella* out of the total 10000 names (Aptroot 2006), excluding names of thousands of asexual species. The germination pattern of the ascospores was introduced as new character by Park & Keane (1982a, b), and was followed by other authors as a diagnostic feature in species recognition (Crous 1998). The morphology of the asexual morphs, on the other hand, is quite distinctive and variable, and many species in the family are also polymorphic.

Two informal asexual taxonomic groups are recognized in *Mycosphaerellaceae*, namely the hyphomycetes, which produce solitary conidiophores, fascicles or sporodochia, and the coelomycetes, which produce acervuli or pycnidial conidiomata. The coelomycete genera were largely treated by Sutton (1980) and, to a lesser degree, by Nag Raj (1993). The hyphomycetes, however, have been the subject of several monographs. Chupp (1954) and Pollack (1987) took a wide approach and described all cercosporoid fungi in the genus *Cercospora*. Deighton (1967, 1974, 1976a, 1979) recognised several genera amid the large *Cercospora* concept, and was succeeded by Crous & Braun (2003) who narrowed down the true cercosporoid fungi to *Cercospora*, *Pseudocercospora*, *Stenella* and *Passalora*. The hyaline counterparts of *Cercospora*, including *Ramularia* and allied genera, were treated by Braun (1995, 1998). The separation of these genera relied on the presence or absence of pigmentation in the conidiogenous structures, arrangement and branching of conidiophores, the conidiogenous cell placement, proliferation and scar type (conidiogenous loci), and conidial formation, shape and septation. Particular emphasis was placed on the nature of the conidiogenous loci and mode of conidiogenesis. However, many difficulties surrounded the definition of these genera based on these characters including intermediate characters, and species that exhibited more than one mode of conidiogenesis (Crous & Braun 2003). Due to the impact of many of these species on agriculture and forestry, many revisions of cercosporoid species have been published based on country or geographical region, e.g. Japan (Katsuki 1965), Taiwan (Hsieh & Goh 1990), China (Guo & Hsieh 1995), South Africa (Crous & Braun, 1996), Russia (Braun & Mel'nik, 1997), Korea (Shin & Kim 2001), India (Kamal 2010), etc. However, the circumscription of genera was not questioned at the time and authors mainly followed the works of Chupp (1954), Deighton (1967, 1974, 1976a, 1979), Braun (1995, 1998) and Crous & Braun (2003).

Since the first DNA phylogeny paper published on the family (Stewart *et al.* 1999), the concept of *Mycosphaerellaceae* and the genera it contains has been significantly revised (Crous *et al.* 2007a, b, 2009a, c, d, e, 2013a, Quaedvlieg *et al.* 2011, 2013, 2014, Verkley *et al.* 2013, Groenewald *et al.* 2013, Videira *et al.* 2015a, b, 2016). The most significant fact was the realisation that *Mycosphaerellaceae* was poly- and paraphyletic in the *Dothideomycetes*, and that the same variation also applied to the genera and species. The second milestone was the proof that *Mycosphaerella* was not the sexual morph of 40 odd genera as formerly believed (Crous 2009), but that these were in fact distinct genera within the *Dothideomycetes*, for which the names of the asexual genera were available for use.

The widespread use of DNA sequences as an identification tool fuelled an idea that was simmering for a long time among mycologists and plant pathologists alike, namely that dual

nomenclature in fungi is superfluous. In its wake came the one fungus = one name initiative, which culminated in the termination of the dual nomenclature system (Hawksworth *et al.* 2011, Hawksworth 2012, Wingfield *et al.* 2012, Crous *et al.* 2015b). Based on the newly revised International Code of Nomenclature for algae, fungi, and plants (ICN), the asexual morph *Ramularia* was chosen over that of *Mycosphaerella* (Wijayawardene *et al.* 2014, Rossman *et al.* 2015, Videira *et al.* 2015b, 2016), and the remaining taxa assigned to existing genera or newly described genera. The ITS was introduced as the official barcode for fungi due to its ease of amplification and its ability to distinguish species across the kingdom (Schoch *et al.* 2012). Frequently, in *Mycosphaerellaceae*, the ITS is insufficient to distinguish closely related species and a combination of ITS and a secondary barcode (Stielow *et al.* 2015) has been proposed for each genus, such as *tef1*-α or *tub2* for *Septoria* and allied genera (Verkley *et al.* 2013), *rpb2* or *actA* for *Ramularia* and allied genera (Videira *et al.* 2016), *cal* and *his3* for *Cercospora* (Groenewald *et al.* 2013), *actA* and/or *tef1*-α (Crous *et al.* 2013a) or *rpb2* (Nakashima *et al.* 2016) for *Pseudocercospora*, and *rpb2* (present study) for many genera in the *Mycosphaerellaceae*. The *rpb2* gene is used to resolve higher levels of classification due to the ease of alignment as the sequence has no introns, and also to discriminate at species level due to the high variability of the sequence data. The main disadvantage of *rpb2* is that it is not always easy to amplify. In this regard, the primer RPB2-F4 was revealed to be very effective among numerous genera. Although the coding genes frequently have a higher discriminatory power between species, there are usually less available data in the public databases to compare them to (Quaedvlieg *et al.* 2013). However, this is slowly being overcome with the increasing amount of newly generated sequence data.

The present study aimed to clarify the phylogenetic position of the genera currently accepted to belong to *Mycosphaerellaceae*, and thus provides a broad framework and phylogeny for the family, laying a foundation for additional genera and species to be recognised and described. Recent studies have already clearly defined several genera (e.g. *Cercospora*, *Pseudocercospora*, *Pseudocercosporella*, *Ramularia*, *Septoria* and *Zymoseptoria*) but it was clear that genera such as *Passalora*, *Zasmidium*, *Stenella* and *Ramichloridium* remained para- and polyphyletic (Arzanlou *et al.* 2007, 2008, Crous *et al.* 2009c). The sequencing of the type species of *Ramichloridium* and *Stenella* revealed them to belong to *Teratosphaeriaceae*, and the taxa remaining in *Mycosphaerellaceae* were therefore combined into existing genera (e.g. *Zasmidium*), or new genera (e.g. *Pachyramichloridium*).

The genera *Phaeoramularia*, *Fulvia* and *Mycovellosiella* were previously considered synonyms of *Passalora* (Crous & Braun 2003) since the morphological characters appeared to overlap among them. In the present study, based on the phylogenetic placement of good representative material, these four genera are revived and distinguished from one another. Previous generic definitions can no longer be applied to these genera in their current circumscription, and the description of new species is strongly reliant on the availability of DNA sequence data. *Mycovellosiella*, based on the present phylogeny is a monotypic genus, but with more collections new species may emerge. *Mycovellosiella* was previously distinguished from *Passalora* and *Phaeoramularia* by the formation of superficial mycelium with solitary conidiophores formed *in vivo*, but these traits are phylogenetically and taxonomically not significant and deemed unreliable. Other non-type species with mycovellosiella-like morphology cluster in the present trees at quite different positions (e.g. *Paramycovellosiella* and *Distomycovellosiella*). The formation of conidia in chains or singly, previously used to differentiate between *Passalora* (incl. *Cercosporidium*) and *Phaeoramularia*, is still somewhat reliable considering the species included in the present

phylogeny, since the type of *Passalora* and species of *Cercosporidium* produce single conidia, whereas *Phaeoramularia* and *Ragnhildiana* produce catenate conidia. With the inclusion of more species this distinguishing character may, however, become less reliable. The genus *Passalora* is now restricted to species with pale brown conidiophores with apical conidiogenous cell with multiple rim-like conidiogenous loci, thickened and darkened, and single obclavate 1–2-septate conidia with a thickened and darkened hilum. New passalora-like species to be described cannot be assigned without molecular data and, if molecular data are not available, should tentatively be assigned to *Passalora s. lat*. This interim solution will be necessary considering the large number of species involved globally.

The particularly problematic situation pertaining to the genera *Zasmidium*, *Periconiella*, *Verrucisporota* and *Ramichloridium*, previously observed by Arzanlou *et al.* (2008) and Crous *et al.* (2009a, 2012), was addressed in the present study by taking a broad approach to the generic definition of *Zasmidium*, due to strong phylogenetic support of the basal branches and morphological similarity of the species involved.

The genus *Phaeophleospora* appeared to be polyphyletic, as previously observed by Crous *et al.* (2009b), and the two species that were not congeneric with the type, *Phaeophleospora atkinsonii* and *Phaeophleospora stonei*, were reassigned to the new genus *Pseudophaeophleospora*. The conundrum surrounding *Phaeophleospora* and *Lecanosticta* was discussed by Crous *et al.* (2009c). The genus *Lecanosticta* produces phaeophleospora-like conidia in acervular conidiomata, in contrast to the pycnidial conidiomata in *Phaeophleospora*. In the present phylogeny, these two genera cluster in sister clades with a strong basal support to both genera, low support for the *Phaeophleospora* basal branch, but strong support for the *Lecanosticta* basal branch. Surprisingly, the species *Cytostagonospora martiniana* clustered in the *Phaeophleospora* clade, and *Phaeophleospora parsonsiae* seemed to have some affinity to *Lecanosticta*. Until more species and further data are available to clarify this situation, however, we refrain from proposing any new combinations, since our phylogenies will always suffer from undersampling, given the many thousands of taxa included in the family.

One of the major challenges encountered in the present study was that several isolates were sterile (e.g. *Sirosporium celtidis* and *Passalora daleae*) irrespective of all the attempts with changing culture media, incubation conditions, and adding plant substrates. This was either due to the age of the isolate, or isolates requiring their respective hosts to sporulate. Fortunately, some isolates could be linked to their original works and respective morphological descriptions (e.g. *Asperisporium vitiphyllum*). In addition, despite the large number of taxa in the family, many have been described without the deposit of a culture in a public collection, and will therefore need to be recollected in order to resolve their phylogenetic position, which will require an enormous effort. This problem extends in retrospective to many old and obscure genera, and therefore a review of the genera associated with *Mycosphaerellaceae* has been included in the present study in order to motivate the recollection of these obscure fungi, which will enable us to resolve their phylogenetic relationships.

The present study addresses several problematic taxa in *Mycosphaerellaceae* in the light of phylogenetic analysis and morphological characterisation. Although the type species of several genera have been reliably identified and typified, many genera remain unresolved or are in need of a more in-depth study (e.g. *Paramycosphaerella*). The reference cultures used in this paper have, however, been deposited in a public culture collection in order to promote further research on this important family of plant pathogenic fungi. What was known as *Mycosphaerella sensu* Aptroot (2006), now represents a great number of different genera accommodated in different families within *Dothideomycetes*. As more cultures become available, new patterns of

coevolution with different fungal genera and their associated host families will emerge, which we hope will eventually lead to more clarity.

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CHAPTER 6

General discussion

The present thesis focuses mainly on the taxonomic review and circumscription of genera within the family *Mycosphaerellaceae* with particular emphasis on the genera *Ramularia*, *Passalora* and *Zasmidium*. The concept of *Mycosphaerellaceae* and the genera it contains has been significantly revised over the years since the introduction of DNA sequencing and phylogenetic analyses into the field of fungal systematics (Stewart *et al.* 1999, Crous *et al.* 2007a, b, 2009a–e, 2013a, Quaedvlieg *et al.* 2011, 2013, 2014, Verkley *et al.* 2013, Groenewald *et al.* 2013, Videira *et al.* 2015a, b, 2016). The reduced morphology of *Mycosphaerella* made it a large genus that, based on molecular evidence, was found to be poly- and paraphyletic within the *Dothideomycetes*. As a consequence, many genera were distributed among other families like *Schizothyriaceae* (Batzer *et al.* 2008), *Cladosporiaceae* (Schubert *et al.* 2007, Dugan *et al.* 2008, Bensch *et al.* 2012, 2015), *Dissoconiaceae* and *Teratosphaeriaceae*. This meant that *Mycosphaerella* was not the sexual morph of 40 odd genera as formerly believed (Crous 2009), but that these were in fact distinct genera within the *Dothideomycetes*, for which the names of the asexual genera were available for use. Therefore, the selection of the name *Ramularia* over that of *Mycosphaerella* (Wijayawardene *et al.* 2014, Chapters 3, 4) to refer to *Mycosphaerella* s. str. based on the newly revised International Code of Nomenclature for algae, fungi, and plants (ICN) was only logical. Based on phylogenetic analyses, the morphological traits used to distinguish genera (i.e. mode of conidiogenesis and conidiogenous loci) are not always confined to a single lineage which suggests these are traits that evolved multiple times (Chapters 4, 5). Therefore, the fundamental monographs that based their taxonomic groupings on morphology only, were in urgent need of revision under the light of new phylogenetic data.

Recent studies had already circumscribed several genera based on the phylogenetic placement of their type species (e.g. *Cercospora*, *Pseudocercospora*, *Septoria*) while the taxa not congeneric with the type were then reassigned to new genera (e.g. *Amycosphaerella*, *Caryophylloseptoria*, *Microcyclosporella*). The sequencing of the type species of *Ramichloridium* and *Stenella* revealed them to belong to *Teratosphaeriaceae*, and the taxa remaining in *Mycosphaerellaceae* were therefore combined into existing genera (e.g. *Zasmidium*). However, several strains present in the general phylogenies remained unassigned to a specific genus and required further treatment (e.g. *Pachyramichloridium*, Chapter 4). In addition, a few genera that included economically important species remained phylogenetically unresolved (e.g. *Ramularia*, *Passalora*). Based on the present work (Chapters 4, 5), many genera have been circumscribed based on the phylogenetic placement of their type species but many remain to be treated (Table 1). The taxa in these genera are mostly known by their morphological description in literature and their associated fungarium specimen. The recollection of these species will represent an enormous expenditure of time and resources that could have been avoided if only a culture had been deposited in a collection. This could have been a challenging task a few decades ago, but not any longer, with the ease in transport and the free deposit policy of most biobanks. Nevertheless, among the 41 novel *Ramularia* names released on MycoBank (2000–2015), only 13 included cultures and DNA sequence data while the rest relied only on morphological descriptions based on fungarium specimens. The deposit of cultures should be made compulsory with the description of a new species if we want to promote further advances in research of these organisms. Even if the culture later becomes sterile, it remains a valuable resource. As more cultures become available, new patterns of coevolution with different fungal genera and their associated host families will emerge, which will eventually lead to more clarity.

The circumscription of genera and species in the present work mostly followed the Consolidated Species Concept (CSC) (Quaedvlieg *et al*. 2014) which incorporates the genealogical concordance of the GCPSR (Taylor *et al.* 2000) and the criteria of ecology and morphology to provide a more natural classification of these organisms. These concepts and

Table 1. Genera in the *Mycosphaerellaceae*.

Genera with phylogenetic data	
Acervuloseptoria	*Lecanosticta*
Amycosphaerella	*Madagascaromyces**
Annellosympodiella	*Megaloseptoria*[2, 3 [*Melanommataceae*], 4 [*Gemmamyces*]]
*Apseudocercosporella**	*Microcyclosporella*
Asperisporium	*Micronematomyces**
*Australosphaerella**	*Miuraea*
Brunneosphaerella	*Mycodiella*
*Brunswickiella**	*Mycosphaerelloides**
Camptomeriphila[2]	*Mycovellosiella*
Caryophylloseptoria	*Neoceratosperma*
*Catenulocercospora**	*Neocercospora*
*Cercoramularia**	*Neocercosporidium**
Cercospora	*Neodeightoniella*
Cercosporella	*Neomycosphaerella*
Cercosporidium	*Neopenidiella*
*Chuppomyces**	*Neophloeospora**
Clarohilum	*Neopseudocercosporella**
Clypeosphaerella	*Neoseptoria*
*Collarispora**	*Nothopassalora**
Colletogloeum[2]	*Nothopericoniella**
*Coremiopassalora**	*Nothophaeocryptopus**
Cytostagonospora	*Pachyramichloridium**
*Deightonomyces**	*Pallidocercospora*
*Devonomyces**	*Pantospora*
Distocercospora	*Paracercospora*
*Distocercosporaster**	*Paracercosporidium**
*Distomycovellosiella**	*Paramycosphaerella*
Dothistroma	*Paramycovellosiella**
*Epicoleosporium**	*Parapallidocercospora**
*Exopassalora**	*Passalora*
Exosporium	*Periconiella*[4 [*Zasmidium*]]
*Exutisphaerella**	*Phacellium*[1, 4 [*Ramularia*]]
Filiella	*Phaeocercospora*
Fulvia	*Phaeophloeospora*
*Fusoidiella**	*Phaeoramularia*
Gloeocercospora[3[*Xylariales*], 4[*Microdochium*]]	*Phloeospora*
*Graminopassalora**	*Pleopassalora**
*Hyalocercosporidium **	*Pleuropassalora**
*Hyalozasmidium**	*Pluripassalora**
Janetia[1,2]	*Polyphialoseptoria*

Table 1. (Continued).

Prathigada[4 |*Pseudocercospora*]	*Sirosporium*[1]
Protostegia[2]	*Sonderhenia*
Pseudocercospora	*Sphaerulina*
Pseudocercosporella	*Stenella*[3 |*Teratosphaeriaceae*]
*Pseudopericoniella**	*Stromatoseptoria*
*Pseudophaeophleospora**	*Sultanimyces**
*Pseudozasmidium**	*Trochophora*
Ragnhildiana	*Utrechtiana*[2, 3 |*Pyriculariaceae*]
Ramichloridium[3 |*Teratosphaeriaceae*]	*Uwemyces*
Ramularia	*Verrucisporota*[1, 4 |*Zasmidium*]
Ramulariopsis	*Virosphaerella**
Ramulispora	*Xenomycosphaerella*
*Rhachisphaerella**	*Xenoramularia**
*Rosisphaerella**	*Xenosonderhenia*
Ruptoseptoria	*Xenosonderhenioides**
Scirrhia	*Zasmidium*
Scolecostigmina	*Zymoseptoria*
Septoria	
Genera lacking phylogenetic data	
Acrodesmis	*Cercosporiopsis*[4 |*Passalora* s. lat.]
Acrocladium	*Cercostigmina*[4 |*Pseudocercospora*]
Achorodothis	*Ciferriella*[4 |*Pseudocercospora*]
Achrotheca[4 |*Ramularia*]	*Cladosporiella*
Allantophomoides	*Clypeispora*
Anematidium	*Cucurbitariopsis*
Anguillosporella	*Cyclodothis*
Annellophora	*Davisoniella*
Annelophragmia	*Dearnessia*
Annelosympodia	*Deightoniella*
Asteromidium	*Denticularia*
Berteromyces[4 |*Passalora* s. lat.]	*Dictyocephala*[4 |*Pseudocercospora*]
Biharia	*Dictyodesmium*
Bryopelta	*Didymaria*[4 |*Ramularia*]
Camptomeris	*Didymellina*
Ceratosperma	*Didymochora*
Cercocladospora[4 |*Pseudocercospora*]	*Elletevera*
Cercodeuterospora[4 |*Mycovellosiella*]	*Eriocercospora*
Cercoseptoria[4 |*Pseudocercospora*]	*Eriocercosporella*
Cercosphaerella	*Euryachora*
Cercosperma	*Fusicladiella*
Cercosporina[4 |*Cercospora*]	*Gillotia*

Table 1. (Continued).

Gomphinaria	*Phlyctaeniella*
Haplographium[4] [*Dematioscypha*]	*Placocrea*
Hawksworthiana	*Pleurovularia*
Helicomina[4] [*Pseudocercospora*]	*Polysporella*
Hoornsmania	*Polythrincium*
Hyalodictys[4] [*Miuraea*]	*Pseudocercosporidium*
Hyalodothis	*Pseudodidymaria*
Isariella	*Pseudophaeoramularia*[4] [*Pseudocercospora*]
Isariopsella[4] [*Phacellium*]	*Pseudopuccinia*
Isariopsis[4] [*Phacellium*]	*Pseudostigmidium*
Jackzewskiella	*Pseudovularia*[4] [*Ramularia*]
Jahniella	*Quasiphloeospora*
Laocoön	*Ramularisphaerella*
Lecanostictopsis	*Rasutoria*
Lembosiopsis	*Rhabdospora*
Lophiosphaerella	*Rhopaloconidium*[4] [*Pseudocercospora*]
Marcosia[4] [*Stigmina*]	*Rosenscheldiella*
Melanodothis	*Semipseudocercospora*
Microcyclus	*Septocylindrium*[4] [*Ramularia*]
Micronectriella[4] [*Sphaerulina*]	*Septocyta*
Mycoporis	*Septopatella*
Neoovularia	*Septoriopsis*
Neoramularia	*Septorisphaerella*
Oedothea	*Sphaerellothecium*
Ophiocarpella	*Spilosphaeria*
Ophiocladium[4] [*Ramularia*]	*Stenellopsis*
Oreophilla	*Stenospora*
Ormathodium	*Stictosepta*
Ovosphaerella	*Stigmidium*
Ovularia[4] [*Ramularia*]	*Stigmina*[4] [*Pseudocercospora*]
Parastenella	*Tandonella*
Periconia	*Tapeinosporium*
Phaeoisariopsis[4] [*Pseudocercospora*]	*Virgasporium*[4] [*Cercospora*]
Phaeophloeosporella	*Walkeromyces*
Pharcidia[4] [*Stigmidium*]	

*genera introduced in the present thesis.

[1]not based on the type species but on the phylogenetic position of other species of the same genus.

[2]not used here in the phylogenetic analysis.

[3]reassigned to a different family based on the phylogenetic position of the type species.

[4]type species currently synonymized under a different genus.

respective criteria do not have hard boundaries and the final decision of what constitutes a species, a genus or a family is most of the times a personal decision of the researcher based on the coherence of the analysed data. However, the phylogenetic analysis is rather reliant on the taxa used, on the sequence alignment, on the phylogenetic method and the evolutionary models used to calculate a final tree. To atone for the inherent errors in methods, several multigene analyses using concordant genes are performed with two or more different methods. If the resulting phylogenetic trees have the same topology, it shows that the outcome is more likely true. However, the bias created by the undersampling of biodiversity is difficult to overcome. Increasing the variety and number of taxa can have a strong impact on the outcome, as it could be observed with the genus *Paramycosphaerella* that was first expanded based on phylogeny (Guatimosim *et al*. 2016) and later more narrowly redefined based on a different phylogenetic analysis (Chapter 5).

The ITS was introduced as the official barcode for fungi due to its ease of amplification and its ability to distinguish species across the kingdom (Schoch *et al.* 2012). Frequently, in *Mycosphaerellaceae*, the ITS is insufficient to distinguish closely related species and a combination of ITS and a secondary barcode (Stielow *et al.* 2015) is required. Unfortunately, a universal secondary barcode has not been found yet and it is usually proposed for each genus according to its effectiveness. For the *Mycosphaerellaceae* genera, the present work relied mostly on the *rpb2* as a secondary barcode (Chapters 2–5). The *rpb2* gene is used to resolve higher levels of classification due to the ease of alignment and is also able to distinguish taxa at species level due to the high variability of the sequence data. The difficulty of amplifying the partial *rpb2* sequence was overcome by designing new primers among which the primer RPB2-F4 was found to be very effective among numerous genera (Chapters 4, 5). Secondary barcodes such as *tef1*-α or *tub2* were proposed for *Septoria* and allied genera (Verkley *et al.* 2013), *rpb2* or *actA* for *Ramularia* and allied genera (Chapter 4), *cmdA* and *his3* for *Cercospora* (Groenewald *et al.* 2013), *actA* and/or *tef1*-α (Crous *et al.* 2013a) or *rpb2* (Nakashima *et al.* 2016) for *Pseudocercospora*. Although the protein-coding genes frequently have a higher discriminatory power between species, there are usually less available data in the public databases for comparison (Quaedvlieg *et al.* 2013). However, this is slowly being overcome with the increasing amount of newly generated sequence data. Once we provide a stable genetic backbone capturing fungal biodiversity, we will be able to accommodate novelties obtained via environmental sequencing platforms like metabarcoding, metatranscriptomics or metagenomics. A recent study used a metagenomic approach to determine the pathogens involved in Citrus greasy spot (CGS) disease and determined that the genera *Ramularia* and *Septoria* were the most abundant ones in the total detected sequences (Abdelfattah *et al*. 2017). Further research would now be required, however, to clarify which of these taxa actually play a role in this disease complex. Nevertheless, these metagenomics findings would not have been possible without DNA species databases for *Ramularia* and *Septoria*.

The genera *Ramularia*, *Passalora* and *Zasmidium*

The delimitation of *Ramularia* (Chapter 4) was of particular importance since it includes the type of the genus *Mycosphaerella*, *Mycosphaerella punctiformis* (=*Ramularia endophylla*), which is the anchor of the *Mycosphaerellaceae*. From the phylogenetic analysis performed it clustered among other *Ramularia* species including the type of *Ramularia*, *R. pusilla*. Following the one fungus = one name decision, and according to the criteria for pleomorphic genera under the ICN Art. 57.2, the older name *Ramularia* (Unger 1833) was selected over the name *Mycosphaerella*

(Johanson 1884b) and included in a list of protected names (Chapter 3, Wijayawardene *et al*. 2014). The morphological traits used to distinguish *Ramularia* consisted mostly of hyaline conidiophores and conidia, produced singly or in chains, with distinct, thickened, darkened, refractive conidiogenous loci and conidial hila. These characters can still be used to determine if a species belongs to *Ramularia* but caution must be used since similar characters can also be observed in *Teratoramularia*, a genus newly introduced in *Teratosphaeriaceae* (Chapter 4). The use of DNA sequencing of the *rpb2* or *actA* partial genes in addition to the ITS barcode is advised in order to obtain a more reliable species identification in this genus. In addition, the genetic data that suggested that several species may be hidden under one species name (cryptic species or species complexes) or at an infraspecific rank (special forms or varieties) was correct. Based on the multigene analysis, morphological and ecological characters, the species complex of *Ramularia eucalypti* was divided into six species (Chapter 2), namely *R. eucalypti*, *R. haroldporteri*, *R. glennii*, *R. mali*, *R. miae* and *R. plurivora*, while the species complex of *Ramularia endophylla* was divided into three species (Chapter 3), namely *R. endophylla*, *R. unterseheri* and *R. vizellae*. The species *Ramularia lamii* var. *lamii* actually represented a total of three species (Chapter 4), namely *R. agastaches*, *R. lami* var. *lami* and *R. leonuri*, that clustered in different lineages in the phylogenetic analyses.

The use of MALDI-TOF MS as an identification tool has proven to be reliable not only in previous studies but also in the present one (Chapter 2). However, it sometimes fails to distinguish between closely related species such as those in a species complex (e.g. *R. glennii* and *R. mali*). Minor discrepancies between phylogenetic and MALDI-TOF MS-based results have been previously observed when comparing closely related *Alternaria* species (Brun *et al*. 2013). The MALDI-TOF MS pathogen identification relies on the quality and quantity of the reference database mass spectra. Identification is given as a final result of a comparison process between the unknown organism and reference in database, where presence/absence of particular peaks of proteins is analysed. The mass spectrum should be seen as species specific mass fingerprint where ribosomal proteins are most abundantly visible in the spectra, although other proteins are detected as well. Species differentiation is therefore closely comparable to that achieved by the use of the 16S rDNA sequence databases in yeast. Therefore, species with similar ribosomal protein sequences are harder to distinguish by MALDI-TOF MS (Wieser *et al*. 2012). The use of MALDI-TOF MS for strain typing of filamentous fungi is still in its early stages due to their more complex nature when compared to yeasts or bacteria. Filamentous fungi have complicated phylogenetic relationships that require multiple genes to be resolved and have a more complex morphology with thick cell walls and more than one phenotype (e.g. hyphae, spores and synasexual morphs) that influence the protein extraction process. MALDI-TOF-MS is a technique that is easily applied in the clinical laboratory workflow, is quick in providing accurate results and cheaper than the DNA-based identification. Its major limitation is the lack of a comprehensive and efficient reference spectrum libraries that are also open sourced (Normand *et al*. 2017). For MALDI-TOF MS to become a widely used tool for filamentous fungi identification, large databases of MSP spectra need to be established based on reliably identified cultures and, most importantly, following the same protocol. The MSP spectra of filamentous fungi may differ for the same fungus depending on factors unrelated to genuine taxonomic reasons (e.g. if they are generated from spores or from mycelia; if the presence of secondary metabolites like melanin inhibits ionization). The development of standardized protocols for culturing and isolating proteins from filamentous fungi has only recently become the focus of research (Normand *et al*. 2017). Standardized protocols (incubation time, temperature, and culture medium) can reduce filamentous fungi pleomorphism and increase the similarity of

the protein mass spectra derived from a given isolate which improves the reliability of the identification. As with DNA sequencing, this enterprise will require an investment in time and resources until it becomes widely used.

All these techniques and work that are put into identifying cryptic species usually leads to the question of why is it so important to recognise cryptic species? The answer is that what we do not know may harm us. Failure to recognise cryptic species of pathogens might complicate efforts toward disease diagnosis, control and eradication programs. Researchers usually rely on species-specific interactions between pathogen and host to develop control strategies and they need to know the species they are dealing with. An intriguing question is also whether cryptic species co-occur on hosts by accident or whether there is a functional relationship. In living tissue, we assume that the latter is most likely. The multiple species in the complex might depend on each other to colonize their host by sharing different effector genes or sharing particular growth substances. Alternatively, they might keep each other in control by expression of antagonistic metabolite or effector genes in order not to colonise their host abundantly and causing too much damage. When a host and its cryptic species enters different environments via global trade or climate change, "peaceful co-existence" of cryptic species might be disturbed and one of them might become dominant and cause serious damage. Such is the case with the pathogen *Pseudocercospora musicola* (Yellow Sigatoka) that was rapidly displaced by the more aggressive *P. fijiensis* (Black Sigatoka) almost everywhere where banana is cultivated (Gomes *et al*. 2013, Chang *et al*. 2016). Identifying cryptic species complexes also has an impact on conservation since introduced invasive species cause significant damage to native populations in wild habitats. Prevalence of cryptic species also influences the estimate of the number of species of fungi on Earth that currently ranges from 1.5 million (Hawksworth & Rossman 1997) to 3.8 million (Hawksworth & Lücking 2017). The existence of cryptic species may also hamper the search for new pharmaceuticals in fungi since natural products with potential medicinally valuable properties, such as antibiotic activity, can go undetected within cryptic species complexes. With *Ramularia* species, as with other groups of fungi, there has been a tradition of describing species as new if the fungus is found on a new host plant, which can lead to an unnecessary proliferation of species names. The *Ramularia* species analysed in this thesis generally agree with the concept presented in literature (Braun 1998), which regards them as being host-specific but more work needs to be done since only a small percentage of taxa were analysed.

The genus *Passalora*, as previously defined, used to include a wide range of species that produced similar morphological characters and genera such as *Phaeoramularia*, *Fulvia* and *Mycovellosiella* were considered to be synonyms of *Passalora* (Crous & Braun 2003). Upon the recollection of the type species of *Passalora*, *P. bacilligera*, and the introduction of its partial DNA sequences on several phylogenetic analyses, most species previously considered to belong in *Passalora* were found not to be congeneric with the type (Chapter 5). *Passalora* is now restricted to species with pale brown conidiophores with apical conidiogenous cells with multiple rim-like conidiogenous loci, thickened and darkened, and single obclavate 1–2-septate conidia with a thickened and darkened hilum. In order to accommodate the species no longer included in *Passalora*, the previously synonymised genera were resurrected (e.g. *Cercosporidium*, *Fulvia*, *Mycovellosiella*, *Phaeoramularia*) and new genera were introduced (e.g. *Distomycovellosiella*, *Neocercosporidium*). New passalora-like species to be described cannot be assigned without molecular data and, if molecular data are not available, should tentatively be assigned to *Passalora* s. lat. In addition to the ITS barcode, for the passalora-like species, the amplification of the *rpb2* partial gene is recommended, due to the long and variable sequence obtained and to the availability of the new data obtained here for comparison. The phylogenetic analysis performed with the passalora-like species (Chapter 5) was the largest of its kind to date but the phylogenetic position of many species described in literature

remains unknown until they are recollected and subjected to DNA sequencing. As observed, based on the phylogeny, morphological and ecological characters, several of the newly introduced genera were monotypic (e.g. *Graminopassalora*, *Sultanimyces*, *Collarispora*). These mainly include species that have an economic impact in agriculture, and many undescribed species are to be expected to exist in association with less known hosts and in non-disturbed habitats. Among vertebrate and plant genera, studies that evaluated the evolution of the taxonomic process suggest that both the excess or deficiency of monotypic and large genera is an artefact inherent to the taxonomic practice which is attenuated with further taxonomic revisions of existing species and with the description of new species (Chamberlin 1924, Cronk 1989, Scotland & Sanderson 2004, Strand & Panova 2015). Taxonomic rank allocations (e.g. genera, families) are non-standardised, which means that at the same rank, different amounts of phenotypic and genetic information may be applied (Avise & Mitchel 2007). This can be observed when comparing several of the genera as circumscribed in the present work such as *Phaeoramularia* and *Zasmidium* (Chapter 5). In addition, rank allocations are usually influenced by previous rank allocations within the group (Bertrand *et al*. 2006, Laurin 2010). Thus, fitting the data in an existing framework has influenced many of the decisions that led to the presented generic circumscriptions (Chapters 2–5). In the end, the genus rank both partly reflects the evolutionary process and partly represents a subjective and artificial category (Clayton 1972, Strand & Panova 2015).

The genus *Zasmidium* is based on the type species, *Z. cellare*, that has been neotypified in the present study (Chapter 5). Based on the phylogenetic analyses performed, only the basal and terminal branches were strongly supported while the intermediate branches were not significantly supported. In addition, the morphological characters appeared multiple times in different lineages, so a clear separation was not possible (Chapter 5). Therefore, based on phylogenetic, morphological and ecological data, the concept of *Zasmidium* has been broadened to include the genera *Periconiella*, *Verrucisporota* and ramichloridium-like species (Fig. 1). The use of additional genes (e.g. *actA*, *tef1*-α, *tub2*) in the phylogenetic analysis may be necessary to clarify the phylogenetic history of this group of species that includes important pathogens such as *Zasmidium citri-griseum*. Based on an *in-silico* gene selection process for alternative candidate barcodes, the *tef1*-α gene, amplified with the primers EF1-1018F/EF1-1620R, appears to be the most promising candidate as a universal secondary barcode and should be prioritized in this effort (Stielow *et al*. 2011).

General conclusions

The present work has changed how we classify several species within the *Mycosphaerellaceae* and has enriched the biodiversity databases that are a valuable tool to plant pathologists, breeders and medical mycologists in the development of their own research. Research lines in genomics and proteomics in *Mycosphaerellaceae* are still poorly explored. Among them, only *Zymoseptoria tritici* (*Mycosphaerella graminicola*) (Goodwin *et al*. 2011), *Fulvia fulva* (*Cladosporium fulvum*; Wit *et al*. 2012) *Pseudocercospora fijiensis* (*Mycosphaerella fijiensis*) (Arango *et al*. 2016), *P. musae* and *P. eumusae* (Chang *et al*. 2016), and *Ramularia collo-cygni* (McGrann *et al*. 2016) have had their genomes sequenced. Genomic analysis of pathogenic species is likely to provide valuable insights into their genetic diversity, their biological cycles and their ability to produce effector proteins and secondary metabolites that are required for pathogenesis, and that can lead to the development of more appropriate control measures.

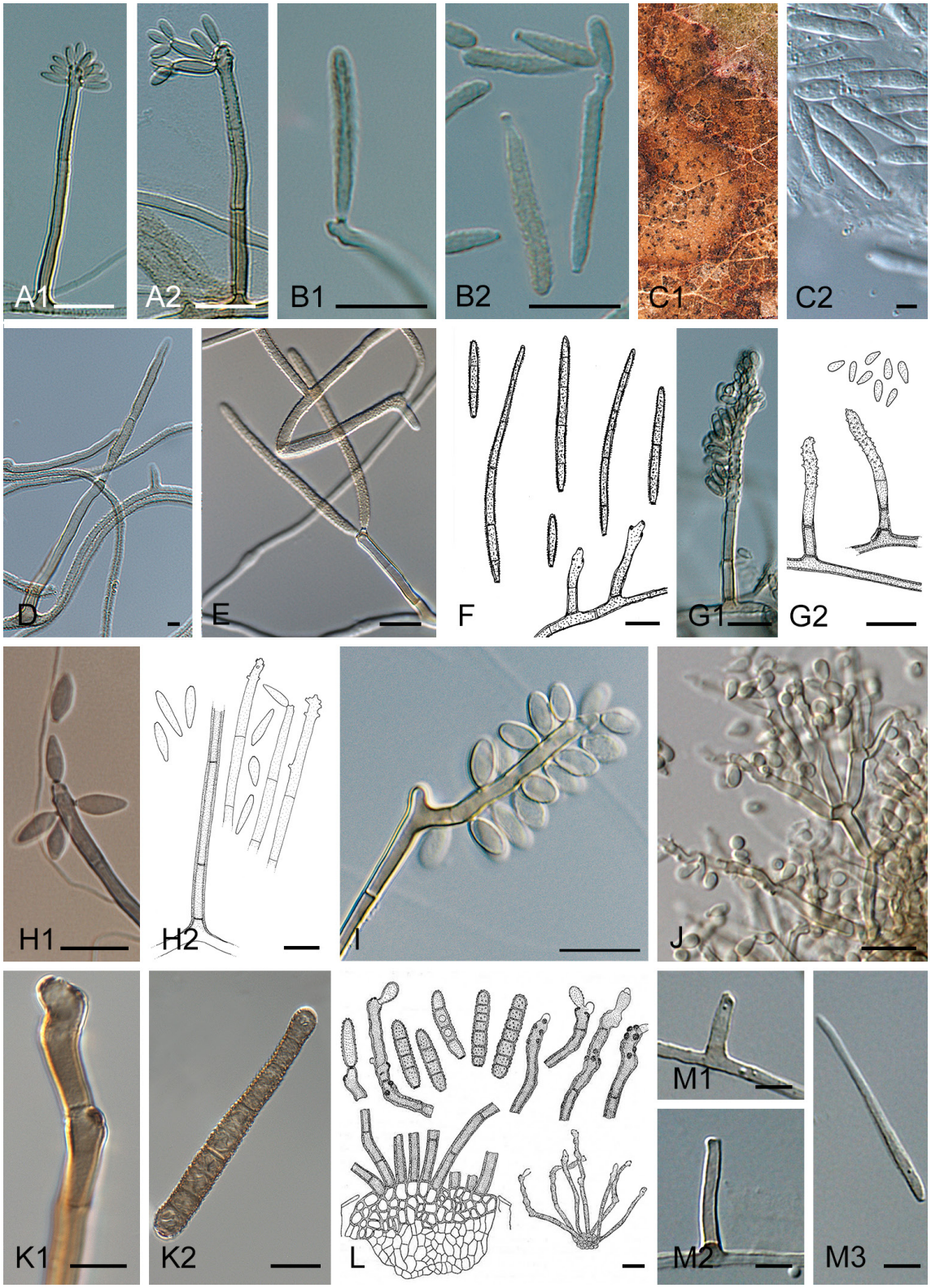

Fig. 1. Morphological characteristics of species belonging to *Zasmidium*. A. *Z. cerophilum* (Arzanlou *et al*. 2007). A1, A2. Conidiophore and conidia. B. *Z. cellare* (Arzanlou *et al*. 2007). B1. Terminal conidiogenous cell and conidium. B2. Ramoconidia and terminal conidia. C. *Z. eucalyptorum* (Crous *et al*. 2006c). C1. Leaf symptoms of the sexual morph development. C2. Ascospores. D. *Z. pseudoparkii*, conidiophore and conidium (Crous *et al*. 2006c). E. *Z. musicola*, conidiophore and conidium (Arzanlou *et al*. 2008). F. *Z. citri-griseum*, conidiophore and conidia (Braun *et al*. 2014). G. *Z. strelitziae* (Arzanlou *et al*. 2007).

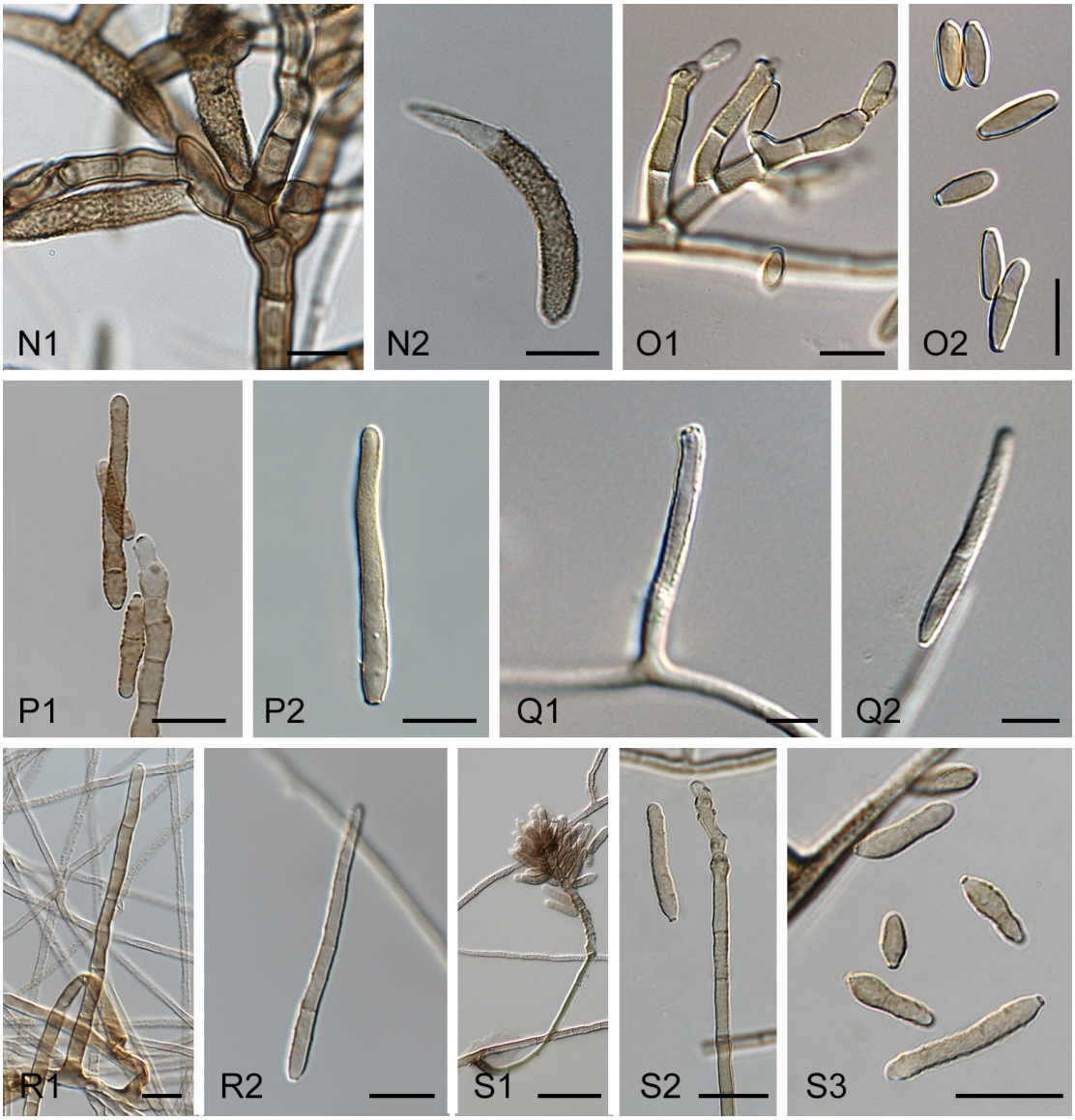

Fig. 1. (Continued). G1, G2. Conidiophore and conidia. H. *Z. musae-banksii* (Arzanlou *et al*. 2007). H1. Conidiogenous cell and conidia. H2. Drawing of the conidiophore and conidia. I. *Z. musigenum*, conidiophore and conidia (Arzanlou *et al*. 2007). J. *Z. biverticillatum*, conidiophores and conidia (Arzanlou *et al*. 2007). K. *Z. grevilleae* (Crous *et al*. 2009a). K1. Partial conidiophore, intercalary and terminal conidiogenous cell. K2. Conidium. L. *Z. proteacearum*, drawing representing conidiophores and conidia (Ellis 1971). M. *Z. musae* (Braun *et al*. 2014). M1, M2. Simple conidiophore emerging from mycelium. M3. Conidium solitary, septate, hyaline. N. *Z. arcuatum* (Arzanlou *et al*. 2007). N1. Partial conidiophore, branched, geniculate-sinuous, verruculose, pigmented. N2. Conidium solitary, with elongated apical beak, verruculose, curved. O. *Z. velutinum* (Arzanlou *et al*. 2007). O1. Conidiophore branched, pigmented, finely verruculose, intercalary and terminal conidiogenous cell, single conidia. O2. Conidia single, septate, finely verruculose, pigmented. P. *Z. hakeae*. P1. Partial conidiophore, finely verruculose, conidiogenous cell terminal and with multiple conidiogenous loci, conidia. P2. Conidium solitary, septate, pigmented, finely verruculose. Q. *Z. queenslandicum* (Arzanlou *et al*. 2008). Q1. Simple conidiophore emerging from mycelium. Q2. Solitary conidium. R. *Z. schini*. R1. Simple conidiophore emerging from mycelium, straight, pigmented. R2. Conidium solitary, septate. S. *Z. elaeocarpi*. S1. Conidiophore emerging from mycelium, slightly curved, with intercalary and terminal conidiogenous cell forming rachis. S2. Partial conidiophore with apical conidiogenous cell and conidium. S3. Solitary conidia, septate, finely verruculose.

APPENDIX

REFERENCES

SUMMARY

ACKNOWLEDGEMENTS

CURRICULUM VITAE

LIST OF PUBLICATIONS

EDUCATION STATEMENT

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SUMMARY

Ramularia is a species-rich genus in the order *Capnodiales* that harbours hyphomycetes with hyaline conidiophores and conidia with distinct, thickened, darkened, refractive conidiogenous loci and conidial hila. The sexual morph of *Ramularia* species belongs to *Mycosphaerella* but the number of experimentally proven links is small and some species may be true asexual holomorphs. Currently *Ramularia* species are accepted as being host-specific, although some exceptions are known. Most species are phytopathogenic and associated with leaf spots, necrosis or chlorosis, but some species can be saprobic or even hyperparasitic. The most important *Ramularia* plant pathogens are *R. collo-cygni* and *R. beticola* that cause severe economic losses to barley and sugar beet crops, respectively. Protecting crops from damage by weeds, animal pests and pathogens is of major importance in order to increase productivity to meet the global increase in demand for food, feed and bioenergy. The present study serves as a backbone for future studies on the taxonomy of *Ramularia* and allied genera since it includes the largest number of *Ramularia* isolates and species ever subjected to DNA sequence analyses. Combined with morphological descriptions and photo plates of several species, it provides a powerful tool to better understand and promote further research on *Ramularia* and allied genera. More than 1 000 names are known in *Ramularia* alone, and this study covered only 88 taxa, which means many species still need to be recollected and characterised based on their DNA sequence data. In addition, the present study aimed to clarify the phylogenetic position of the genera currently accepted to belong to *Mycosphaerellaceae*, thus providing a broad framework and phylogeny for the family and laying a foundation for additional genera and species to be recognised and described. Recent studies have already clearly defined several genera, but it was clear that genera such as *Passalora*, *Zasmidium*, *Stenella* and *Ramichloridium* remained para- and polyphyletic. Although the type species of several genera have been reliably identified and typified, many genera remain unresolved or are in need of a more in-depth study. What was known as *Mycosphaerella sensu* Aptroot (2006), now represents a great number of different genera accommodated in different families within *Dothideomycetes*. The fundamental work performed in this thesis will provide plant pathologists with the resources to facilitate a more reliable identification of the pathogens they work with, as well as provide a solid platform to base their research on, while at the same time also giving more stability to the names which are used to communicate about these fungi.

Chapter 1 gives a general introduction to the genera *Mycosphaerella*, *Ramularia* and allied genera. Their taxonomic history and their economic importance as plant pathogens are detailed. The importance of the morphological characteristics in identification versus the molecular approach is introduced. The introduction of the one species = one name and its impact on the taxonomy of *Ramularia* and allied genera is explained.

Chapter 2 provides an in-depth view on the *Ramularia eucalypti* species complex. *Ramularia eucalypti* was the only species of this genus known to infect *Eucalyptus* by causing severe leaf-spotting symptoms. Isolates of *R. eucalypti* obtained from other plant hosts, environmental samples and human clinical specimens were heterogeneous based on their ITS sequence data and morphology. Therefore, a polyphasic approach involving morphology, multi-gene phylogeny and matrix assisted laser desorption ionization time of flight mass spectrometry (MALDI-TOF MS) was applied in order to resolve the taxa representing this species complex. A six-gene alignment (ITS, *actA, tef1-α, his3, gapdh* and *rpb2*) including 44 isolates of *R. eucalypti* s. lat.

and closely related species was used in both Bayesian and parsimony phylogenetic analysis. The resulting phylogenetic trees showed significant support for separation of seven species: two previously described species (*R. eucalypti* and *R. miae*), four newly introduced (*R. haroldporteri*, *R. glennii*, *R. mali* and *R. plurivora*) and one undescribed *Ramularia* species (sterile). There are now two *Ramularia* spp. known to infect *Eucalyptus* hosts, namely *R. eucalypti* and *R. glennii*. The pathogen responsible for causing lenticel rot in fruits of apple and pear in Italy is the newly described *R. mali*. The ITS barcode was not sufficient to achieve species level identification but any of the partial genes *tef1-α*, *rpb2* or *gapdh* could be used as a secondary barcode to efficiently identify these species. The growth curve analysis of the studied isolates revealed that one strain of *R. plurivora* obtained from a clinical sample was able to grow at 40 °C by changing its morphology from a filamentous fungus to an arthroconidial yeast. The MALDI-TOF is a popular diagnostics tool in clinical samples that allows the identification of microorganisms by analysing their unique protein peak pattern and comparing it with a database of reference main mass spectra (MSPs). Main mass spectra (MSPs) of several *R. eucalypti* s. lat. strains were generated using MALDI-TOF MS and were compared through a Principal Component Analysis (PCA) dendogram. The PCA dendrogram supported three clades containing *R. plurivora*, *R. glennii* / *R. mali* and *R. eucalypti* / *R. miae*. Although the dendrogram separation of species differed from the phylogenetic analysis, the clinically relevant strains of *R. plurivora* and *R. glennii* were successfully identified by MALDI-TOF MS.

Chapter 3 focuses on the resolution of the species complex of *Ramularia endophylla* and on the known links between asexual and sexual morphs among *Ramularia* species. *Ramularia endophylla* (syn. *M. punctiformis*) is an endophyte often associated with broad-leaved trees worldwide. The ITS sequences of several isolates from different hosts appeared to be heterogenous. In order to evaluate the presence of cryptic species a polyphasic approach involving morphology and multi-gene phylogeny was employed. A total of 81 isolates of *R. endophylla* s. lat. and 32 isolates representing 11 *Ramularia* species were targeted for the amplification of eleven genes (LSU, ITS, *actA, tef1-α, his3, gapdh* and *rpb2*, *cmdA*, *tub2*, MAT1-1-1 and MAT1-2-1). The amplification of *cal* and *tub2* was often unsuccessful and the sequences obtained were not used in the multigene analysis. The amplification of the mating-type loci was not successful for all the strains and was particularly challenging for the MAT1-2-1 with the use of the available primers. A Bayesian phylogenetic analysis, as well as a parsimony analysis, was performed on a combined five-locus dataset and the resulting trees showed significant support for three species within the complex, including the previously described *R. endophylla* and *R. vizellae*, and the newly introduced *Ramularia unterseheri*. The ITS barcode alone proved to be insufficient for species level identification and the partial gene sequences of *actA*, *rpb2* and *gapdh* individually proved to be good complementary phylogenetic markers since they successfully separated the three species. The parsimony analyses performed separately with the mating-type gene sequences (MAT1-1-1 and MAT1-2-1) generated trees that were in accordance with those of the multigene analysis. There are presently five *Ramularia* species with an experimentally confirmed link between the asexual ramularia-like and the sexual mycosphaerella-like morph (*R. endophylla*, *R. grevilleana*, *R. inaequalis*, *R. phacae-frigidae* and *R. variabilis*). A total of 15 other links found in literature are either doubtful or have not been experimentally proven and await further collections and study. The taxa identified as *Mycosphaerella* in much of the plant pathology literature needs to be revisited.

Chapter 4 treats the species within the genus *Ramularia* and its closest allied genera. *Ramularia* is a species-rich genus that harbours hyphomycetes with hyaline conidiophores and conidia with distinct, thickened, darkened, refractive conidiogenous loci and conidial hila. Because of its simple morphology closely related species can be difficult to distinguish and several allied genera are frequently confused with *Ramularia*. In the present study a polyphasic approach based on phylogenetic, morphological and cultural data were used in order to improve species and genus circumscription. A total of 420 isolates were targeted for the amplification and sequencing of six partial genes. Five congruent genes were used in the phylogenetic analysis based on three methods that included Bayesian, Maximum-Likelihood and Parsimony methods. Although *Ramularia* and *Ramulariopsis* proved to be monophyletic, *Cercosporella* and *Pseudocercosporella* were polyphyletic. The genus *Phacellium* is tentatively reduced to synonymy with *Ramularia* since all the studied isolates clustered in the *Ramularia* clade and the current phylogenetic position of the type species is unknown. *Cercosporella* and *Pseudocercosporella* isolates that were not congeneric with the ex-type strains of the type species of those genera were assigned to existing genera or to the newly introduced genera *Teratoramularia* and *Xenoramularia*, respectively. The genera *Apseudocercosporella*, *Filiella* and *Neopseudocercosporella* are newly introduced to include pseudocercosporella-like species non-congeneric with their purported type. The genus *Fusoidiella* was introduced to accommodate a passalora-like species closely related to *Filiella*. The genera *Epicoleosporium* and *Mycosphaerelloides* were newly introduced to accommodate ramularia-like species non-congeneric with *Ramularia*. Several isolates included in the genus *Ramularia* were morphologically and molecularly characterised, nine new species were described, 12 species were epitypified, two new combinations and two new names were proposed, and a new sexual-asexual link was observed in *R. hydrangeae-macrophyllae*. Based on the individual genes, ITS was able to distinguish 58 % of the species while *tef1*-α recognised 62 %, *actA* 72%, *gapdh* 76 % and *rpb2* 84 % of the species. The K2P test showed that the ITS barcode has a lower ability to distinguish species than protein-coding genes and that the *rpb2* gene would be a good candidate for a secondary barcode gene. *Ramularia* and allied genera are much undersampled and are frequently described without culture or DNA sequence data.

Chapter 5 introduces a revision of the current taxonomic knowledge of the genera within the *Mycosphaerellaceae*. The *Mycosphaerellaceae* contains numerous genera that include thousands of fungal species. Most of these species are plant pathogens and some can cause significant harm to crops we depend on for food, feed and fuel. Nevertheless, the taxonomy of many genera belonging to this family remains unclear to this day mostly due to the scarcity of cultures and the difficulty of identification based on morphological characters. Therefore, a multigene phylogenetic analysis was performed in order to resolve the phylogenetic relationships among the genera currently recognised within the family and to clarify the position of the cercosporoid fungi among them. The alignment was based on three genes (LSU, ITS and *rpb2*), contained 415 isolates representing 297 taxa and included ex-type strains when available. Based on the analysis, the genera *Passalora*, *Zasmidium*, *Stenella* and *Ramichloridium* are shown to be para- and polyphyletic. As a consequence, several old generic names including *Cercosporidium*, *Fulvia*, *Mycovellosiella*, *Phaeoramularia* and *Raghnildiana* are resurrected to accommodate the species non-congeneric with the *Passalora* type and 19 genera are newly introduced for the remaining passalora-like species (e.g. *Graminopassalora*, *Pleuropassalora*). Previous generic definitions can no longer be applied to these genera in their current circumscription, and the description of new species is strongly reliant on the availability of DNA sequence data. New passalora-like species to be described cannot be assigned without molecular data

and, if molecular data are not available, should tentatively be assigned to *Passalora* s. lat. Species of *Ramichloridium* and *Stenella* in *Mycosphaerellaceae* which were not congeneric with the respective type species currently in *Teratosphaeriaceae*, were combined into existing genera (e.g. *Zasmidium*), or newly described genera (e.g. *Pachyramichloridium*). The genera *Periconiella* and *Verrucisporota* were combined under a broader concept of *Zasmidium*, due to strong phylogenetic support of the basal branches and morphological similarity of the species involved. The genus *Phaeophleospora* was polyphyletic and species non-congeneric with the type were reassigned to the new genus *Pseudophaeophleospora*. The *rpb2* gene proved to be effective in both species and genera separation within the family and is recommended for future phylogenetic work as a secondary barcode. Based on MycoBank, the *Mycosphaerellaceae* contains 213 genera but, based on the phylogenetic data from the present study only 120 genera are known to belong in the family. The phylogenetic position of the remaining genera remains unresolved until fresh collections and DNA data are obtained.

Chapter 6 discusses the results of the performed studies for the present thesis. The main focus is the impact of the use of molecular tools in modern classification as well as how it impacts other scientific fields besides taxonomy and systematics.

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CURRICULUM VITAE

Sandra I. R. Videira was born on June 8th 1984 in Coimbra, Portugal. In 2008, she completed her bachelor in Biology and in 2009 a master in Biodiversity and Plant Biotechnology.

During graduation she collaborated in several projects in progress at the time at Departamento das Ciencias da Vida (DCV) in the University of Coimbra. From 2007–2009, she collaborated in a project that aimed to evaluate the ecology and management of the commercially harvested *Tricholoma flavovirens* in maritime pine forests of Beira Litoral in Portugal (POCI/AGR/57669/2004). During this work she participated in the field trips to the marked areas where the overall abundance of several species of economic importance was calculated throughout the mushroom season over several years. From 2009–2010 she participated in a project that evaluated the fungal diversity present on historical documents through molecular identification and the implementation of control strategies based on gamma radiation for the preservation of the archive patrimony (PTDC/HAH/652662/2006). During this work she learned how to perform microfungi isolation and maintenance in culture, DNA extraction, PCR amplification, DNA sequencing and BLAST. Also from 2009–2010, she participated in a joint project between DCV and the Oryzon Energias company that aimed to inventory the macrofungi present in Póvoa Dão, an historical village, for promotion of biodiversity tourism. During this work she collected, identified and preserved many mushroom specimens and constructed a database with information regarding the species found with respective photographs for public consultation.

After graduation she worked as a research technician at DCV in the University of Coimbra, on a project funded by Fundação para a Ciência e Tecnologia (FCT). The project aimed at detecting the presence or absence of *Fusarium circinatum* in *Pinus* sp. and *Pseudotsuga* sp. from forest and nursery samples, since it is a quarantine pathogen that needs to be controlled. During this work she acquired further experience with microfungi isolation, DNA extraction, PCR amplification of different partial genes and DNA sequencing.

Due to end of the project in early 2011, she applied for a PhD position at the Westerdijk Fungal Biodiversity Institute (then called CBS-KNAW Fungal Biodiversity Centre), in the Evolutionary Phytopathology group of Pedro Crous, on which this thesis is based.

LIST OF PUBLICATIONS

Videira SIR, Groenewald JZ, Nakashima C, Braun U, Barreto RW, de Wit PJGM, Crous PW (2017). *Mycosphaerellaceae* – chaos or clarity? *Studies in Mycology* **87**: 257–421.

Wang XW, Lombard L, Groenewald JZ, Li J, **Videira SIR**, Samson RA, Liu XZ, Crous PW (2016). Phylogenetic reassessment of the *Chaetomium globosum* species complex. *Persoonia* **36**: 83–133.

Videira SIR, Groenewald JZ, Braun U, Shin HD, Crous PW (2016). All that glitters is not *Ramularia*. *Studies in Mycology* **83**: 49–163.

Videira SIR, Groenewald JZ, Verkley GJM, Braun U, Crous PW (2015). The rise of *Ramularia* from the *Mycosphaerella* labyrinth. *Fungal Biology* **119**(9): 823–843.

Videira SIR, Groenewald JZ, Kolecka A, Haren L van, Boekhout T, Crous PW (2015). Elucidating the *Ramularia eucalypti* species complex. *Persoonia* **34**: 50–64.

Gomes RR, Glienke C, **Videira SIR**, Lombard L, Groenewald JZ, Crous PW (2013). *Diaporthe*: a genus of endophytic, saprobic and plant pathogenic fungi. *Persoonia* **31**: 1–41.

Hawksworth DL, Crous PW, Redhead SA, Reynolds DR, Samson RA, Seifert KA, Taylor JW, Wingfield MJ, Abaci O, Aime C, Asan A, Bai FY, Beer ZW de, Begerow D, Berikten D, Boekhout T, Buchanan PK, Burgess T, Buzina W, Cai L, Cannon PF, Crane JL, Damm U, Daniel HM, Diepeningen AD van, Druzhinina I, Dyer PS, Eberhardt U, Fell JW, Frisvad JC, Geiser DM, Geml J, Glienke C, Gräfenhan T, Groenewald JZ, Groenewald M, Gruyter J de, Guého-Kellermann E, Guo LD, Hibbett DS, Hong SB, Hoog GS de, Houbraken J, Huhndorf SM, Hyde KD, Ismail A, Johnston PR, Kadaifciler DG, Kirk PM, Kõljalg U, Kurtzman CP, Lagneau PE, Lévesque CA, Liu X, Lombard L, Meyer W, Miller A, Minter DW, Najafzadeh MJ, Norvell L, Ozerskaya SM, Oziç R, Pennycook SR, Peterson SW, Pettersson OV, Quaedvlieg W, Robert VA, Ruibal C, Schnürer J, Schroers HJ, Shivas R, Slippers B, Spierenburg H, Takashima M, Taşkın E, Thines M, Thrane U, Uztan AH, Raak M van, Varga J, Vasco A, Verkley G, **Videira SIR**, Vries RP de, Weir BS, Yilmaz N, Yurkov A, Zhang N (2011). The Amsterdam Declaration on Fungal Nomenclature. *IMA Fungus* **2**: 105–112.

Portugal A, Mesquita N, **Videira S**, Rodriguez-Echeverría S, Bandeira AML, Santos MJA, Cabo-Verde S, Botelho ML, Freitas H (2009). Fungal diversity in ancient documents. A case study on the archive of the University of Coimbra. *International Biodeterioration & Biodegradation* **63**: 626–629.

Education Statement of the Graduate School

Experimental Plant Sciences

Issued to: Sandra Isabel Rodrigues Videira
Date: 16 Oct 2018
Group: Laboratory of Phytopathology
University: Wageningen University & Research

1) Start-up phase	date
► **First presentation of your project**	
Phylogeny and Systematics of *Ramularia* and allied genera	Sep 2011
► **Writing or rewriting a project proposal**	
Phylogeny and Systematics of *Ramularia* and allied genera	Apr-Jul 2011
► **Writing a review or book chapter**	
► **MSc courses**	
► **Laboratory use of isotopes**	
Subtotal Start-up Phase	*5.5 credits**

2) Scientific Exposure	date
► **EPS PhD student days**	
EPS PhD student day, Wageningen, the Netherlands	May 20 2011
KNAW PhD afternoon, Utrecht, the Netherlands	14 Sep 2011
EPS PhD student day, Wageningen, the Netherlands	Nov 30 2012
► **EPS theme symposia**	
EPS theme 2 symposium - Willie Commelin Scholten day 'Interactions between plants and biotic agents', Utrecht, the Netherlands	24 Jan 2013
EPS theme 2 symposium - Willie Commelin Scholten day 'Interactions between plants and biotic agents', Utrecht, the Netherlands	20 Feb 2015
► **National meetings (e.g. Lunteren days) and other National Platforms**	
KNVvM Mycology Day: Fungal Adaptation, Utrecht, the Netherlands	29 Nov 2013
► **Seminars (series), workshops and symposia**	
CBS Seminar Series, Utrecht, the Netherlands	2011-2015
CBS Symposium: One Fungus One Name (1F=1N), Amsterdam, the Netherlands	19-20 Apr 2011
CBS Symposium: One Fungus which Name (1F=?N), Amsterdam, the Netherlands	12-13 Apr 2012
CBS Symposium: One Fungus which gene (1F=?gene), Amsterdam, the Netherlands	10-11 Apr 2013
CBS Symposium: Genera and Genomes, Amsterdam, the Netherlands	24-25 Apr 2014
CBS Symposium: Second International Workshop on Ascomycete Systematics, Amsterdam, the Netherlands	22-24 Apr 2015
Mini-symposium: Intraspecific Pathogen Variation - Implications and Opportunities, Wageningen, the Netherlands	22 Jan 2013
Symposium: DNA barcoding Symposium, Utrecht, the Netherlands	03 Jun 2015
► **Seminar plus**	
► **International symposia and congresses**	
10th International Mycological Congress (IMC10), Bangkok, Thailand	03-08 Aug 2014
ISHAM: The Future of Barcoding, Utrecht, the Netherlands	12-13 Apr 2013
ISHAM: Diversity and Barcoding of Medical Fungi, Utrecht, the Netherlands	22-23 Apr 2013
► **Presentations**	
Poster: EMBO Computational Molecular Evolution - Phylogeny and taxonomy of *Ramularia* and allied genera	29 Apr 2012
Poster: APS/MSA joint meeting 2013 - *Ramularia eucalypti* species complex untangled	4 Aug 2013
Talk: CBS Seminar series - Phylogenetic lineages in *Ramularia*	10 Jun 2013
Talk: CBS Seminar series - *Ramularia eucalypti* in the spotlight	14 Apr 2014
Talk: Laboratory of Phytopathology: *Ramularia* and allied genera	13 Jun 2014
Talk: 10th International Mycological Congress (IMC10): Radiating *Ramularia* Revisited	5 Aug 2014
Talk: DNA Barcoding Symposium - Barcoding of *Ramularia* and allied genera	3 Jun 2015
Talk: CBS seminar series - The Passalora Puzzle	14 Dec 2015
► **IAB interview**	
► **Excursions**	
Subtotal Scientific Exposure	*19.5 credits**

3) In-Depth Studies	date
► **EPS courses or other PhD courses**	
EMBO Practical Course 'Computational Molecular Evolution', Crete, Greece	29 Apr-10 May 2012
CBS-KNAW Fungal Biodiversity, Utrecht, the Netherlands	04-15 Feb 2013
► **Journal club**	
► **Individual research training**	
Subtotal In-Depth Studies	*6.0 credits**

4) Personal development	date
► **Skill training courses**	
Information Literacy including EndNote Introduction (ILP), Wageningen, the Netherlands	01-02 Nov 2011
Science Communication Course for PhD Students, Utrecht, the Netherlands	13 Jan-17 Feb 2012
Basic training Photoshop for Publications, Utrecht, the Netherlands	28 Mar-18 Apr 2012
Mini-symposium 'How to write a world-class paper', Wageningen, the Netherlands	17 Oct 2013
Rathenau Institute and CWTS 'Crafting your career', Utrecht, the Netherlands	30 Oct 2013
WGS PhD Workshop Carousel, Wageningen, the Netherlands	2 Jun 2014
Entrepreneurship in and out Science, Wageningen, the Netherlands	08 Dec 2014 - 2 Jan 2015
Career Orientation, Wageningen, the Netherlands	19 Nov-14 Dec 2015
► **Organisation of PhD students day, course or conference**	
► **Membership of Board, Committee or PhD council**	
Subtotal Personal Development	*6.0 credits**

The research described in this thesis, was conducted at the Westerdijk Fungal Biodiversity Institute, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands.

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Manon van den Hoeven-Verweij.

Front and back cover:

Background picture in both front and back cover: Culture surface of *Ramularia vizellae*.

Front cover pictures (top to bottom and left to right): Conidia of *Ramularia eucalypti*, culture surface of *R. hydrangea-macrophyllae*, *R. plurivora*, and *R. acris*.

Back cover insets (left to right): Conidiophores and conidia of *Mycovellosiella cajani*, partial conidiophores and conidia of *Passalora bacilligera* and *Phaeoramularia gomphrenicola*.

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