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Highlights of the *Didymellaceae*: A polyphasic approach to characterise *Phoma* and related pleosporalean genera

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Abstract: Fungal taxonomists routinely encounter problems when dealing with asexual fungal species due to poly- and paraphyletic generic phylogenies, and unclear species boundaries. These problems are aptly illustrated in the genus *Phoma*. This phytopathologically significant fungal genus is currently subdivided into nine sections which are mainly based on a single or just a few morphological characters. However, this subdivision is ambiguous as several of the section-specific characters can occur within a single species. In addition, many teleomorph genera have been linked to *Phoma*, three of which are recognised here. In this study it is attempted to delineate generic boundaries, and to come to a generic circumscription which is more correct from an evolutionary point of view by means of multilocus sequence typing. Therefore, multiple analyses were conducted utilising sequences obtained from 28S nrDNA (Large Subunit - LSU), 18S nrDNA (Small Subunit - SSU), the Internal Transcribed Spacer regions 1 & 2 and 5.8S nrDNA (ITS), and part of the β-tubulin (TUB) gene region. A total of 324 strains were included in the analyses of which most belonged to *Phoma* taxa, whilst 54 to related pleosporalean fungi. In total, 206 taxa were investigated, of which 159 are known to have affinities to *Phoma*. The phylogenetic analysis revealed that the current Boeremaean subdivision is incorrect from an evolutionary point of view, revealing the genus to be highly polyphyletic. *Phoma* species are retrieved in six distinct clades within the *Pleosporales*, and appear to reside in different families. The majority of the species, however, including the generic type, clustered in a recently established family, *Didymellaceae*. In the second part of this study, the phylogenetic variation of the species and varieties in this clade was further assessed. Next to the genus *Didymella*, which is considered to be the sole teleomorph of *Phoma s. str*., we also retrieved taxa belonging to the teleomorph genera *Leptosphaerulina* and *Macroventuria* in this clade. Based on the sequence data obtained, the *Didymellaceae* segregate into at least 18 distinct clusters, of which many can be associated with several specific taxonomic characters. Four of these clusters were defined well enough by means of phylogeny and morphology, so that the associated taxa could be transferred to separate genera. Aditionally, this study addresses the taxonomic description of eight species and two varieties that are novel to science, and the recombination of 61 additional taxa.

Key words: *Boeremia*, coelomycetes, *Didymella*, *Didymellaceae*, DNA phylogeny, *Epicoccum*, *Leptosphaerulina*, *Macroventuria*, *Peyronellaea*, *Phoma*, *Pleosporales*, taxonomy, *Stagonosporopsis*.

Taxonomic novelties: New genus: *Boeremia* Aveskamp, Gruyter & Verkley. **New species:** *Phoma brasiliensis* Aveskamp, Gruyter & Verkley, *Ph. bulgarica* Aveskamp, Gruyter & Verkley, *Ph. dactylidis* Aveskamp, Gruyter & Verkley, *Ph. dimorpha* Aveskamp, Gruyter & Verkley, *Ph. longicolla* Aveskamp, Gruyter & Verkley, *Ph. minor* Aveskamp, Gruyter & Verkley, *Ph. pedeiae* Aveskamp, Gruyter & Verkley, *Ph. saxea* Aveskamp, Gruyter & Verkley. **New varieties:** *Boeremia exigua* var. *gilvescens* Aveskamp, Gruyter & Verkley, *B. exigua* var. *pseudolilacis* Aveskamp, Gruyter & Verkley. **New combinations:** ***Boeremia*** *crinicola* (Siemasko) Aveskamp, Gruyter & Verkley, *B. diversispora* (Bubák) Aveskamp, Gruyter & Verkley, *B. exigua* var. *exigua* (Desm.) Aveskamp, Gruyter & Verkley, *B. exigua* var. *heteromorpha* (Schulzer & Sacc.) Aveskamp, Gruyter & Verkley, *B. exigua* var. *lilacis* (Sacc.) Aveskamp, Gruyter & Verkley, *B. exigua* var. *linicola* (Naumov & Vassiljevsky) Aveskamp, Gruyter & Verkley, *B. exigua* var. *populi* (Gruyter & Scheer) Aveskamp, Gruyter & Verkley, *B. exigua* var. *coffeae* (Henn.) Aveskamp, Gruyter & Verkley, *B. exigua* var. *viburni* (Roum. ex. Sacc.) Aveskamp, Gruyter & Verkley, *B. foveata* (Foister) Aveskamp, Gruyter & Verkley, *B. lycopersici* (Cooke) Aveskamp, Gruyter & Verkley, *B. noackiana* (Allesch.) Aveskamp, Gruyter & Verkley, *B. sambuci-nigrae* (Sacc.) Aveskamp, Gruyter & Verkley, *B. strasseri* (Moesz) Aveskamp, Gruyter & Verkley, *B. telephii* (Vestergr.) Aveskamp, Gruyter & Verkley, ***Epicoccum*** *pimprinum* (P.N. Mathur, S.K. Menon & Thirum.) Aveskamp, Gruyter & Verkley, *E. sorghi* (Sacc.) Aveskamp, Gruyter & Verkley, ***Peyronellaea*** *americana* (Morgan-Jones & J.F. White) Aveskamp, Gruyter & Verkley, *Pey. alectorolophi* (Rehm.) Aveskamp, Gruyter & Verkley, *Pey. anserina* (Marchal) Aveskamp, Gruyter & Verkley, *Pey. arachidicola* (Khokhr.) Aveskamp, Gruyter & Verkley, *Pey. aurea* (Gruyter, Noordel. & Boerema) Aveskamp, Gruyter & Verkley, *Pey. calorpreferens* (Boerema, Gruyter & Noordel.) Aveskamp, Gruyter & Verkley, *Pey. coffeae-arabicae* (Aveskamp, Verkley & Gruyter) Aveskamp, Gruyter & Verkley, *Pey. curtisii* (Berk.) Aveskamp, Gruyter & Verkley, *Pey. eucalyptica* (Sacc.) Aveskamp, Gruyter & Verkley, *Pey. gardeniae* (S. Chandra & Tandon) Aveskamp, Gruyter & Verkley, *Pey. lethalis* (Ellis & Bartholomew) Aveskamp, Gruyter & Verkley, *Pey. pomorum* var. *pomorum* (Thüm.) Aveskamp, Gruyter & Verkley, *Pey. pomorum* var. *circinata* (Kusnezowa) Aveskamp, Gruyter & Verkley, *Pey. pomorum* var. *cyanea* (Jooste & Papendorf) Aveskamp, Gruyter & Verkley, *Pey. obtusa* (Fuckel) Aveskamp, Gruyter & Verkley, *Pey. pinodella* (L.K. Jones) Aveskamp, Gruyter & Verkley, *Pey. pinodes* (Berk. & A. Bloxam) Aveskamp, Gruyter & Verkley, *Pey. protuberans* (Lév.) Aveskamp, Gruyter & Verkley, *Pey. sancta* (Aveskamp, Gruyter & Verkley) Aveskamp, Gruyter & Verkley, *Pey. subglomerata* (Boerema, Gruyter & Noordel.) Aveskamp, Gruyter & Verkley, *Pey. zeae-maydis* (Arny & R.R. Nelson)Aveskamp, Gruyter & Verkley, ***Phoma*** *clematidis-rectae* (Petr.) Aveskamp, Woudenberg & Gruyter, *Ph. noackiana* (Allesch.) Aveskamp, Gruyter & Verkley, ***Stagonosporopsis*** *ajacis* (Thüm.) Aveskamp, Gruyter & Verkley, *S. andigena* (Turkenst.) Aveskamp, Gruyter & Verkley, *S. artemisiicola* (Hollós) Aveskamp, Gruyter & Verkley, *S. astragali* (Cooke & Harkn.) Aveskamp, Gruyter & Verkley, *S. caricae* (Sydow & P. Sydow) Aveskamp, Gruyter & Verkley, *S. crystalliniformis* (Loer., R. Navarro, M. Lôbo & Turkenst.) Aveskamp, Gruyter & Verkley, *S. cucurbitacearum* (Fr.) Aveskamp, Gruyter & Verkley, *S. dorenboschii* (Noordel. & Gruyter) Aveskamp, Gruyter & Verkley, *S. heliopsidis* (H.C. Greene) Aveskamp, Gruyter & Verkley, *S. ligulicola* var. *ligulicola* (K.F. Baker, Dimock & L.H. Davis) Aveskamp, Gruyter & Verkley, *S. ligulicola* var. *inoxydabilis* (Boerema) Aveskamp, Gruyter & Verkley, *S. loticola* (Died.) Aveskamp, Gruyter & Verkley, *S. oculo-hominis* (Punith.) Aveskamp, Gruyter & Verkley, *S. rudbeckiae* (Fairm.) Aveskamp, Gruyter & Verkley, *S. trachelii* (Allesch.) Aveskamp, Gruyter & Verkley, *S. valerianellaea* (Gindrat, Semecnik & Bolay) Aveskamp, Gruyter & Verkley. **New names:** ***Peyronellaea*** *australis* Aveskamp, Gruyter & Verkley, ***Phoma*** *fungicola* Aveskamp, Gruyter & Verkley, *Ph. novae-verbascicola* Aveskamp, Gruyter & Verkley.

INTRODUCTION

Coelomycetous fungi (Grove 1935) are geographically widespread and are found in numerous ecological niches. Sutton (1980) mentions exponents of this anamorph group inhabiting soil, organic debris, and water, as well as species that parasitise other fungi, lichens, insects and vertebrates. A substantial percentage of the coelomycetes is associated with plant material, either as opportunists or as primary pathogens (Sutton 1980).

Difficulties in morphological identification have resulted in a poor understanding of the generic and species boundaries in the coelomycetes (Sutton 1977, 1980, Nag Raj 1981, Van der Aa *et al.* 1990, Torres *et al.* 2005a, b, De Gruyter *et al*. 2009). In an attempt to improve the classification of the coelomycetes, Sutton (1980) proposed to divide the order into six suborders, which unfortunately proved to be highly artificial from an evolutionary perspective (De Gruyter *et al*. 2009).

The current common procedure for isolate identification, which chiefly relies on similarity of DNA sequences to those found in public DNA libraries (Hyde & Soytong 2007), combined with the high level of incorrectly identified sequences in these databases (Bridge *et al.* 2003, 2004, Nilsson *et al.* 2006) placed the likelihood of achieving correct identifications of coelomycetous fungi under intense scrutiny. As pointed out by De Gruyter *et al.* (2009), for appropriate morphological identifications within the coelomycete genera *in vitro* studies are essential, for example in the cases in which quarantine pathogens are involved (Aveskamp *et al.* 2008). For the current generic delimitation of this class, the use of conidiogenesis characters as taxonomic criteria is of major importance (Hughes 1953; Boerema 1965, Boerema & Bollen 1975, Sutton 1964, 1977, 1980, Singh *et al.* 1997).

Phoma

The genus *Phoma* Sacc. emend. Boerema & G.J. Bollen (*Pleosporales*) is a good example of a coelomycetous genus made fascinating by its great ecological diversity, but taxing investigators with profound difficulties in making identifications. The majority of the taxa within this mitosporic genus have been found in association with land plants, causing mainly leaf and stem spots (Aveskamp *et al*. 2008, Zhang *et al.* 2009). Approximately 50 % of the *Phoma* taxa that were redescribed by Boerema *et al.* (2004) are recognised as relevant phytopathogenic fungi, including a series of pathogens with quarantine status (Boerema *et al.* 2004, Aveskamp *et al*. 2008). Although most taxa are continuously present in the environment as saprobic soil organisms, many species switch to a pathogenic lifestyle when a suitable host is encountered (Aveskamp *et al*. 2008). The genus further comprises several species and varieties that are recognised as endophytic, fungicolous and lichenicolous fungi (*e.g.* Hawksworth 1981, Xianshu *et al*. 1994, Sullivan & White 2000, Hawksworth & Cole 2004, Diederich *et al.* 2007, Schoch *et al*. 2009a). In addition, approximately 10 species are known as pathogens of humans (*e.g.* De Hoog *et al*. 2000, Balis *et al.* 2006) and other vertebrates, such as cattle (Costa *et al.* 1993) and fish (Ross *et al*. 1975, Hatai *et al*. 1986, Voronin 1989, Faisal *et al*. 2007). Next to such an active role in vertebrate pathology, *Phoma* spp. may indirectly affect animal health by the production of toxic secondary metabolites (Bennett 1983, Pedras & Biesenthal 2000, Rai *et al*. 2009), as is known for *Ph. sorghina* in straw roofs in South Africa (Rabie *et al.* 1975) and may be the case in *Ph. pomorum* in cattle feed (Sørensen *et al.* 2009). An almost completely unexplored habitat of *Phoma* spp. is the marine environment (Kohlmeyer & Volkmann-Kohlmeyer 1991), in which *Phoma* species are regularly found that are completely new to science (*e.g.* Osterhage *et al*. 2000, Yarden *et al*. 2007).

The genus *Phoma* has always been considered to be one of the largest fungal genera, with more than 3 000 infrageneric taxa described (Monte *et al*. 1991). The number of species described in *Phoma* rose to this level due to the common practice of host associated nomenclature, in combination with the paucity in micromorphological characters and a high variability in cultural characteristics. These factors have resulted in the fact that the systematics of the genus never has been fully understood (Aveskamp *et al.* 2008). Based on various morphological features depicted by earlier workers, probably less than one-tenth of the 3 200 species listed in MycoBank (www.mycobank.org, Crous *et al.* 2004, Robert *et al.* 2005) can currently still be recognised as a separate *Phoma* taxon. Many of those names were thus already reduced to synonymy after an extensive study of the genus (Boerema *et al*. 2004), and after a thoroughly revised generic concept of the morphologically similar genera *Ascochyta* (Boerema & Bollen 1975) and *Phyllosticta* (Van der Aa 1973, Van der Aa & Vanev 2002). Many other species could be recombined into other coelomycete genera, such as *Asteromella*, *Microsphaeropsis*, *Phomopsis*, *Pleurophoma*, *Pyrenochaeta* and *Stagonospora* (Sutton 1964, 1980, Boerema & Bollen 1975). In addition, *Coniothyrium* and *Paraconiothyrium* have regularly been mistaken for *Phoma* (Verkley *et al.* 2004, Damm *et al.* 2008, Woudenberg *et al*. 2009). In their studies, Boerema *et al.* (2004) recognised a total of 215 *Phoma* taxa and eight teleomorph species with an unnamed *Phoma* anamorph, although this is probably just the tip of the iceberg as, thus far, only 40 % of the herbarium species mentioned in literature could be recovered and studied properly. Additionally, novel species are described regularly in this genus (*e.g.* Hawksworth & Cole 2004, Torres *et al.* 2005a, Li *et al.* 2006, Diederich *et al.* 2007, Aveskamp *et al.* 2009a, Davidson *et al.* 2009).

A subdivision of the asexual genus *Phoma* that is currently widely applied divides the genus into nine sections, including the sections *Phoma*, *Heterospora*, *Macrospora, Paraphoma*, *Peyronellaea*, *Phyllostictoides*, *Pilosa, Plenodomus* and *Sclerophomella* (Boerema 1997). These sections are primarily based on just a few morphological or physiological characters and have not been confirmed as biologically realistic by molecular biological studies. The number of taxa per section may vary, ranging from almost 70 species in section *Phoma* to only two in section *Pilosa*. In Table 1, a list is provided with the main characters of every section (Boerema 1997). This subdivision into sections has led to an identification system that is considered to be extremely helpful in morphological identification (Boerema *et al.* 2004). However, as was hypothesised by Boerema *et al.* (2004), the classification has proved to be artificial. Molecular evidence has shown that the sections are linked to phylogenetically distinct teleomorph genera (Reddy *et al*. 1998, Torres *et al.* 2005b, De Gruyter *et al*. 2009). Even these teleomorph genera are not always monophyletic (Morales *et al.* 1995, Câmara *et al.* 2002, Kodsueb *et al*. 2006, Inderbitzin *et al.* 2009). In addition, characters that are thought to be specific for a certain section appeared to be polyphyletic, as is illustrated for dictyochlamydospores and setose pycnidia, the main characters for the sections *Peyronellaea* (Aveskamp *et al.* 2009a) and *Paraphoma* (Grondona *et al*. 1997, De Gruyter *et al.* 2010) respectively. Furthermore, *Phoma* section *Phoma*, a group of species which is characterised by the absence of chlamydospores, septate conidia, and pycnidial ornamentation or wall thickening, is

Table 1. Overview of the characters of the various *Phoma* sections in the Boeremaean classification system. Adapted from Boerema *et al*. (2004).

Section	Teleomorph	Synanamorph	Sectional character
Heterospora	–	*Stagonosporopsis*	Production of distinctly large conidia in addition to the regular conidia
Macrospora	*Mycosphaerella*	–	Conidia large, measuring 8–19 × 3–7 µm
Paraphoma	–	–	Setose pycnidia
Peyronellaea	–	*Epicoccum**	Multicellular chlamydospores
Phoma	*Didymella*	*Phialophora**	–
Phyllostictoides	*Didymella*	–	Small septate conidia in addition to the regular conidia
Pilosa	*Pleospora*	–	Pycnidia covered by pilose outgrows
Plenodomus	*Leptosphaeria*	*Sclerotium**	Pycnidia scleroplectenchymatous
		*Phialophora**	
Sclerophomella	*Didymella*	–	Pycnidia thick-walled

*Synanamorph only recorded in a single species.

considered to be a repository for degenerated and insufficiently understood species that could not be placed elsewhere.

The genus *Phoma* is typified by *Phoma herbarum* (Boerema 1964). This species has thus far not been linked to any teleomorph, but several other species that are currently accommodated in *Phoma* do have a sexual state. The species in the section *Pilosa* are linked to the teleomorph genus *Pleospora*, while many species in the section *Plenodomus* have a sexual state in *Leptosphaeria*. As mentioned above, *Leptosphaeria* is para- or possibly polyphyletic (Morales *et al.* 1995, Câmara *et al.* 2002). A teleomorph in the poorly studied genus *Didymella* is associated with approximately 40 *Phoma* species placed in sections *Phoma*, *Phyllostictoides* and *Sclerophomella* (Boerema *et al*. 2004). Moreover, *Phoma* has been linked in literature to several other teleomorph genera, such as *Mycosphaerella* (Corlett 1991, De Gruyter 2002, Crous *et al*. 2009a, b), *Belizeana* (Kohlmeyer & Volkmann-Kohlmeyer 1987), *Atradidymella* (Davey & Currah 2009) and *Fenestella*, *Cucurbitaria*, *Preussia*, and *Westerdykella* (Von Arx 1981, Zhang *et al*. 2009). None of these hypothesised teleomorph-anamorph linkages is supported by molecular evidence. All must be investigated by study of type material. However, these associations are unlikely as the mentioned teleomorph genera are not linked to the *Pleosporales*. The species and teleomorph relations are also not recognised by Boerema *et al*. (2004), except for two *Phoma* species of the section *Macrospora*, *Ph. rabiei* and *Ph. zeae-maydis* which were linked to "*Mycosphaerella*" teleomorphs as *M. rabiei* (Kaiser 1997, De Gruyter 2002) and *M. zeae-maydis* (Mukunya & Boothroid 1973) respectively. Both species also have names in *Didymella*. The use of those names is recommended, since *Mycosphaerella* has been shown to be phylogenetically widely separated from all known *Phoma* species (De Gruyter *et al.* 2009, Crous *et al*. 2009a, b).

Characteristic strains of the genus concerned have been used in a Multilocus Sequence Typing (MLST) study of the *Dothideomycetes*, which indicated that *Phoma* is phylogenetically embedded in the *Pleosporales* (Schoch *et al*. 2006, 2009b, Zhang *et al*. 2009). A similar, but smaller scale study aiming to delineate the species in the unofficial suborder Phialopycnidiineae (Sutton 1980), revealed that *Phoma* is highly polyphyletic, as reference species of the various sections were recovered in distinct clades of the reconstructed phylogeny (De Gruyter *et al.* 2009). Type species of the sections *Heterospora, Plenodomus*, *Paraphoma* and *Pilosa* appeared to be ancestral to a cluster comprising types of the other sections, as well as to members of the anamorph genera *Ascochyta*, *Microsphaeropsis*, *Chaetasbolisia, Coniothyrium* and *Paraconiothyrium.* This group has been elevated to family level and is now recognised as the *Didymellaceae* (De Gruyter *et al.* 2009). A Blast-search in public sequence libraries revealed a high genetic similarity between species ascribed to the *Didymellaceae* and two other teleomorph genera, *Macroventuria* and *Leptosphaerulina*, although these genera are morphologically clearly distinct from *Didymella* (Van der Aa 1971, Von Arx 1981, Zhang *et al*. 2009). The genetic similarity between those two genera has been observed before by Kodsueb *et al.* (2006), but the phylogenetic relationship with the genus *Didymella* was not noted in their study. Members of these two genera have therefore also been included in this study.

To solve the problems in quarantine species identification of isolates taken from samples obtained during phytosanitary border controls, a comprehensive taxonomic system is required (Aveskamp *et al.* 2008). As DNA-based techniques do become more and more important in identification and detection of plant pathogens (Bridge 2002), such a taxonomic system should be in line with sequence data. One of the major initiatives in this field is the development of DNA Barcodes (Hebert *et al.* 2003, Summerbell *et al*. 2005), which has been promising in the rapid detection of potentially serious plant pathogens (Armstrong & Ball 2005).

Three genes have in recent years been proposed as standard loci for use in DNA barcoding in fungi. These comprise the internal transcribed spacers (ITS) of the rDNA operon ITS region (Druzhinina *et al.* 2005), actin (ACT, Aveskamp *et al.* 2009b), and cytochrome *c* oxidase subunit I (COI, Seifert *et al.* 2007). The last locus was successfully applied in DNA Barcoding of *Penicillium* (Seifert *et al.* 2007, Chen *et al.* 2009). However, COI analysis applied to a subset of *Ph. exigua* related strains, did not reveal taxon-specific conserved SNPs (Aveskamp *et al.* 2009b), whilst in an attempt to barcode *Aspergillus*, COI was found to have limited value (Geiser *et al.* 2007). Although ACT has proven helpful in resolving the phylogeny of *Phoma exigua* below species level (Aveskamp *et al.* 2009b), it could not be applied in the present study, as interspecific variation proved to be too high to align the obtained sequences properly. The use of ITS as fungal barcode locus is most popular (Seifert 2009) and has been applied in several taxonomic groups, such as *Trichoderma* and *Hypocrea* (Druzhinina *et al*. 2005), and *Trichophyton* (Summerbell *et al.* 2007) and in ecological groups such as wood-inhabiting fungi (Naumann *et al.* 2007). The power of this locus for barcoding lies in the multiple copies that are present within each cell; this phenomenon results in lower detection

thresholds than can be obtained with single-copy loci. Despite the general practicality of using ITS in barcoding, the locus is relatively conservative and may oversimplify species delimitations or blur generic boundaries in some groups (Nilsson *et al.* 2008). In the present study, a combination of four loci is therefore applied. These include two loci that are renowned for their capacity to resolve phylogenies above family level, namely parts of the LSU (Large Subunit – 28S) and SSU (Small Subunit – 18S) nrDNA. Additinally two loci were applied that mainly provide resolution at species level – or even below. In addition to the abovementioned ITS regions, also part of the β-tubulin gene was utilised, which was successfully applied in a preliminary study on *Phoma* species of the section *Peyronellaea* (Aveskamp *et al.* 2009a).

For the present study, four objectives were defined. The main objective of this study was to reach consensus on the circumscription of the genus *Phoma*. A modified definition of the genus is not only helpful in taxonomy, but will also be of interest to plant quarantine officers (Aveskamp *et al.* 2008). Teleomorph associations of *Phoma* are still uncertain, and here we attempt to shed light on the sexual state of *Phoma s. str*. Species representing all *Phoma* sections were included and DNA sequences were compared with those of other species in the *Pleosporales*.

Secondly, we aimed to integrate morphological and cultural features with DNA sequence data to resolve the generic limits of taxa currently placed in the *Didymellaceae*. The number of genera in this family is still unclear. Although De Gruyter *et al.* (2009) found a series of genera that, according to their reconstructed phylogeny, clustered in this family, many were not clearly defined or were morphologically distant from each other, although all anamorph taxa found are accommodated in the coelomycetes (Sutton 1980). Examples of these taxa were included in this study, although the number of *Ascochyta*, *Coniothyrium* and *Microsphaeropsis* species is too high to take all infrageneric taxa of these adjacent genera into account.

Further, we aimed to validate the *Phoma* sections, which are widely applied in *Phoma* species recognition. Are the sections representing evolutionary units, and what is the taxonomical value of the characters used to define the sections? To judge the value of the Boeremaean taxonomic system, representative species of all sections were studied, including the sectional type species. The main focus was, however, to resolve the sections associated with *Didymellaceae*. A single generic name, based on priority but regardless of whether it is an “anamorph” or “teleomorph” genus, is used for all unambiguous monophyletic phylogenetic lineages (Crous *et al*. 2006, 2009a, b). Finally, we aimed to assess the molecular variation within species that have historically been placed in *Phoma*. Genes were tested for their potential reliability as standard barcoding genes for *Phoma* species.

For this study, a sequence data set was generated and morphological data assembled for the more than 300 well-vouchered strains available in the culture collections of CBS (CBS-KNAW Fungal Biodiversity Centre, Utrecht, the Netherlands) and PD (Plantenziektenkundige Dienst, Dutch Plant Protection Service, Wageningen, the Netherlands). In addition, five species recognised in a recent study in the section *Peyronellaea* (Aveskamp *et al.* 2009a) have also been included, as well as several strains that could not be associated with any of the species that were accepted in *Phoma* by Boerema *et al.* (2004), and that were maintained as unnamed *Phoma* species in the culture collections mentioned above. These strains were recognised as taxonomic novelties and are described at species or variety level in the present paper. Furthermore, several species were relocated to more appropriate genera based on the results obtained.

MATERIALS AND METHODS

Strain selection

A total of 324 strains, belonging to 206 species were selected for the present study. The majority of these species (159) belonged to the genus *Phoma* or its associated teleomorphs, the remainder to genera that are regularly confused with this genus and that belong to the *Pleosporales* according to the studies published by De Gruyter *et al.* (2009). Besides the anamorphous species that were included, representatives of the teleomorph genera *Didymella*, *Leptosphaeria*, *Leptosphaerulina*, *Macroventuria* and *Pleospora* were also included. The recently described genus *Atradidymella* (Davey & Currah 2009) was not available for study and therefore excluded.

Strains were obtained from CBS and PD culture collections in lyophilised form or from the liquid nitrogen collection. Freeze-dried strains were revived overnight in 2 mL malt/peptone (50 % / 50 %) liquid medium. Subsequently, the cultures were transferred and maintained on oatmeal agar (OA, Crous *et al.* 2009c). The strains that were stored at -196 °C were directly plated on the same agar medium.

DNA extraction, amplification and sequence analysis

Genomic DNA extraction was performed using the Ultraclean Microbial DNA isolation kit (Mo Bio Laboratories, Carlsbad, CA, U.S.A.), according to the instructions of the manufacturer. All DNA extracts were diluted 10 × in milliQ water and stored at 4 ºC before their use as PCR templates.

For nucleotide sequence comparisons fragments of four loci were analysed: LSU, SSU, ITS, and TUB. Amplification of LSU and SSU was conducted utilising the primer combination LR0R (Rehner & Samuels 1994) and LR7 (Vilgalys & Hester 1990) for LSU sequencing and the primer pair NS1 and NS4 (White *et al.* 1990) for SSU. The PCRs were performed in a 2720 Thermal Cycler (Applied Biosystems, Foster City, California) in a total volume of 12.5 µL. The PCR mixture contained 0.5 µL 10 × diluted genomic DNA, 0.2 µM of each primer, 0.5 Unit Taq polymerase E (Genaxxon Bioscience, Germany), 0.04 mM (SSU) or 0.06 mM (LSU) of each of the dNTP, 2 mM $MgCl_2$ and 1 × PCR buffer E incomplete (Genaxxon Bioscience). Conditions for amplification for both regions were an initial denaturation step of 5 min at 94 °C, followed by 35 cycles of denaturation, annealing and elongation and a final elongation step of 7 min at 72 °C. For the SSU amplification, the 35 cycles consisted of 30 s at 94 °C, 50 s at 48 °C and 90 s at 72 °C; for the LSU 45 s at 94 °C, 45 s at 48 °C and 2 min at 72 °C. The loci ITS and TUB were amplified as described by Aveskamp *et al*. (2009a), using the primer pairs V9G (De Hoog & Gerrits van den Ende 1998) and ITS4 (White *et al.* 1990) for ITS sequencing and the BT2Fw and BT4Rd primer pair (Aveskamp *et al.* 2009a) for sequencing of the TUB locus. PCR products were analysed by electrophoresis in a 1.0 % (w/v) agarose gel containing 0.1 ug/mL ethidium bromide in 1 × TAE buffer (0.4 M Tris, 0.05 M glacial acetetic acid 0.01 M ethylenediamine tetraacetic acid [EDTA], pH 7.85). The amplicons were visualised under UV light. Hyperladder I (Bioline, Luckenwalde, Germany) was applied as size standard.

The obtained amplicons were sequenced in both directions using the same primer combinations, except for LSU, where an additional primer, LR5 (White *et al.* 1990) was further required

to assure complete coverage of the locus. Sequencing reactions were prepared with the BigDye terminator chemistry v. 3.1 (Applied Biosystems) according to the manufacturer's recommendations. Sequence products were purified with Sephadex G-50 Fine (Amersham Biosciences, Roosendaal, the Netherlands) and subsequently separated and analysed on an ABI Prism 3730 DNA Sequencer (Applied Biosystems). Consensus sequences were computed from the forward and reverse sequences using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium). The consensus sequences are deposited in GenBank (For GenBank accession numbers see Tables 2, 3).

Obtained consensus sequences were assembled and aligned using the same BioNumerics software and adjusted manually where necessary. As SSU was highly conserved in deeper node phylogenies, revealing almost no phylogenetic informative nuclear polymorphisms, and as ITS and TUB proved to be unalignable due to a high level of polymorphism if all taxa studied would be taken into account, it was decided to conduct two separate analyses. The first analysis comprised SSU and LSU loci, and was applied to 76 taxa of which most species included belonged to genera that were often confused with *Phoma* (Sutton 1980, De Gruyter *et al.* 2009). A second set of analyses was conducted on 274 taxa, and focussed on the species that had proven to be related to the *Didymellaceae* from preliminary studies.

Each of the phylogenetic analyses consisted of two methods: Bayesian Interference (BI) and Maximum Likelihood (ML). For BI analysis, the nucleotide substitution models were determined for each locus separately with MrModeltest v. 2.2 (Nylander 2004). According to this software, the General Time Reversible substitution was determined to be the best model for SSU, TUB and LSU in both data sets, with inverse gamma rates and dirichlet base frequencies (GTR + I + G). For the ITS dataset, the software suggested the Symmetrical Model as the best model for substitution of nucleotides. Also in this locus, the inverse gamma rates and dirichlet base frequencies were used (SYM + I + G). The actual Bayesian calculations were performed in MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001). One tree was saved per 100 generations, and the run was automatically ended when the standard deviation of split frequencies was below 0.01. The temperature value of the Bayesian run was set at 0.2. To avoid suboptimal trees being taking into account for the consensus tree, a burn-in of 25 % of the saved trees was used. The resulting "50 % majority rule consensus" trees were visualised with TreeView v. 1.6.6 (Page 1996).

A second measure of branch support was obtained by conducting a ML analysis using RAxML software (Stamatakis *et al.* 2005) through the CIPRES Website (www.phylo.org). The same partitions were used as in the BI analyses, but because RAxML implements only the GTR substitution model, the symmetrical model for the ITS partition was waived. The robustness of trees in the ML analyses was evaluated by bootstrapping the datasets. The number of bootstrap replicates was automatically determined by the RAxML software (Stamatakis *et al.* 2008). The obtained trees in both analyses are lodged with TreeBASE (www.treebase.org).

Morphology

Morphological studies of the strains were performed on OA, malt extract agar (MEA) and cherry decoction agar (CHA) (Crous *et al*. 2009c). The cultures were incubated according to the methodologies described by Boerema *et al*. (2004). Eight days after inoculation, the colony growth was measured. At the 15th day after incubation, the colony colours were rated using the colour charts of Rayner (1970). Micromorphological features were studied after maturation of the pycnidia. Therefore, fungal structures were mounted in tap water using a scalpel blade and examined under a stereo light microscope. Perennial structures that were formed in the agar medium, such as chlamydospores, were cut out from the medium, and mounted in lactic acid. Remaining agar was removed from these samples by gently heating the glass slides. The sizes of the various structures were determined by averaging the measurements of 30 samples of each structure, except for conidiogenous cells and pycnidial wall characters, of which the size ranges were estimated based on 5–10 samples. Fifth and 95th percentiles were determined for all measurements and are provided in parentheses. By application of a droplet of 1N NaOH, the production of metabolite E+ was determined (Dorenbosch 1970, Noordeloos *et al*. 1993). The structure of the pycnidial wall and shape of conidiogenous cells were studied using microtome sections of 6 µm thickness, prepared with a Leica CM3050 freezing microtome and mounted in lactic acid. Taxonomic recombinations and novel species and descriptions were deposited in MycoBank.

RESULTS

Systematics of the genus *Phoma*

DNA phylogenetical analysis

Due to alignment difficulties multiple datasets, consisting of different sets of loci, were utilised. For a generic overview, LSU and SSU were included in the first alignment, which consisted of 76 taxa. A list of species names and numbers, original substrates, geographical origins and GenBank accession numbers of the strains used in this study is provided in Table 2. The aligned sequence matrix had a total length of 2 210 characters including alignment gaps (LSU: 1 258 and SSU: 952 bp). Of those characters, 1 809 (LSU: 994 and SSU: 815) were constant and 401 were variable (LSU: 264 and SSU: 137). The Bayesian analysis run was aborted after 10 000 000 generations as a point of stationarity was reached in the average standard deviation of split frequencies, at a value of 0.0288. The applied "burn-in" percentage of 25 % was well after stationarity in the probability of the trees was reached. The tree topologies and support values of the ML analysis, differed only slightly from the trees obtained from the Bayesian analyses, supporting the probability of the tree. The tree is rooted to *Pseudorobillarda phragmitis* (CBS 398.61).

Based on the LSU-SSU phylogenetic study performed here for the various anamorph and teleomorph species in the *Phoma* complex, eight clades were revealed (Fig. 1), including one which only comprises the outgroup specimen. The various clades will be treated below, but for additional synonymy on the *Phoma* species we refer to Boerema *et al.* (2004). The findings in these clades are largely in congruence with the observations of De Gruyter *et al.* (2009).

Species that were ascribed to the *Phoma* section *Phoma* by Boerema *et al.* (2004) appear to be genetically highly heterogeneous, as these species are recovered in almost every clade. Species that were ascribed to *Phoma* section *Heterospora* appear to be linked to at least three distinct clades. Also polymorphism is observed for sections *Paraphoma*, *Peyronellaea* and *Sclerophomella*, as well as for *Coniothyrium* and *Ascochyta*. The type species of this latter genus, *A. pisi*, is not included in the present tree, but is genetically similar to the *Didymellaceae*.

Table 2. Isolates of *Phoma* and related genera used for DNA analyses. The GenBank accession numbers in bold have been obtained from other studies.

Strain no.[1]	Holomorph[2]	GenBank no.		Original substrate	Locality
		SSU	LSU		
CBS 129.79	*Ampelomyces quisqualis*	**EU754029**	**EU754128**	Mildew on *Cucumis sativus*	Canada
CBS 543.70	*Aposphaeria populina*	**EU754031**	**EU754130**	*Populus canadensis*	Netherlands
CBS 246.79; PD 77/655	*Ascochyta caulina* T	**EU754032**	**EU754131**	*Atriplex hastata*	Germany
CBS 544.74	*Ascochyta hordei* var. *hordei*	**EU754035**	**EU754134**	*Triticum aevestum*	South Africa
CBS 117477	*Ascochyta* sp.	GU238202	GU237926	*Salicornia australis*	New Zealand
CBS 265.94	*Asteromella tiliae*	**EU754040**	**EU754139**	*Tilia platyphilos*	Austria
CBS 431.74; PD 74/2447	*Boeremia exigua* var. *exigua* B	**EU754084**	**EU754183**	*Solanum tuberosum*	Netherlands
CBS 341.67; CECT 20055; IMI 331912	*Boeremia foveata* B	GU238203	GU237947	*Solanum tuberosum*	U.K.
CBS 148.94	*Chaetasbolisia erysiphoides*	**EU754041**	**EU754140**	Unknown	Unknown
CBS 216.75; PD 71/1030	*Chaetosphaeronema hispidulum*	**EU754045**	**EU754144**	*Anthyllis vulneraria*	Germany
CBS 589.79	*Coniothyrium concentricum*	**EU754053**	**EU754152**	*Yucca* sp.	Netherlands
CBS 797.95	*Coniothyrium fuckelii*	GU238204	GU237960	*Rubus* sp.	Denmark
CBS 400.71	*Coniothyrium palmarum*	**EU754054**	**EU754153**	*Chamaerops humilis*	Italy
CBS 122787; PD 03486691	*Coniothyrium* sp.	**EU754052**	**EU754151**	Unknown	Germany
CBS 183.55	*Didymella exigua* T	**EU754056**	**EU754155**	*Rumex arifolius*	France
CBS 524.77	*Didymella fabae*	**EU754034**	**EU754133**	*Phaseolus vulgaris*	Belgium
CBS 581.83A	*Didymella rabiei*	GU238205	GU237970	*Cicer arietinum*	Syria
CBS 173.73; ATCC 24428; IMI 164070	*Epicoccum nigrum* T	GU238206	GU237975	*Dactylis glomerata*	U.S.A.
CBS 298.36	*Leptosphaeria biglobosa*	GU238207	GU237980	*Brassica napus* var. *napobrassica*	Unknown
CBS 127.23; MUCL 9930	*Leptosphaeria maculans*	**EU754090**	**EU754189**	*Brassica* sp.	Netherlands
CBS 939.69	*Leptosphaerulina australis*	**EU754068**	**EU754167**	Soil	Netherlands
CBS 525.71	*Macroventuria anomochaeta* T	GU238208	GU237984	Decayed canvas	South Africa
CBS 442.83	*Microsphaeropsis olivacea*	**EU754072**	**EU754171**	*Taxus baccata*	Netherlands
CBS 331.37	*Neottiosporina paspali*	**EU754073**	**EU754172**	*Paspalum notatum*	U.S.A.
CBS 122786; PD 99/1064-1	*Paraconiothyrium minitans*	**EU754075**	**EU754174**	Unknown	Unknown
CBS 626.68; IMI 108771	*Peyronellaea gardeniae* T	**GQ387534**	**GQ387595**	*Gardenia jasminoides*	India
CBS 528.66; PD 63/590	*Peyronellaea glomerata* B	**EU754085**	**EU754184**	*Chrysanthemum* sp.	Netherlands
CBS 531.66	*Peyronellaea pinodella* B	GU238209	GU238017	*Trifolium pratense*	U.S.A.
CBS 235.55	*Peyronellaea pinodes*	GU238210	GU238021	Unknown	Netherlands
CBS 588.69	*Peyronellaea zeae-maydis* T	**EU754093**	**EU754192**	*Zea mays*	U.S.A.
CBS 110110	*Phaeosphaeria oryzae*	**GQ387530**	**GQ387591**	*Oryza sativa*	South Korea
CBS 297.74	*Phialophorophoma litoralis*	**EU754078**	**EU754177**	Sea water	Montenegro
CBS 285.72	*Phoma apiicola* B	GU238211	GU238040	*Apium graveolens* var. *rapaceum*	Germany
CBS 337.65; ATCC 16195; IMI 113693	*Phoma capitulum* B	GU238212	GU238054	Soil	India
CBS 522.66	*Phoma chrysanthemicola* T	**GQ387521**	**GQ387582**	*Chrysanthemum morifolium*	U.K.
CBS 100311	*Phoma complanata*	**EU754082**	**EU754181**	*Heracleum sphondylium*	Netherlands
CBS 345.78; PD 76/1015	*Phoma dimorphospora*	GU238213	GU238069	*Chenopodium quinoa*	Peru
CBS 527.66	*Phoma eupyrena* B	GU238214	GU238072	Soil	Germany
CBS 161.78	*Phoma fallens* B	GU238215	GU238074	*Olea europaea*	New Zealand
CBS 170.70; ATCC 22707; CECT 20011; IMI 163514; PD 70/Alk	*Phoma fimeti* T	**GQ387523**	**GQ387584**	*Apium graveolens*	Netherlands

Table 2. (Continued).

Strain no.[1]	Holomorph[2]	GenBank no.		Original substrate	Locality
		SSU	LSU		
CBS 178.93; PD 82/1062	*Phoma flavescens* T	GU238216	GU238075	Soil	Netherlands
CBS 314.80	*Phoma flavigena* T	GU238217	GU238076	Water	Romania
CBS 633.92; ATCC 36786; VKM MF-325	*Phoma fungicola*	**EU754028**	**EU754127**	*Microsphaera alphitoides* on *Quercus* sp.	Ukraine
CBS 284.70	*Phoma glaucispora* B	GU238218	GU238078	*Nerium oleander*	Italy
CBS 175.93; PD 92/370	*Phoma haematocycla* T	GU238219	GU238080	*Phormium tenax*	New Zealand
CBS 615.75; PD 73/665, IMI 199779	*Phoma herbarum* B	**EU754087**	**EU754186**	*Rosa multiflora*	Netherlands
CBS 448.68	*Phoma heteromorphospora* B	**EU754088**	**EU754187**	*Chenopodium album*	Netherlands
CBS 467.76	*Phoma incompta* B	GU238220	GU238087	*Olea europaea*	Greece
CBS 253.92; PD 70/998	*Phoma lini* B	GU238221	GU238093	Water	U.S.A.
CBS 529.66; PD 66/521	*Phoma macrostoma* var. *macrostoma* B	GU238222	GU238098	*Malus sylvestris*	Netherlands
CBS 316.90	*Phoma medicaginis* var. *medicaginis*	GU238223	GU238103	*Medicago sativa*	Czech Republic
CBS 509.91; PD 77/920	*Phoma minutispora*	GU238224	GU238108	Saline soil	India
CBS 501.91; PD 83/888	*Phoma multipora* B	GU238225	GU238109	Unknown	Egypt
CBS 376.91; CBS 328.78, PD 77/1177	*Phoma opuntiae* B	GU238226	GU238123	*Opuntia ficus-indica*.	Peru
CBS 560.81; PD 92/1569; PDDCC 6614	*Phoma paspali* T	GU238227	GU238124	*Paspalum dilatatum*	New Zealand
CBS 445.81; PDDCC 7049	*Phoma pratorum* T	GU238228	GU238136	*Lolium perenne*	New Zealand
CBS 111.79; PD 76/437; IMI 386094	*Phoma radicina* B	**EU754092**	**EU754191**	*Malus sylvestris*	Netherlands
CBS 138.96; PD 82/653	*Phoma samarorum* B	**GQ387517**	**GQ387578**	*Phlox paniculata*	Netherlands
CBS 343.85; IMI 386097	*Phoma terricola* T	**GQ387563**	**GQ387624**	*Globodera pallida*	Netherlands
CBS 630.68; PD 68/141	*Phoma valerianae* B	GU238229	GU238150	*Valeriana phu*	Netherlands
CBS 539.63	*Phoma vasinfecta* T	GU238230	GU238151	*Chrysanthemum* sp.	Greece
CBS 306.68	*Phoma violicola* B	GU238231	GU238156	*Viola tricolor*	Unknown
CBS 523.66; PD 66/270	*Pleospora betae* B	**EU754080**	**EU754179**	*Beta vulgaris*	Netherlands
CBS 191.86; IMI 276975	*Pleospora herbarum* T	GU238232	GU238160	*Medicago sativa*	India
CBS 257.68; IMI 331911	*Pleurophoma cava*	**EU754100**	**EU754199**	Soil	Germany
CBS 398.61; IMI 070678	*Pseudorobillarda phragmitis* T	**EU754104**	**EU754203**	*Phragmites australis*	U.K.
CBS 122789; PD 03486800	*Pyrenochaeta acicola*	**EU754105**	**EU754204**	*Hordeum vulgare*	Unknown
CBS 306.65	*Pyrenochaeta lycopersici* T	**EU754106**	**EU754205**	*Lycopersicon esculentum*	Germany
CBS 407.76	*Pyrenochaeta nobilis* T	**EU754107**	**EU754206**	*Laurus nobilis*	Italy
CBS 252.60; ATCC 13735	*Pyrenochaeta romeroi* T	**EU754108**	**EU754209**	Man	Venezuela
CBS 524.50	*Sporormiella minima*	**DQ678003**	**DQ678056**	Goat dung	Panama
CBS 343.86	*Stagonospora neglecta* var. *colorata*	**EU754119**	**EU754218**	*Phragmites australis*	France
CBS 101.80; PD 75/909; IMI 386090	*Stagonosporopsis andigena* B	GU238233	GU238169	*Solanum* sp.	Peru
CBS 133.96; PD 79/127	*Stagonosporopsis cucurbitacearum*	GU238234	GU238181	*Cucurbita* sp.	New Zealand
CBS 631.68; PD 68/147	*Stagonosporopsis dennisii* B	GU238235	GU238182	*Solidago floribunda*	Netherlands
CBS 164.31	*Stenocarpella macrospora*	**EU754121**	**EU754220**	*Zea mays*	Unknown

[1]ATCC: American Type Culture Collection, Virginia, U.S.A.; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CECT: Colección Española de Cultivos Tipo, Valencia University, Spain; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, U.K.; MUCL: Mycotheque de l'Universite catholique de Louvain, Louvain-la-Neuve, Belgium; PD: Plant Protection Service, Wageningen, the Netherlands; PDDCC: Plant Diseases Division Culture Collection, Auckland, New Zealand; VKM: All-Russian Collection of Microorganisms, Pushchino, Russia.

[2]T: Ex-type strain; B: Reference strain according to Boerema *et al.* (2004).

Table 3. Strains from the *Didymellaceae* used for DNA analyses. The GenBank accession numbers in bold have been obtained from other studies.

Strain no.[1]	Holomorph[2]	GenBank no.			Original substrate	Locality
		LSU	ITS	TUB		
CBS 544.74	*Ascochyta hordei* var. *hordei*	**EU754134**	GU237887	GU237488	*Triticum aevestum*	South Africa
CBS 109.79; PD 77/747	*Boeremia crinicola* B	GU237927	GU237737	GU237489	*Crinum powellii*	Netherlands
CBS 118.93; PD 70/195	*Boeremia crinicola*	GU237928	GU237758	GU237490	*Crinum* sp.	Netherlands
CBS 101194; PD 79/687; IMI 373349	*Boeremia diversispora*	GU237929	GU237716	GU237491	*Phaseolus vulgaris*	Netherlands
CBS 102.80; PD 79/61; CECT 20049; IMI 331907	*Boeremia diversispora* B	GU237930	GU237725	GU237492	*Phaseolus vulgaris*	Kenya
CBS 119730	*Boeremia exigua* var. *coffeae*	GU237942	GU237759	GU237504	*Coffea arabica*	Brazil
CBS 109183; IMI 300060; PD 2000/10506	*Boeremia exigua* var. *coffeae* B	GU237943	GU237748	GU237505	*Coffea arabica*	Cameroon
CBS 431.74; PD 74/2447	*Boeremia exigua* var. e*xigua* B	**EU754183**	**FJ427001**	**FJ427112**	*Solanum tuberosum*	Netherlands
CBS 101150; PD 79/118	*Boeremia exigua* var. e*xigua*	GU237933	GU237715	GU237495	*Cichorium intybus*	Netherlands
CBS 101197; PD 95/721	*Boeremia exigua* var. *forsythiae*	GU237931	GU237718	GU237493	*Forsythia* sp.	Netherlands
CBS 101213; PD 92/959	*Boeremia exigua* var. *forsythiae* B	GU237932	GU237723	GU237494	*Forsythia* sp.	Netherlands
CBS 101196; PD 79/176	*Boeremia exigua* var. *heteromorpha*	GU237934	GU237717	GU237496	*Nerium oleander*	France
CBS 443.94	*Boeremia exigua* var. *heteromorpha* B	GU237935	GU237866	GU237497	*Nerium oleander*	Italy
CBS 569.79; PD 72/741	*Boeremia exigua* var. *lilacis* B	GU237936	GU237892	GU237498	*Syringa vulgaris*	Netherlands
CBS 114.28	*Boeremia exigua* var. *linicola*	GU237937	GU237752	GU237499	*Linum usitatissimum*	Netherlands
CBS 116.76; ATCC 32332; CECT 20022; CECT 20023; IMI 197074	*Boeremia exigua* var. *linicola* B	GU237938	GU237754	GU237500	*Linum usitatissimum*	Netherlands
CBS 100167; PD 93/217	*Boeremia exigua* var. *populi* T	GU237939	GU237707	GU237501	*Populus* (x) *euramericana*	Netherlands
CBS 101202; PD 82/942	*Boeremia exigua* var. *populi*	GU237940	GU237719	GU237502	*Salix* sp.	Netherlands
CBS 101207; PD 94/614	*Boeremia exigua* var. *pseudolilacis* T	GU237941	GU237721	GU237503	*Syringa vulgaris*	Netherlands
CBS 100354; PD 84/448	*Boeremia exigua* var. *viburni* B	GU237944	GU237711	GU237506	*Viburnum opulus*	Netherlands
CBS 101211; PD 93/838	*Boeremia exigua* var. *viburni*	GU237945	GU237722	GU237507	*Viburnum* sp.	Netherlands
CBS 109176; CECT 2828; PD 94/1394	*Boeremia foveata* B	GU237946	GU237742	GU237508	*Solanum tuberosum*	Bulgaria
CBS 341.67; CECT 20055; IMI 331912	*Boeremia foveata* B	GU237947	GU237834	GU237509	*Solanum tuberosum*	U.K.
CBS 366.91; PD 70/811	*Boeremia hedericola*	GU237948	GU237841	GU237510	*Hedera helix*	Netherlands
CBS 367.91; PD 87/229	*Boeremia hedericola* B	GU237949	GU237842	GU237511	*Hedera helix*	Netherlands
CBS 378.67; PD 76/276	*Boeremia lycopersici* B	GU237950	GU237848	GU237512	*Lycopersicon esculentum*	Netherlands
CBS 109172; PD 84/143	*Boeremia lycopersici*	GU237951	GU237739	GU237513	*Lycopersicon esculentum*	Netherlands
CBS 100353; PD 87/718	*Boeremia noackiana* B	GU237952	GU237710	GU237514	*Phaseolus vulgaris*	Guatemala
CBS 101203; PD 79/1114	*Boeremia noackiana*	GU237953	GU237720	GU237515	*Phaseolus vulgaris*	Colombia
CBS 109170; PD 75/796	*Boeremia sambuci-nigrae*	GU237954	GU237738	GU237516	*Sambucus nigra*	Netherlands
CBS 629.68; CECT 20048; IMI 331913; PD 67/753	*Boeremia sambuci-nigrae* T	GU237955	GU237897	GU237517	*Sambucus nigra*	Netherlands
CBS 126.93; PD 73/642	*Boeremia strasseri*	GU237956	GU237773	GU237518	*Mentha* sp.	Netherlands
CBS 261.92; ATCC 244146; PD 92/318	*Boeremia strasseri*	GU237957	GU237812	GU237519	*Mentha piperita*	U.S.A.
CBS 109175; PD 79/524	*Boeremia telephii* B	GU237958	GU237741	GU237520	*Sedum spectabile*	Netherlands
CBS 760.73; PD 71/1616	*Boeremia telephii* B	GU237959	GU237905	GU237521	*Sedum spectabile*	Netherlands
CBS 148.94	*Chaetasbolisia erysiphoides*	**EU754140**	GU237785	GU237522	Unknown	Unknown
CBS 187.83; PD 82/128	*Didymella adianticola* B	GU238035	GU237796	GU237576	*Polystichum adiantiforme*	U.S.A.
CBS 258.92; PD 89/1887	*Didymella adianticola*	GU238036	GU237811	GU237577	*Polystichum adiantiforme*	Costa Rica
CBS 102634; PD 75/248	*Didymella applanata*	GU237997	GU237726	GU237555	*Rubus idaeus*	Netherlands
CBS 205.63	*Didymella applanata* T	GU237998	GU237798	GU237556	*Rubus idaeus*	Netherlands
CBS 234.37	*Didymella cannabis*	GU237961	GU237804	GU237523	*Cannabis sativa*	Unknown
CBS 102635; PD 77/1131	*Didymella catariae*	GU237962	GU237727	GU237524	*Nepeta catenaria*	Netherlands
CBS 183.55	*Didymella exigua* T	**EU754155**	GU237794	GU237525	*Rumex arifolius*	France
CBS 524.77	*Didymella fabae*	GU237963	GU237880	GU237526	*Phaseolus vulgrais*	Belgium
CBS 649.71	*Didymella fabae*	GU237964	GU237902	GU237527	*Vicia faba*	Netherlands

Table 3. (Continued).

Strain no.[1]	Holomorph[2]	GenBank no.			Original substrate	Locality
		LSU	ITS	TUB		
PD 83/492	*Didymella fabae*	GU237965	GU237917	GU237528	*Phaseolus vulgaris*	Netherlands
PD 84/512	*Didymella macropodii*	GU237966	GU237919	GU237529	Crucifer	Unknown
CBS 100190; PD 82/736	*Didymella macropodii*	GU237967	GU237708	GU237530	*Brassica napus*	Germany
CBS 126.54	*Didymella pisi*	GU237968	GU237772	GU237531	*Pisum sativum*	Netherlands
CBS 122785; PD 78/517	*Didymella pisi*	GU237969	GU237763	GU237532	*Pisum sativum*	Netherlands
CBS 534.65	*Didymella rabiei*	GU237970	GU237886	GU237533	*Cicer arietinum*	India
CBS 581.83a	*Didymella rabiei*	GU237971	GU237894	GU237534	*Cicer arietinum*	Syria
CBS 121.75; ATCC 32164; IHEM 3403; IMI 194767; PD 73/584	*Didymella urticicola* T	GU237972	GU237761	GU237535	*Urtica dioica*	Netherlands
PD 73/570	*Didymella urticicola*	GU237973	GU237914	GU237536	*Urtica dioica*	Netherlands
CBS 454.64	*Didymella vitalbina*	**FJ515646**	**FJ515605**	**FJ515623**	*Clematis vitalba*	France
CBS 138.25	*Diplodina coloradensis*	**EU754158**	GU237784	GU237537	*Senecio* sp.	Unknown
CBS 172.34	*"Dothiorella ulmi"*	**EU754160**	GU237789	GU237538	*Ulmus* sp.	U.S.A.
CBS 125.82; IMI 1331914; CECT 20044	*Epicoccum nigrum*	GU237974	**FJ426995**	**FJ427106**	Human	Netherlands
CBS 173.73; ATCC 24428; IMI 164070	*Epicoccum nigrum* T	GU237975	**FJ426996**	**FJ427107**	*Dactylis glomerata*	U.S.A.
CBS 246.60; ATCC 22237; ATCC 16652; IMI 081601	*Epicoccum pimprinum* T	GU237976	**FJ427049**	**FJ427159**	Soil	India
PD 77/1028	*Epicoccum pimprinum*	GU237977	**FJ427050**	**FJ427160**	Unknown	Unknown
CBS 179.80; PD 76/1018	*Epicoccum sorghi*	GU237978	**FJ427067**	**FJ427173**	*Sorghum vulgare*	Puerto Rico
CBS 627.68; PD 66/926	*Epicoccum sorghi*	GU237979	**FJ427072**	**FJ427178**	*Citrus* sp.	France
CBS 213.55	*Leptosphaerulina americana*	GU237981	GU237799	GU237539	*Trifolium pretense*	U.S.A.
CBS 275.59; ATCC 13446	*Leptosphaerulina arachidicola*	GU237983	GU237820	GU237543	*Arachis hypochea*	Taiwan
CBS 317.83	*Leptosphaerulina australis*	**EU754166**	GU237829	GU237540	*Eugenia aromatica*	Indonesia
CBS 939.69	*Leptosphaerulina australis*	**EU754167**	GU237911	GU237541	Soil	Netherlands
CBS 235.58	*Leptosphaerulina trifolii*	GU237982	GU237806	GU237542	*Trifolium* sp.	Netherlands
CBS 525.71	*Macroventuria anomochaeta* T	GU237984	GU237881	GU237544	decayed canvas	South Africa
CBS 502.72	*Macroventuria anomochaeta*	GU237985	GU237873	GU237545	*Medicago sativa*	South Africa
CBS 526.71	*Macroventuria wentii*	GU237986	GU237881	GU237546	Unidentified plant material	U.S.A.
CBS 432.71	*Microsphaeropsis olivacea*	GU237987	GU237863	GU237548	*Sorothamus* sp.	Netherlands
CBS 233.77	*Microsphaeropsis olivacea*	GU237988	GU237803	GU237549	*Pinus laricio*	France
CBS 442.83	*Microsphaeropsis olivacea*	**EU754171**	GU237865	GU237547	*Taxus baccata*	Netherlands
CBS 132.96; PD 93/853	*Peyronellaea alectorolophi* T	GU237989	GU237778	GU237550	*Rhinanthus major*	Netherlands
CBS 185.85; PD 80/1191	*Peyronellaea americana* B	GU237990	**FJ426972**	**FJ427088**	*Zea mays*	U.S.A.
CBS 568.97; PD 94/1544; ATCC 44494	*Peyronellaea americana*	GU237991	**FJ426974**	**FJ427090**	*Glycine max*	U.S.A.
PD 82/1059	*Peyronellaea americana*	GU237992	**FJ426980**	**FJ427096**	Nematode cyst	Unknown
CBS 360.84	*Peyronellaea anserina* B	GU237993	GU237839	GU237551	Potatoflour	Netherlands
CBS 363.91; PD 79/712	*Peyronellaea anserina*	GU237994	GU237840	GU237552	*Pisum sativum*	Netherlands
CBS 315.90; PD 80/1190	*Peyronellaea arachidicola*	GU237995	GU237827	GU237553	*Arachis hypogaea*	Zimbabwe
CBS 333.75; ATCC 28333; IMI 386092; PREM 44889	*Peyronellaea arachidicola* T	GU237996	GU237833	GU237554	*Arachis hypogaea*	South Africa
CBS 269.93; PD 78/1087	*Peyronellaea aurea* B	GU237999	GU237818	GU237557	*Medicago polymorpha*	New Zealand
CBS 444.81; PDDCC 6546	*Peyronellaea australis* T	GU238000	GU237867	GU237558	*Actinidia chinensis*	New Zealand
PD 77/919	*Peyronellaea australis*	GU238001	GU237915	GU237559	*Actinidea chinensis*	Unknown
CBS 109.92; PD 73/1405	*Peyronellaea calorpreferens* T	GU238002	**FJ426983**	**FJ427098**	Undefined food material	Netherlands
CBS 630.97; ATCC 96683; IMI 361196; PD 96/2022	*Peyronellaea calorpreferens*	GU238004	GU237925	GU237560	*Heterodera glycines*	U.S.A.
CBS 875.97; PD 93/1503	*Peyronellaea calorpreferens*	GU238003	GU237908	GU237561	Indoor environment	U.S.A.
CBS 123380; PD 84/1013	*Peyronellaea coffeae-arabicae* T	GU238005	**FJ426993**	**FJ427104**	*Coffea arabica*	Ethiopia

Table 3. (Continued).

Strain no.[1]	Holomorph[2]	GenBank no.			Original substrate	Locality
		LSU	ITS	TUB		
CBS 123398; PD 84/1014	*Peyronellaea coffeae-arabicae*	GU238006	**FJ426994**	**FJ427105**	*Coffea arabica*	Ethiopia
PD 92/1460	*Peyronellaea curtisii*	GU238012	**FJ427041**	**FJ427151**	*Sprekelia*	Netherlands
CBS 251.92; PD 86/1145	*Peyronellaea curtisii* B	GU238013	**FJ427038**	**FJ427148**	*Nerine* sp.	Netherlands
CBS 377.91; PD 79/210	*Peyronellaea eucalyptica* B	GU238007	GU237846	GU237562	*Eucalyptus* sp.	Australia
CBS 508.91; PD 73/1413	*Peyronellaea eucalyptica*	GU238008	GU237878	GU237563	Water	Croatia
CBS 302.79; PD 79/1156	*Peyronellaea gardeniae*	**GQ387596**	**FJ427002**	**FJ427113**	Air	Netherlands Antilles
CBS 626.68; IMI 108771	*Peyronellaea gardeniae* T	**GQ387595**	**FJ427003**	**FJ427114**	*Gardenia jasminoides*	India
CBS 464.97; MUCL 9882	*Peyronellaea glomerata*	GU238009	**FJ427012**	**FJ427123**	Indoor environment	Netherlands
CBS 528.66; PD 63/590	*Peyronellaea glomerata* B	**EU754184**	**FJ427013**	**FJ427124**	*Chrysanthemum* sp.	Netherlands
CBS 103.25	*Peyronellaea lethalis*	GU238010	GU237729	GU237564	Unknown	Unknown
CBS 463.69	*Peyronellaea musae* B	GU238011	**FJ427026**	**FJ427136**	*Mangifera indica*	India
CBS 377.93; PD 80/976	*Peyronellaea obtusa* B	GU238014	GU237847	GU237565	*Daucus carota*	Netherlands
CBS 391.93; PD 80/87	*Peyronellaea obtusa* B	GU238015	GU237858	GU237566	*Spinacia oleracea*	Netherlands
CBS 318.90; PD 81/729	*Peyronellaea pinodella*	GU238016	**FJ427051**	**FJ427161**	*Pisum sativum*	Netherlands
CBS 531.66	*Peyronellaea pinodella* B	GU238017	**FJ427052**	**FJ427162**	*Trifolium pratense*	U.S.A.
CBS 100580; PD 98/1135	*Peyronellaea pinodella*	GU238018	GU237713	GU237567	*Glycine max*	Hungary
CBS 567.97; PD 97/2160	*Peyronellaea pinodella*	GU238019	GU237891	GU237568	*Glycine max*	Hungary
CBS 159.78b	*Peyronellaea pinodes*	GU238020	GU237786	GU237569	*Pisum sativum*	Iraq
CBS 285.49	*Peyronellaea pinodes*	GU238022	GU237823	GU237571	*Primula auricula*	Switzerland
CBS 235.55	*Peyronellaea pinodes*	GU238021	GU237805	GU237570	Unknown	Netherlands
CBS 525.77	*Peyronellaea pinodes*	GU238023	GU237883	GU237572	*Pisum sativum*	Belgium
CBS 525.77a	*Peyronellaea pinodes*	GU238024	GU237882	GU237573	*Pisum sativum*	Belgium
CBS 539.66; ATCC 16791; IMI 122266; PD 64/914	*Peyronellaea pomorum* var. *pomorum* B	GU238028	**FJ427056**	**FJ427166**	*Polygonum tataricum*	Netherlands
CBS 285.76; ATCC 26241; IMI 176742; VKM F-1843	*Peyronellaea pomorum* var. *circinata* T	GU238025	**FJ427053**	**FJ427163**	*Heracleum dissectum*	Russia
CBS 286.76; ATCC 26242; IMI 176743; VKM F-1844	*Peyronellaea pomorum* var. *circinata*	GU238026	**FJ427054**	**FJ427164**	*Allium nutans*	Russia
CBS 388.80; PREM 45736	*Peyronellaea pomorum* var. *cyanea* T	GU238027	**FJ427055**	**FJ427165**	*Triticum* sp.	South Africa
CBS 381.96; PD 71/706	*Peyronellaea protuberans* B	GU238029	GU237853	GU237574	*Lycium halifolium*	Netherlands
CBS 281.83	*Peyronellaea sancta* T	GU238030	**FJ427063**	**FJ427170**	*Ailanthus altissima*	South Africa
LEV 15292	*Peyronellaea sancta*	GU238031	**FJ427065**	**FJ427172**	*Gleditsia triacantha*	Unknown
CBS 110.92; PD 76/1010	*Peyronellaea subglomerata* B	GU238032	**FJ427080**	**FJ427186**	*Triticum* sp.	U.S.A.
PD 78/1090	*Peyronellaea subglomerata*	GU238033	**FJ427081**	**FJ427187**	*Zea mays*	Unknown
CBS 588.69	*Peyronellaea zeae-maydis* T	**EU754186**	**FJ427086**	**FJ427190**	*Zea mays*	U.S.A.
CBS 179.97	*Phoma acetosellae*	GU238034	GU237793	GU237575	*Rumex hydrolapathum*	Netherlands
CBS 379.93; PD 82/945	*Phoma aliena*	GU238037	GU237851	GU237578	*Berberis* sp.	Netherlands
CBS 877.97; PD 94/1401	*Phoma aliena*	GU238038	GU237910	GU237579	*Buxus sempervirens*	Netherlands
CBS 381.91; PD 79/1110	*Phoma anigozanthi* B	GU238039	GU237852	GU237580	*Anigozanthus maugleisii*	Netherlands
CBS 107.96; PD 73/598	*Phoma aquilegiicola* B	GU238041	GU237735	GU237582	*Aconitum pyramidale*	Netherlands
CBS 108.96; PD 79/611	*Phoma aquilegiicola* B	GU238042	GU237736	GU237583	*Aquilegia* sp.	Netherlands
CBS 125.93; PD 77/1029	*Phoma arachidis-hypogaeae* B	GU238043	GU237771	GU237584	*Arachis hypogaea*	India
CBS 383.67; PD 65/223	*Phoma aubrietiae* B	GU238044	GU237854	GU237585	*Aubrietia hybrida* cv. Superbissima	Netherlands
CBS 627.97; PD 70/714	*Phoma aubrietiae* B	GU238045	GU237895	GU237586	*Aubrietia* sp.	Netherlands
CBS 714.85; PD 74/265	*Phoma bellidis* B	GU238046	GU237904	GU237587	*Bellis perennis*	Netherlands
PD 94/886	*Phoma bellidis*	GU238047	GU237923	GU237581	*Bellis* sp.	Netherlands

Table 3. (Continued).

Strain no.[1]	Holomorph[2]	GenBank no.			Original substrate	Locality
		LSU	ITS	TUB		
CBS 109942; PD 84/402	*Phoma boeremae* T	GU238048	**FJ426982**	**FJ427097**	*Medicago littoralis* cv. Harbinger	Australia
CBS 120105	*Phoma brasiliensis* T	GU238049	GU237760	GU237588	*Amaranthus* sp.	Brazil
CBS 357.84	*Phoma bulgarica* T	GU238050	GU237837	GU237589	*Trachystemon orientale*	Bulgaria
CBS 124515; PD 82/1058	*Phoma bulgarica*	GU238051	GU237768	GU237590	*Trachystemon orientale*	Bulgaria
CBS 448.83	*Phoma calidophila* T	GU238052	**FJ427059**	**FJ427168**	Soil	Egypt
PD 84/109	*Phoma calidophila*	GU238053	**FJ427060**	**FJ427169**	*Cucumis sativus*	Europe
CBS 128.93; PD 79/140	*Phoma chenopodiicola* B	GU238055	GU237775	GU237591	*Chenopodium quinoa* cv. Sajana	Peru
CBS 129.93; PD 89/803	*Phoma chenopodiicola*	GU238056	GU237776	GU237592	*Chenopodium quinoa* cv. Sajana	Peru
CBS 102.66	*Phoma clematidina*	**FJ515630**	**FJ426988**	**FJ427099**	*Clematis* sp.	U.K.
CBS 108.79; PD 78/522	*Phoma clematidina* T	**FJ515632**	**FJ426989**	**FJ427100**	*Clematis* sp.	Netherlands
CBS 507.63; MUCL 9574; PD 07/03486747	*Phoma clematidis-rectae* T	**FJ515647**	**FJ515606**	**FJ515624**	*Clematis* sp.	Netherlands
PD 95/1958	*Phoma clematidis-rectae*	**FJ515648**	**FJ515607**	**FJ515625**	*Clematis* sp.	Netherlands
CBS 100409	*Phoma commelinicicola* B	GU238057	GU237712	GU237593	*Tradescantia* sp.	New Zealand
CBS 100311	*Phoma complanata*	**EU754181**	GU237709	GU237594	*Heracleum sphondylium*	Netherlands
CBS 268.92; PD 75/3	*Phoma complanata*	**EU754180**	GU237815	GU237595	*Angelica sylvestris*	Netherlands
CBS 506.91; IMI 215229; PD 91/876	*Phoma costarricensis* B	GU238058	GU237876	GU237596	*Coffea* sp.	Nicaragua
CBS 497.91; PD 79/209	*Phoma costarricensis*	GU238059	GU237870	GU237597	*Coffea arabica*	Unknown
CBS 193.82	*Phoma crystallifera* T	GU238060	GU237797	GU237598	*Chamaespartium sagittale*	Austria
CBS 124513 ; PD 73/1414	*Phoma dactylidis* T	GU238061	GU237766	GU237599	*Dactylis glomerata*	U.S.A.
CBS 133.93; PD 88/961; IMI 173142	*Phoma destructiva* var. *destructiva*	GU238064	GU237779	GU237602	*Solanum lycopersicum*	Guadeloupe
CBS 378.73; CECT 2877	*Phoma destructiva* var. *destructiva* B	GU238063	GU237849	GU237601	*Lycopersicon esculentum*	Tonga
CBS 162.78; PD 77/725	*Phoma destructiva* var. *diversispora*	GU238062	GU237788	GU237600	*Lycopersicon esculentum*	Netherlands
CBS 507.91; PD 74/148	*Phoma dictamnicola* B	GU238065	GU237877	GU237603	*Dictamnus albus*	Netherlands
CBS 109179; PD 90/835-1	*Phoma digitalis*	GU238066	GU237744	GU237604	*Digitalis* sp.	Netherlands
CBS 229.79; LEV 7660	*Phoma digitalis* B	GU238067	GU237802	GU237605	*Digitalis purpurea*	New Zealand
CBS 346.82	*Phoma dimorpha* T	GU238068	GU237835	GU237606	*Opuntiae* sp.	Spain
CBS 186.83; PD 82/47	*Phoma draconis* B	GU238070	GU237795	GU237607	*Dracaena* sp.	Rwanda
CBS 123.93; PD 77/1148	*Phoma eupatorii* B	GU238071	GU237764	GU237608	*Eupatorium cannabinum*	Netherlands
CBS 374.91; PD 78/391	*Phoma eupyrena* B	GU238072	**FJ426999**	**FJ427110**	*Solanum tuberosum*	Netherlands
CBS 527.66; ATCC 22238	*Phoma eupyrena* B	GU238073	**FJ427000**	**FJ427111**	Soil	Germany
CBS 633.92; ATCC 36786; VKM MF-325	*Phoma fungicola*	**EU754127**	GU237900	GU237609	*Microsphaera alphitoides* on *Quercus* sp.	Ukraine
CBS 112.96	*Phoma glaucii*	GU238077	GU237750	GU237610	*Dicentra* sp.	Netherlands
CBS 114.96; PD 94/888	*Phoma glaucii* B	**FJ515649**	**FJ515609**	**FJ515627**	*Chelidonium majus*	Netherlands
CBS 377.67	*Phoma gossypiicola* B	GU238079	GU237845	GU237611	*Gossypium hirsutum*	U.S.A.
CBS 104.80; PD 74/1017	*Phoma henningsii* B	GU238081	GU237731	GU237612	*Acacia mearnesii*	Kenya
CBS 502.91; PD 86/276	*Phoma herbarum*	GU238082	GU237874	GU237613	*Nerium* sp.	Netherlands
CBS 615.75; PD 73/665; IMI 199779	*Phoma herbarum* B	**EU880896**	**FJ427022**	**FJ427133**	*Rosa multiflora*	Netherlands
CBS 629.97; PD 76/1017	*Phoma herbicola* B	GU238083	GU237898	GU237614	Water	U.S.A.
CBS 105.80; PD 75/908	*Phoma huancayensis* T	GU238084	GU237732	GU237615	*Solanum* sp.	Peru
CBS 390.93; PD 77/1173	*Phoma huancayensis*	GU238085	GU237857	GU237616	*Chenopodium quinoa*	Peru
CBS 220.85	*Phoma humicola* B	GU238086	GU237800	GU237617	*Franseria* sp.	U.S.A.
CBS 123394	*Phoma infossa*	GU238088	**FJ427024**	**FJ427134**	*Fraxinus pennsylvanica*	Argentina
CBS 123395	*Phoma infossa* T	GU238089	**FJ427025**	**FJ427135**	*Fraxinus pennsylvanica*	Argentina
CBS 252.92; PD 80/1144	*Phoma insulana* B	GU238090	GU237810	GU237618	*Olea europaea*	Greece

Table 3. (Continued).

Strain no.[1]	Holomorph[2]	GenBank no.			Original substrate	Locality
		LSU	ITS	TUB		
CBS 124.93; PD 87/269	*Phoma labilis* B	GU238091	GU237765	GU237619	*Solanum lycopersicum*	Netherlands
CBS 479.93; PD 70/93	*Phoma labilis*	GU238092	GU237868	GU237620	*Rosa* sp.	Israel
CBS 347.82	*Phoma longicolla*	GU238094	GU237836	GU237621	*Opuntiae* sp.	Spain
CBS 124514; PD 80/1189; VPRI 1239	*Phoma longicolla* T	GU238095	GU237767	GU237622	*Opuntiae* sp.	Spain
CBS 223.69	*Phoma macrostoma* var. *incolorata* B	GU238096	GU237801	GU237623	*Acer pseudoplatanus*	Switzerland
CBS 109173; PD 83/908	*Phoma macrostoma* var. *incolorata* B	GU238097	GU237740	GU237624	*Malus sylvestris*	Netherlands
CBS 529.66; PD 66/521	*Phoma macrostoma* var. *macrostoma* B	GU238098	GU237885	GU237625	*Malus sylvestris*	Netherlands
CBS 482.95	*Phoma macrostoma* var. *macrostoma*	GU238099	GU237869	GU237626	*Larix decidua*	Germany
CBS 259.92; IMI 286996; PD 91/272	*Phoma matteuciicola* B	GU238100	GU237812	GU237627	*Matteuccia struthiopteris*	Canada
CBS 112.53	*Phoma medicaginis* var. *macrospora* B	GU238101	GU237749	GU237628	*Medicago sativa*	U.S.A.
CBS 404.65; IMI 116999	*Phoma medicaginis* var. *macrospora* B	GU238102	GU237859	GU237629	*Medicago sativa*	Canada
CBS 316.90	*Phoma medicaginis* var. *medicaginis*	GU238103	GU237828	GU237630	*Medicago sativa*	Czech Republic
CBS 105.95	*Phoma microchlamydospora* T	GU238104	**FJ427028**	**FJ427138**	*Eucalyptus* sp.	U.K.
CBS 491.90	*Phoma microchlamydospora*	GU238105	**FJ427029**	**FJ427139**	Unidentified vegetable	U.K.
CBS 315.83	*Phoma minor*	GU238106	GU237826	GU237631	*Syzygium aromaticum*	Indonesia
CBS 325.82	*Phoma minor* T	GU238107	GU237831	GU237632	*Syzygium aromaticum*	Indonesia
CBS 110.79; PD 65/8875; MUCL 8247	*Phoma multirostrata*	GU238110	**FJ427030**	**FJ427140**	*Cucumis sativus*	Netherlands
CBS 274.60; IMI 081598	*Phoma multirostrata* T	GU238111	**FJ427031**	**FJ427141**	Soil	India
CBS 368.65; PD 92/1757; HACC 154	*Phoma multirostrata*	GU238112	**FJ427033**	**FJ427143**	Soil	India
PD 83/48	*Phoma multirostrata*	GU238113	**FJ427037**	**FJ427147**	*Cucumis sativus*	Unknown
CBS 117.93; PD 83/90	*Phoma nebulosa*	GU238114	GU237757	GU237633	*Mercurialis perennis*	Netherlands
CBS 503.75; ATCC 32163; DSM 63391; IMI 194766; PD 75/4	*Phoma nebulosa* B	GU238115	GU237875	GU237634	*Urtica dioica*	Austria
CBS 358.71	*Phoma negriana* B	GU238116	GU237838	GU237635	*Vitis vinifera*	Germany
PD 79/74	*Phoma negriana*	GU238117	GU237916	GU237636	*Vitis vinifera*	Netherlands
CBS 116.96; PD 95/7930	*Phoma nigripycnidia* B	GU238118	GU237756	GU237637	*Vicia cracca*	Russia
CBS 114.93; PD 74/228	*Phoma novae- verbascicola*	GU238119	GU237753	GU237638	*Verbascum* sp.	Netherlands
CBS 127.93; PD 92/347	*Phoma novae-verbascicola* B	GU238120	GU237774	GU237639	*Verbascum densiflorum*	Netherlands
CBS 654.77	*Phoma omnivirens*	GU238122	**FJ427043**	**FJ427153**	Unknown	India
CBS 991.95	*Phoma omnivirens*	GU238121	**FJ427044**	**FJ427154**	Soil	Papua New Guinea
CBS 560.81; PD 92/1569; PDDCC 6614	*Phoma paspali* T	GU238124	**FJ427048**	**FJ427158**	*Paspalum dilatatum*	New Zealand
CBS 561.81; PDDCC 6615	*Phoma paspali*	GU238125	GU237889	GU237640	*Lolium perenne*	New Zealand
CBS 124516; PD 84/453	*Phoma pedeiae*	GU238126	GU237769	GU237641	*Orchidaceae*	Netherlands
CBS 124517; PD 92/612A	*Phoma pedeiae* T	GU238127	GU237770	GU237642	*Schefflera elegantissima*	Netherlands
CBS 267.92; PD 76/1014	*Phoma pereupyrena* T	GU238128	GU237814	GU237643	*Coffea arabica*	India
CBS 268.93; CBS 108.93; PD 88/720	*Phoma piperis* B	GU238129	GU237816	GU237644	*Peperomia pereskifolia*	Netherlands
PD 90/2011	*Phoma piperis*	GU238130	GU237921	GU237645	*Peperomia* sp.	Netherlands
CBS 284.93; PD 75/907	*Phoma plurivora*	GU238131	GU237822	GU237646	*Medicago sativa*	Australia
CBS 558.81; PDDCC 6873	*Phoma plurivora* T	GU238132	GU237888	GU237647	*Setaria* sp.	New Zealand
CBS 109181; PD 83/757	*Phoma polemonii* B	GU238133	GU237746	GU237648	*Polemonium caeruleum*	Netherlands
CBS 116.93; PD 71/884	*Phoma poolensis* B	GU238134	GU237755	GU237649	*Antirrhinum majus*	Netherlands
CBS 113.20; PD 92/774	*Phoma poolensis*	GU238135	GU237751	GU237650	Unknown	Unknown
CBS 372.91; PD 75/690	*Phoma putaminum* B	GU238137	GU237843	GU237651	*Ulmus* sp.	Netherlands
CBS 130.69; CECT 20054; IMI 331916	*Phoma putaminum* B	GU238138	GU237777	GU237652	*Malus sylvestris*	Denmark
CBS 109177; LEV 15165; PD 2000/9941	*Phoma rhei* B	GU238139	GU237743	GU237653	*Rheum rhaponticum*	New Zealand
CBS 298.89	*Phoma saxea*	GU238140	GU237824	GU237654	Limestone	Germany

Table 3. (Continued).

Strain no.[1]	Holomorph[2]	GenBank no.			Original substrate	Locality
		LSU	ITS	TUB		
CBS 419.92	*Phoma saxea* T	GU238141	GU237860	GU237655	Corroded mediterranean marble	Germany
CBS 122.93; PD 77/1049	*Phoma selaginellicola* B	GU238142	GU237762	GU237656	*Selaginella* sp.	Netherlands
CBS 160.78; LEV 11451	*Phoma senecionis* B	GU238143	GU237787	GU237657	*Senecio jacobaea*	New Zealand
CBS 249.92; PD 78/1088	*Phoma subherbarum*	GU238144	GU237808	GU237658	*Solanum* sp.	Peru
CBS 250.92; DAOM 171914; PD 92/371	*Phoma subherbarum* B	GU238145	GU237809	GU237659	*Solanum* sp.	Peru
CBS 305.79A; DAOM 170848	*Phoma subherbarum*	GU238146	GU237825	GU237660	*Zea mays*	Peru
CBS 135.93; PD 83/87	*Phoma sylvatica* B	GU238147	GU237781	GU237661	*Melampyrum pratense*	Netherlands
CBS 874.97; PD 93/764	*Phoma sylvatica* B	GU238148	GU237907	GU237662	*Melampyrum pratense*	Netherlands
CBS 436.75	*Phoma tropica* T	GU238149	GU237864	GU237663	*Saintpaulia ionantha*	Germany
CBS 876.97; PD 82/1008	*Phoma versabilis* B	GU238152	GU237909	GU237664	*Silene* sp.	Netherlands
PD 2000/1379	*Phoma versabilis*	GU238153	GU237913	GU237665	*Stellaria media*	Netherlands
CBS 500.91; PD 83/322	*Phoma viburnicola* B	GU238154	GU237871	GU237666	*Ilex aquifolium*	Netherlands
CBS 523.73; PD 69/800	*Phoma viburnicola* B	GU238155	GU237879	GU237667	*Viburnum cassioides*	Netherlands
CBS 383.68	*Phoma xanthina* B	GU238157	GU237855	GU237668	*Delphinium* sp.	Netherlands
PD 84/407	*Phoma xanthina*	GU238158	GU237918	GU237669	*Delphinium* sp.	Netherlands
CBS 131.93; PD 69/140	*Phoma zantedeschiae*	GU238159	**FJ427084**	**FJ427188**	*Calla* sp.	Netherlands
CBS 105.96; PD 74/230	*Stagonosporopsis actaeae* B	GU238165	GU237733	GU237670	*Cimicifuga simplex*	Netherlands
CBS 106.96; PD 94/1318	*Stagonosporopsis actaeae* T	GU238166	GU237734	GU237671	*Actaea spicata*	Netherlands
CBS 176.93; PD 86/547	*Stagonosporopsis ajacis*	GU238167	GU237790	GU237672	*Delphinium* sp.	Netherlands
CBS 177.93; PD 90/115	*Stagonosporopsis ajacis* T	GU238168	GU237791	GU237673	*Delphinium* sp.	Kenya
CBS 101.80; PD 75/909; IMI 386090	*Stagonosporopsis andigena* B	GU238169	GU237714	GU237674	*Solanum* sp.	Peru
CBS 269.80; PD 75/914	*Stagonosporopsis andigena*	GU238170	GU237817	GU237675	*Solanum* sp.	Peru
CBS 102636; PD 73/1409	*Stagonosporopsis artemisiicola* B	GU238171	GU237728	GU237676	*Artemisia dracunculus*	France
CBS 178.25; MUCL 9915	*Stagonosporopsis astragali* B	GU238172	GU237792	GU237677	*Astragalus* sp.	Unknown
CBS 248.90	*Stagonosporopsis caricae*	GU238175	GU237807	GU237680	*Carica papaya*	Chile
PD 06/03082531	*Stagonosporopsis caricae*	GU238176	GU237912	GU237681	*Carica papaya*	Brazil
CBS 282.76	*Stagonosporopsis caricae*	GU238177	GU237821	GU237682	*Brassica* sp.	Indonesia
CBS 713.85; ATCC 76027; PD 83/826	*Stagonosporopsis crystalliniformis* T	GU238178	GU237903	GU237683	*Lycopersicon esculentum*	Colombia
CBS 771.85; IMI 386091; PD 85/772	*Stagonosporopsis crystalliniformis*	GU238179	GU237906	GU237684	*Solanum tuberosum*	Colombia
CBS 109171; PD 91/310; PDDCC 272	*Stagonosporopsis cucurbitacearum*	GU238180	GU237922	GU237685	*Cucurbita* sp.	Netherlands
CBS 133.96; PD 79/127	*Stagonosporopsis cucurbitacearum*	GU238181	GU237780	GU237686	*Cucurbita* sp.	New Zealand
CBS 631.68; PD 68/147	*Stagonosporopsis dennisii* B	GU238182	GU237899	GU237687	*Solidago floribunda*	Netherlands
CBS 135.96; IMI 19337; PD 95/4756	*Stagonosporopsis dennisii*	GU238183	GU237782	GU237688	*Solidago canadensis*	Canada
CBS 320.90; PD 86/932	*Stagonosporopsis dorenboschii* B	GU238184	GU237830	GU237689	*Physostegia virginiana*	Netherlands
CBS 426.90; IMI 386093; PD 86/551	*Stagonosporopsis dorenboschii* T	GU238185	GU237862	GU237690	*Physostegia virginiana*	Netherlands
CBS 109182; PD 74/231	*Stagonosporopsis heliopsidis* B	GU238186	GU237747	GU237691	*Heliopsis patula*	Netherlands
PD 95/6189; DAOM 221138	*Stagonosporopsis heliopsidis*	GU238187	GU237924	GU237692	*Ambrosia artemisiifolia*	Canada
CBS 104.42	*Stagonosporopsis hortensis* B	GU238198	GU237730	GU237703	Unknown	Netherlands
CBS 572.85; PD 79/269	*Stagonosporopsis hortensis* B	GU238199	GU237893	GU237704	*Phaseolus vulgaris*	Netherlands
CBS 425.90; PD 81/520	*Stagonosporopsis ligulicola* var. *inoxydabilis* T	GU238188	GU237861	GU237693	*Chrysanthemum parthenii*	Netherlands
PD 85/259	*Stagonosporopsis ligulicola* var. *inoxydabilis*	GU238189	GU237920	GU237694	*Matricaria* sp.	Netherlands
CBS 500.63; MUCL 8090	*Stagonosporopsis ligulicola* var. *ligulicola* B	GU238190	GU237872	GU237695	*Chrysanthemum indicum*	Germany
CBS 137.96; PD 84/75	*Stagonosporopsis ligulicola* var. *ligulicola* B	GU238191	GU237783	GU237696	*Chrysanthemum indicum*	Netherlands
CBS 562.81; PDDCC 6884	*Stagonosporopsis loticola* T	GU238192	GU237890	GU237697	*Lotus pedunculatus*	New Zealand
CBS 628.97; PD 79/72; PDDCC 3870	*Stagonosporopsis loticola*	GU238193	GU237896	GU237698	*Lotus tenuis*	New Zealand

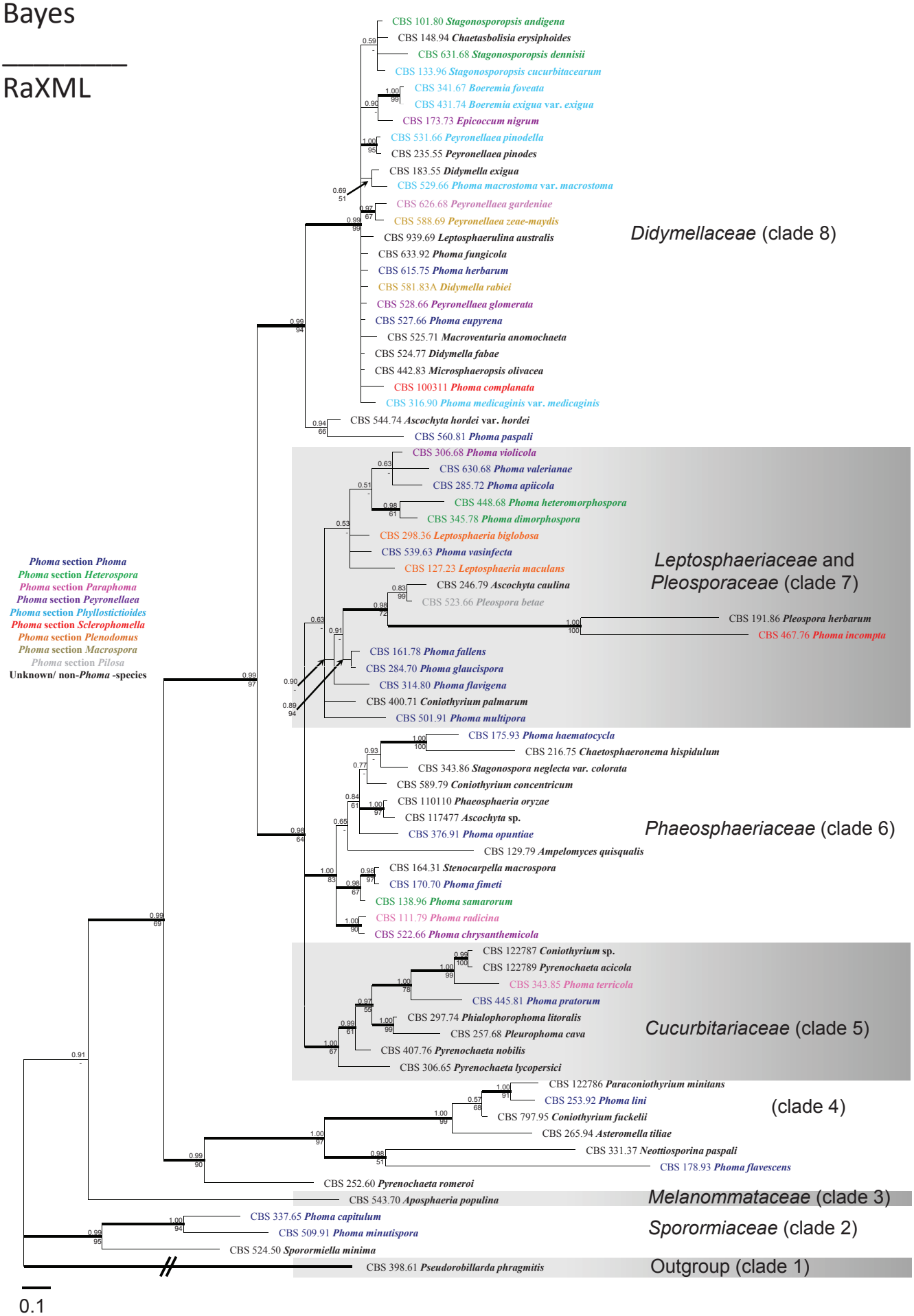
Table 3. (Continued).

Strain no.[1]	Holomorph[2]	GenBank no.			Original substrate	Locality
		LSU	ITS	TUB		
CBS 101494; PD 98/5247	*Stagonosporopsis lupini* B	GU238194	GU237724	GU237699	*Lupinus albus*	U.K.
CBS 375.84; PD 80/1250	*Stagonosporopsis lupini*	GU238195	GU237844	GU237700	*Lupinus mutabilis*	Peru
CBS 634.92; IMI 193307	*Stagonosporopsis oculo-hominis* T	GU238196	GU237901	GU237701	Human	U.S.A.
CBS 109180; PD 79/175	*Stagonosporopsis rudbeckiae* B	GU238197	GU237745	GU237702	*Rudbeckia bicolor*	Netherlands
CBS 379.91; PD 77/675	*Stagonosporopsis trachelii* B	GU238173	GU237850	GU237678	*Campanula isophylla*	Netherlands
CBS 384.68	*Stagonosporopsis trachelii* B	GU238174	GU237856	GU237679	*Campanula isophylla*	Sweden
CBS 273.92; PD 76/1019	*Stagonosporopsis valerianellae*	GU238200	GU237819	GU237705	*Valerianella locusta*	Netherlands
CBS 329.67; PD 66/302	*Stagonosporopsis valerianellae* B	GU238201	GU237832	GU237706	*Valerianella locusta* var. *oleracea*	Netherlands

[1]ATCC: American Type Culture Collection, Virginia, U.S.A.; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CECT: Colección Española de Cultivos Tipo, Valencia University, Spain; DAOM: Canadian Collection of Fungal Cultures, Ottawa, Canada; DSM: Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; HACC: Research Laboratory, Hindustan Antibiotics Ltd., Pimpri Poona, India; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, U.K.; LEV: Plant Health and Diagnostic Station, Auckland, New Zealand; MUCL: Mycotheque de l'Universite catholique de Louvain, Louvain-la-Neuve, Belgium; PD: Plant Protection Service, Wageningen, the Netherlands; PDDCC: Plant Diseases Division Culture Collection, Auckland, New Zealand; PREM: National Collection of Fungi: Culture Collection, Pretoria, South Africa; VKM: All-Russian Collection of Microorganisms, Pushchino, Russia; VPRI: Victorian Plant Disease Herbarium, Victoria, Australia.

[2]T: Ex-type strain; B: Reference strain according to Boerema *et al.* (2004).

Fig. 1. (p. 15) Fifty percent majority rule consensus tree from a BI analysis of Large and Small subunit sequences of *Phoma* and related genera (n = 76). At the nodes the BI Posterior Probabilities are presented above the branch, and bootstrap percentages of the ML analysis are given below the branch. Branches that were less than 50 % supported in the ML analyses are indicated with a hyphen. The bar indicates the number of substitutions per site. The tree is rooted with *Pseudorobillarda phragmitis* (CBS 398.61).


Bayes
RaXML
CBS 101.80 Stagonosporopsis andigena
CBS 148.94 Chaetasbolisia erysiphoides
CBS 631.68 Stagonosporopsis dennisii
CBS 133.96 Stagonosporopsis cucurbitacearum
CBS 341.67 Boeremia foveata
CBS 431.74 Boeremia exigua var. exigua
CBS 173.73 Epicoccum nigrum
CBS 531.66 Peyronellaea pinodella
CBS 235.55 Peyronellaea pinodes
CBS 183.55 Didymella exigua
CBS 529.66 Phoma macrostoma var. macrostoma
CBS 626.68 Peyronellaea gardeniae
CBS 588.69 Peyronellaea zeae-maydis
CBS 939.69 Leptosphaerulina australis
CBS 633.92 Phoma fungicola
CBS 615.75 Phoma herbarum
CBS 581.83A Didymella rabiei
CBS 528.66 Peyronellaea glomerata
CBS 527.66 Phoma eupyrena
CBS 525.71 Macroventuria anomochaeta
CBS 524.77 Didymella fabae
CBS 442.83 Microsphaeropsis olivacea
CBS 100311 Phoma complanata
CBS 316.90 Phoma medicaginis var. medicaginis
CBS 544.74 Ascochyta hordei var. hordei
CBS 560.81 Phoma paspali
Didymellaceae (clade 8)
CBS 306.68 Phoma violicola
CBS 630.68 Phoma valerianae
CBS 285.72 Phoma apiicola
CBS 448.68 Phoma heteromorphospora
CBS 345.78 Phoma dimorphospora
CBS 298.36 Leptosphaeria biglobosa
CBS 539.63 Phoma vasinfecta
CBS 127.23 Leptosphaeria maculans
CBS 246.79 Ascochyta caulina
CBS 523.66 Pleospora betae
CBS 191.86 Pleospora herbarum
CBS 467.76 Phoma incompta
CBS 161.78 Phoma fallens
CBS 284.70 Phoma glaucispora
CBS 314.80 Phoma flavigena
CBS 400.71 Coniothyrium palmarum
CBS 501.91 Phoma multipora
Leptosphaeriaceae and Pleosporaceae (clade 7)
Phoma section Phoma
Phoma section Heterospora
Phoma section Paraphoma
Phoma section Peyronellaea
Phoma section Phyllostictioides
Phoma section Sclerophomella
Phoma section Plenodomus
Phoma section Macrospora
Phoma section Pilosa
Unknown/ non-Phoma -species
CBS 175.93 Phoma haematocycla
CBS 216.75 Chaetosphaeronema hispidulum
CBS 343.86 Stagonospora neglecta var. colorata
CBS 589.79 Coniothyrium concentricum
CBS 110110 Phaeosphaeria oryzae
CBS 117477 Ascochyta sp.
CBS 376.91 Phoma opuntiae
CBS 129.79 Ampelomyces quisqualis
CBS 164.31 Stenocarpella macrospora
CBS 170.70 Phoma fimeti
CBS 138.96 Phoma samarorum
CBS 111.79 Phoma radicina
CBS 522.66 Phoma chrysanthemicola
Phaeosphaeriaceae (clade 6)
CBS 122787 Coniothyrium sp.
CBS 122789 Pyrenochaeta acicola
CBS 343.85 Phoma terricola
CBS 445.81 Phoma pratorum
CBS 297.74 Phialophorophoma litoralis
CBS 257.68 Pleurophoma cava
CBS 407.76 Pyrenochaeta nobilis
CBS 306.65 Pyrenochaeta lycopersici
Cucurbitariaceae (clade 5)
CBS 122786 Paraconiothyrium minitans
CBS 253.92 Phoma lini
CBS 797.95 Coniothyrium fuckelii
CBS 265.94 Asteromella tiliae
CBS 331.37 Neottiosporina paspali
CBS 178.93 Phoma flavescens
(clade 4)
CBS 252.60 Pyrenochaeta romeroi
CBS 543.70 Aposphaeria populina
Melanommataceae (clade 3)
CBS 337.65 Phoma capitulum
CBS 509.91 Phoma minutispora
CBS 524.50 Sporormiella minima
Sporormiaceae (clade 2)
CBS 398.61 Pseudorobillarda phragmitis
Outgroup (clade 1)
0.1

Treatment of the clades

Clade 1, Outgroup:
Pseudorobillarda phragmitis was selected as outgroup on the basis of the studies conducted by De Gruyter *et al*. (2009). This species, although being recognised as a coelomycete, is not only phylogenetically, but also morphologically distinct from *Phoma*, although Sutton (1980) classified it in the Phialopycnidiineae.

Clade 2, Sporormiaceae:
In the basal lineages, *Sporormiella minima* (CBS 524.50) was recovered, representing the *Sporormiaceae*, which was recently recircumscribed (Barr 2000). In the same clade, two species were recovered that are described in *Phoma* section *Phoma*: *Ph. capitulum* and *Ph. minutispora*. Both species are distinguishable from other species in this Boeremaean section by the production of relatively small subglobose conidia (measuring *ca*. 2–5 × 1.5–3 µm) with a few, large guttules. Within the *Sporormiaceae*, teleomorphs species have been reported with phoma-like anamorphs, such as *Westerdykella dispersa* (Von Arx 1981). Two *Sporormiaceae*-associated genera, *Sporormia* and *Preussia*, have been mentioned as possible teleomorph for *Ph. deserticola* (Von Arx & Storm 1967), a species that was regarded as miscellaneous by Boerema *et al.* (2004). Also these anamorphs produce minute (sub-) globose conidia (Von Arx 1981, Boerema *et al.* 2004). Although the *Sporormiaceae* belongs to the *Pleosporales* (Barr 2000, 2002, Shearer *et al*. 2009, Suetrong *et al.* 2009), it forms a rather basal clade to most of the other *Phoma* species, and a taxonomic revision of *Ph. capitulum* and *Ph. minutispora* should therefore be considered.

Clade 3, Melanommataceae:
One species that belongs to the *Melanommataceae* was included in the phylogenetical reconstruction of the phomoid *Pleosporales*. This species, *Aposphaeria populina* (CBS 543.70), is recovered in the basal lineages of the reconstructed tree (Mugambi & Huhndorf 2009, Suetrong *et al.* 2009, Tanaka *et al*. 2009). The close association of this family with the *Sporormiaceae* and their phylogenetic placement in the basal lineages of the *Pleosporales* is in congruence with results obtained in earlier studies (Kruys *et al.* 2006, De Gruyter *et al.* 2009). Although some earlier workers regularly mistook several *Phoma* species for members of the genus *Aposphaeria* (*e.g.* Saccardo 1884), none of the *Phoma* species included in this study were clustering with the *Melanommataceae*.

Clade 4:
This clade comprises a range of species that almost all belong to different genera. *Phoma lini* and *Ph. flavescens* are the two *Phoma* representatives found in this clade, although they are not sister species. Based on morphological data, both species were accommodated in *Phoma* section *Phoma* (De Gruyter *et al*. 1993). Both species produce a yellow diffusible pigment *in vitro*, although a positive reaction to NaOH is only observed in *Ph. lini*. Both *Ph. flavescens* and *Ph. lini* are closely related to *Paraconiothyrium minitans* (≡ *Coniothyrium minitans*; Verkley *et al.* 2004). With this formal recombination into *Paraconiothyrium*, it was aimed to differentiate *Par. minitans*, which produces complex, thick-walled pycnidia from other *Coniothyrium* species that normally produce more phomoid pycnidia (Verkley *et al.* 2004). The close relationship between *Par. minitans* with *C. fuckelii* that is found here is in congruence with the observations of Damm *et al.* (2008), although the teleomorph name, *Leptosphaeria coniothyrium*, would suggest a association with the *Leptosphaeriaceae* (clade 8).

The likeliness of the findings of *Pyrenochaeta romeroi* (CBS 252.60), *Asteromella tiliae* (CBS 265.94) and *Neottiosporina paspali* (CBS 331.37) in this clade was already discussed by De Gruyter *et al.* (2009).

Clade 5, Cucurbitariaceae:
Clade 5 comprises mainly taxa with setose pycnidia, including several representative species of the genus *Pyrenochaeta.* In addition, a *Coniothyrium* sp., *Phialophorophoma litoralis* and *Pleurophoma cava* grouped in this clade, as well as two *Phoma* species, *Ph. pratorum* (section *Phoma*) *and Ph. terricola*, (section *Paraphoma*). Another representative of the section *Paraphoma* that is included in this study is *Ph. radicina*, which is however found in clade 6. The taxonomy of setose species that are currently classified in *Phoma* section *Paraphoma*, *Pyrenochaeta* and *Pleurophoma* is revised (De Gruyter *et al.* 2010). Also in several non-*Paraphoma* species in the genus *Phoma* setose or semi-pilose pycnidia do occur incidentally (Boerema *et al.* 2004). However, thus far, no setae-forming *Ph. pratorum* strains have been recorded. The finding of this species in the present clade is thus highly remarkable.

The *Coniothyrium* strain in this clade (CBS 122787) was previously identified as *C. cerealis*, and is found to be closely related to *Pyrenochaeta acicola* (BPP = 0.99, RBS = 100 %). As was illustrated in a previous study of Muthumeenakshi *et al.* (2001) *C. cerealis* is quite distantly related to other *Coniothyrium* species. However, based on comparison with sequence data available in GenBank, it is unlikely that its previous identification was correct. This finding further illustrates the polyphyly of the genus *Coniothyrium*, which further has been retrieved in clades 4, 6 (*Phaeosphaeriaceae*), 7 (*Leptosphaeriaceae* and *Pleosporaceae*) and 8 (*Didymellaceae*). As mentioned before, some species of this genus have been associated with the teleomorph genus *Leptosphaeria*, and are thus expected to cluster with the *Leptosphaeriaceae* (clade 7). None of the species recovered in clade 5 has been associated with a teleomorph.

Clade 6, Phaeosphaeriaceae:
The species that are found in the well-supported clade 6 (BPP = 1.00; RBS = 83 %), belong to the morphologically heterogeneous group of the *Phaeosphaeriaceae* (Boehm *et al*. 2009, Zhang *et al.* 2009). Most findings in this clade have already been discussed in the previous paper of De Gruyter *et al.* (2009). In addition to that study, six *Phoma* species are retrieved in this clade. *Phoma radicina*, type of *Phoma* section *Paraphoma*, is found in close association with *Ph. chrysanthemicola* (BPP = 1.00; RBS = 90 %). The association between *Ph. radicina* and the *Phaeosphaeriaceae* is further discussed by De Gruyter *et al.* (2010). Its close association with *Ph. chrysanthemicola* has been observed before by Aveskamp *et al.* (2008a), but the link with the *Phaeosphaeriaceae* has not been established. Strains of *Ph. chrysanthemicola* exhibit some semi-setose pycnidia that are, however, often fully covered by mycelial hairs (Boerema 1993). This is a feature that is in common with *Ph. radicina*, which has, as type species of the section *Paraphoma*, clearly visible setae. In contrast, the main characteristic of *Ph. chrysanthemicola*, the presence of pseudosclerotioid masses, has never been observed in the latter species. However, also not all strains of *Ph. chrysanthemicola* exhibit this character (Dorenbosch 1970).

Phoma fimeti forms a subclade with *Ph. samarorum* and a strain that was previously identified as *Stenocarpella macrospora* (BPP = 0.98; RBS = 67 %), but that is probably misidentified (De

Gruyter *et al.* 2009). Especially the finding of *Ph. samarorum* is noteworthy, as it is found rather distinct from two clusters of other species belonging to the section *Heterospora*, which are retrieved among the *Leptosphaeriaceae* and *Didymellaceae* (clades 7 and 8). In contrast to these other *Heterospora* species, the large conidia of *Ph. samarorum* that can be observed *in planta* are clearly distinct by the subulate top cells, and measures up to 17 × 3.5 µm (Boerema *et al.* 1997). The strain identified as *Stenocarpella macrospora* is now sterile and therefore not studied morphologically. This species is known to produce similar-shaped, septate conidia, which are however pigmented and considerably larger, 44–82 × 7.5–11.5 µm (Sutton 1980). The close association with *Ph. fimeti* is therefore remarkable as this species is known to produce only minute, aseptate conidia, measuring (2–)2.5–4(–5) × (1.5–)2–2.5(–3) µm (De Gruyter & Noordeloos 1992).

The remaining two *Phoma* species in this clade, *Ph. haematocycla* and *Ph. opuntiae*, also produce such minute conidia. *Phoma haematocyla*, a flax-associated species from New Zealand, is retrieved in a subclade that also accommodates *Chaetasphaeronema hispidulum* (BPP = 1.00; RBS = 100 %).

All *Phoma* species found here are morphologically rather distinct, hence their placement in four different *Phoma* sections (Boerema *et al.* 2004). None of the *Phoma* species accommodated in this clade is associated with a teleomorph. The main teleomorph associated with the *Phaeosphaeriaceae* is *Phaeosphaeria,* although also incidentally a *Leptosphaeria* species is associated with this family (Câmara *et al.* 2002). An anamorph genus that is often confused with *Phoma* is *Microsphaeropsis* (Boerema 1997), which is linked to *Phaeosphaeria* (Câmara *et al.* 2002). Both anamorph genera differ in conidial pigmentation, which is commonly only present in mature conidia of *Microsphaeropsis*. Younger conidia are, however, often colourless. It may be that the *Phoma* species in this clade actually belong to what is now known as *Microsphaeropsis*, but have lost the pigmentation character during evolution.

Clade 7, Leptosphaeriaceae and *Pleosporaceae*:

Clade 7 is a large clade comprising many *Phoma* species from various Boeremaean sections. Three reference species encountered here have been associated with the *Leptosphaeriaceae* before, these include *Leptosphaeria maculans*, *L. biglobosa* and *Coniothyrium palmarum* (Reddy *et al.* 1998, Verkley *et al.* 2004, De Gruyter *et al.* 2009), or with the *Pleosporaceae*, such as *Pleospora herbarum*, *Ascochyta caulina* and *Ph. betae* (Dong *et al.* 1998, Kodsueb *et al.* 2006, Inderbitzin *et al.* 2009, De Gruyter *et al.* 2009).

The two *Leptosphaeria* species in this study that were associated with a *Phoma* anamorph cluster together in the present clade: *L. maculans* (anam *Ph. lingam*) and *L. biglobosa*, which produces an unnamed, phomoid anamorph that is highly similar to *Ph. lingam* (Shoemaker & Brun 2001). Both species are serious pathogens of *Brassicaceae* (Fitt *et al.* 2006). *Leptosphaeria biglobosa* was found to be closely related to *Ph. lingam* in previous studies (Mendes-Perreira *et al.* 2003) and was for a long time recognised as a weakly pathogenic variety of the latter species (Johnson & Lewis 1990, Schäfer & Wöstemeyer 1992, Morales *et al*. 1993, Pongam *et al*. 1999, Williams & Fitt 1999, Purwantara *et al*. 2000, Shoemaker & Brun 2001, Voigt *et al*. 2001).

The phylogenic relation of *Phoma* species currently classified in sections *Pleonodomus* and *Pilosa* is currently investigated (De Gruyter *et al*. in prep.). However, the present results reveal that a number of species from other *Phoma* sections fits in the *Leptosphaeriaceae* and *Pleosporaceae*. These include *Ph. apiicola*, *Ph. fallens*, *Ph. flavigena*, *Ph. glaucispora*, *Ph. multipora*, *Ph. valerianeae* and *Ph. vasinfecta*. In contrast to the species that are accommodated in sections *Pilosa* and *Plenodomus*, pilose or scleroplectenchymatous pycnidia have never been recorded in these seven species; hence the placements in section *Phoma*.

Phoma multipora was ascribed to section *Phoma*. However, the original morphological description mentions the presence of elongated conidiophores (Pawar *et al.* 1967), which indicates that this species does not belong to the genus *Phoma* according to the present-day concept.

In addition, some representatives of other sections are found in clade 7, such as *Ph. incompta* (section *Sclerophomella*) and *Ph. violicola*, which is associated with the section *Peyronellaea*. Based on previous studies in the section *Peyronellaea* however, also *Ph. chrysanthemicola* and *Ph. schachtii* may be expected to cluster with the species in this clade (Aveskamp *et al*. 2009a). Remarkably, also two representatives of the section *Heterospora* are found in this clade. *Phoma heteromorphospora* is the assigned type species of this section (Boerema *et al.* 1997), whereas *Ph. dimorphospora* is morphologically closely allied, in congruence with the molecular results obtained here. Both species have a slow growth-rate and occur on *Chenopodium* spp., but can be distinguished by the absence of the conidial dimorphism in *Ph. dimorphospora in vitro*. Moreover, the latter species is commonly found in North and South America, whilst *Ph. heteromorphospora* occurs mainly in Europe (Boerema *et al*. 2004).

With the exception of *Ph. samarorum* (clade 6 – *Phaeosphaeriaceae*), the other species of the section *Heterospora* are found in clade 8, which represents the *Didymellaceae*. The major difference between the *Heterospora* species in the present clade in contrast to those in the *Didymellaceae* is the size of the septate conidia, which are up to 9 × larger *in vivo* than the regular conidia in *Ph. heteromorphospora* and *Ph. dimorphospora*, whereas, in the *Didymellaceae* clade, the septate conidia are only 1.5–4.5 × larger.

Also, *Coniothyrium palmarum*, which represents the type of its genus, clusters in this clade. Just as in *Phoma*, the species in *Coniothyrium* have only a limited number of morphological features that can aid in taxonomy. This has led to an unwanted situation in which species morphologically placed in this genus have been shown in phylogenetic examination to be dispersed among multiple families (Verkley *et al*. 2004). Although, based on type species, an anamorph-teleomorph link has been established between *Coniothyrium* and *Leptosphaeria* (Crous 1998), many heterogeneous species are *Coniothyrium*-like, and belong phylogenetically to different families or even classes (Cortinas *et al*. 2006). In this study we found "*Coniothyrium*" species accommodated in at least three different clades (Fig. 1). *Coniothyrium clematidis-rectae* is phylogenetically linked to the *Didymellaceae* (Fig. 2 – see below). *Phoma* and *Coniothyrium* are considered to be highly similar and are only distinguished on basis of the pigmentation of the conidia and the structure of the pycnidial wall (Boerema *et al*. 2004).

This clade also accommodates *Pleospora betae*, a notorious leaf and seed pathogen of beet (*Beta vulgaris*, Bugbee & Cole 1981), and *Pl. herbarum*, which is the type species of the genus *Pleospora*. The genetic distance between the two species was already observed in a study utilising SSU nrDNA sequences (Dong *et al*. 1998). Also three *Phoma* species that are found in close association with these "true" *Pleosporaceae* and that are found basal to this clade, *Ph. fallens*, *Ph. flavigena* and *Ph. glaucispora*

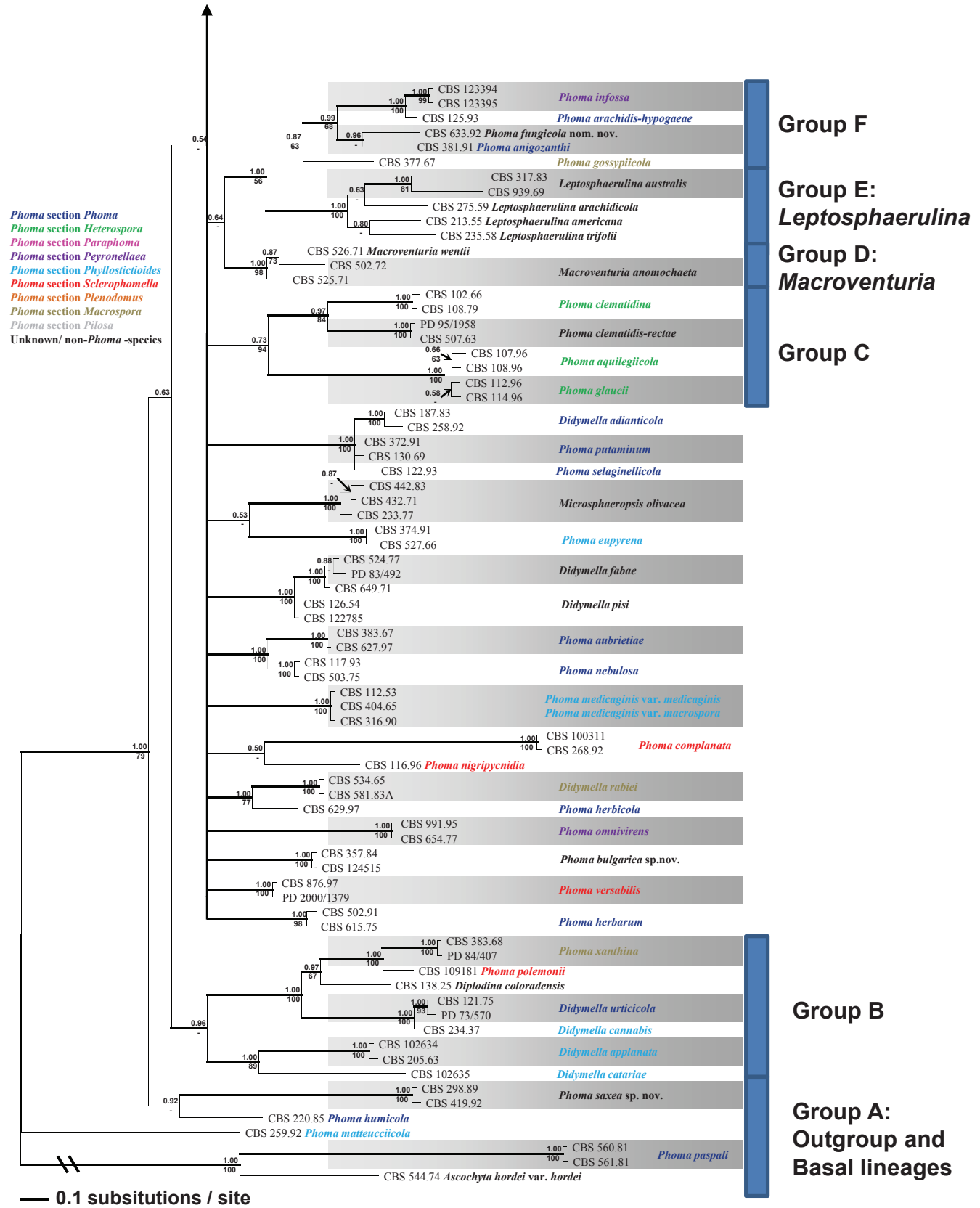


Fig. 2. Fifty percent majority rule consensus tree from a BI analysis of LSU, ITS and TUB sequences of *Didymellaceae* (n = 274). At the nodes the BI Posterior Probabilities are presented above the branch, and bootstrap percentages of the analysis are given below the branch. Branches that were less than 50 % supported in the ML analyses are indicated with a hyphen. The bar indicates the number of substitutions per site. The tree is rooted with *Ascochyta hordei* var. *hordei* (CBS 544.74) and *Phoma paspali* (CBS 560.81 & CBS 561.81).

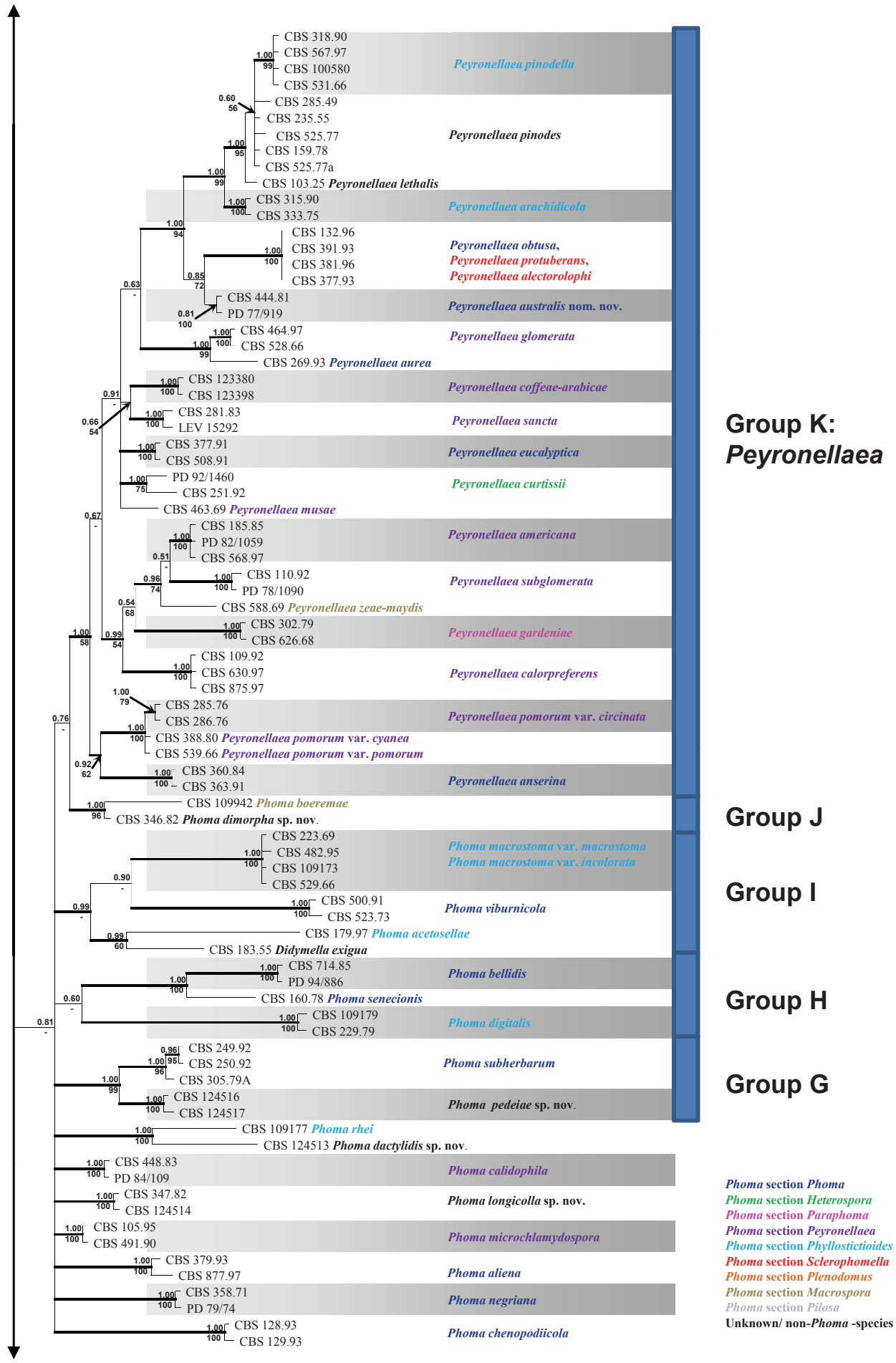


Fig. 2. (Continued).

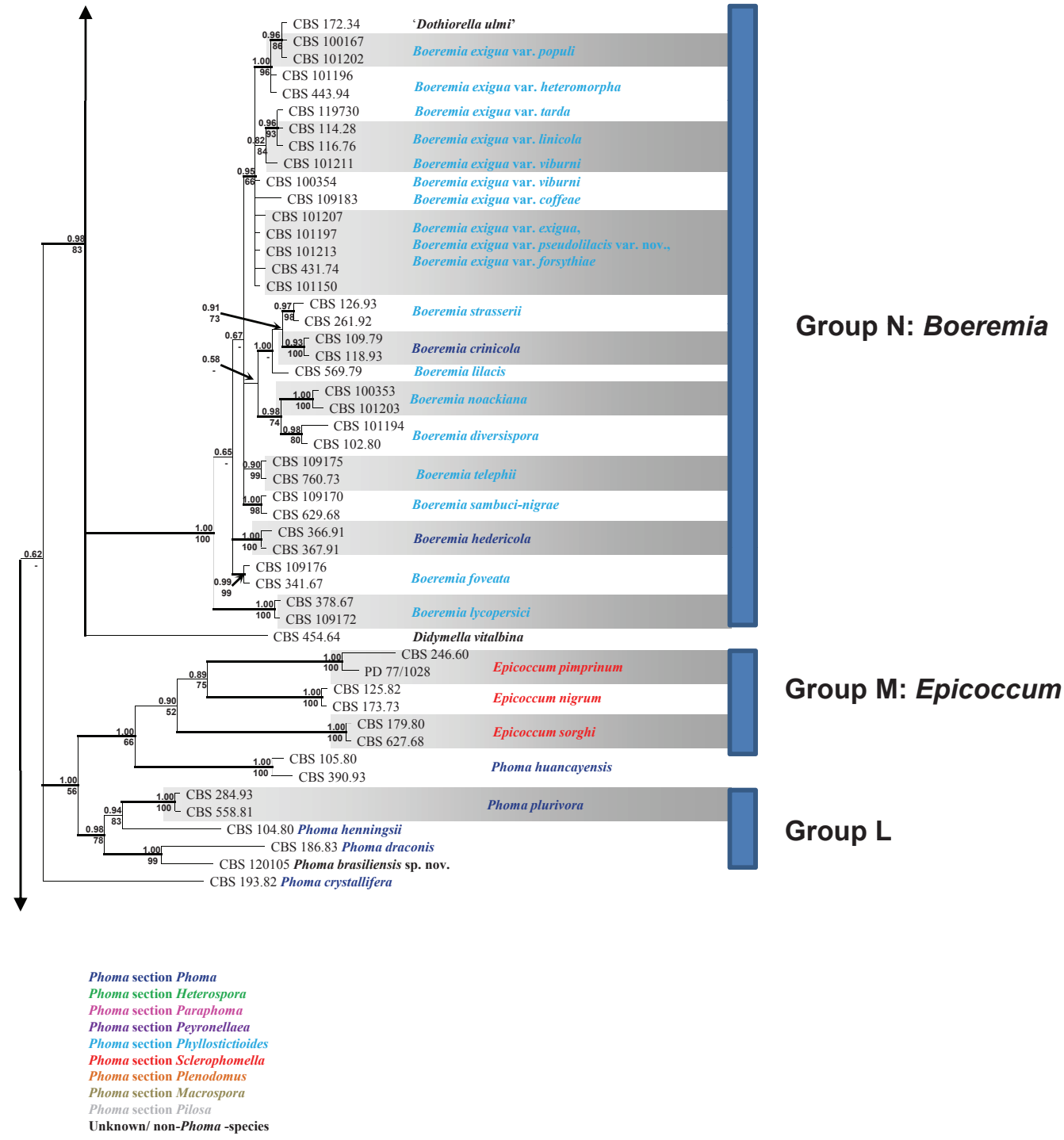


Fig. 2. (Continued).

have glabrous pycnidia and, like *Ph. betae*, aseptate conidia, hence their link to *Phoma* section *Phoma*. Absence of an ostiole is only recorded in *Ph. glaucispora* (De Gruyter *et al*. 1998).

Pleospora is linked to the anamorph genus *Stemphylium* (Simmons 1969), *Alternaria* and *Dendryphion* (Von Arx 1981). The pluriform nature of the *Pleospora* anamorphs strongly contrasts with the relatively uniform morphology of the teleomorphic structures (Holm 1962, Kodsueb *et al*. 2006, Inderbitzin *et al*. 2009). The polyphyletic nature of *Pleospora* has been hypothesised by Holm (1962) and Berbee (1996), but only recently have molecular studies confirmed its taxonomic complexity (Dong *et al*. 1998, Kodsueb *et al*. 2006, Inderbitzin *et al*. 2009).

Clade 8, Didymellaceae:

The major cluster observed in the generic phylogeny is the top clade in Fig. 1, which represents the *Didymellaceae* clade. This clade is well supported (BPP = 0.99, RBS = 94 %), but with the loci used, a high level of basal polytomy is recorded within the clade. The ancestral species in this clade are the *Graminae*-pathogens, *Ascochyta hordei* and *Ph. paspali*. The latter species has been considered to be an indigenous pathogen of grasses in Australia and New Zealand (Johnston 1981, Boerema *et al*. 2004), but based on sequence comparisons this species is probably also present in Europe (Wirsel *et al*. 2001, C. Gueidan pers. comm.).

Clade 8 comprises most *Phoma* species, including CBS 615.75, the representative strain of *Ph. herbarum* (Boerema *et al*.

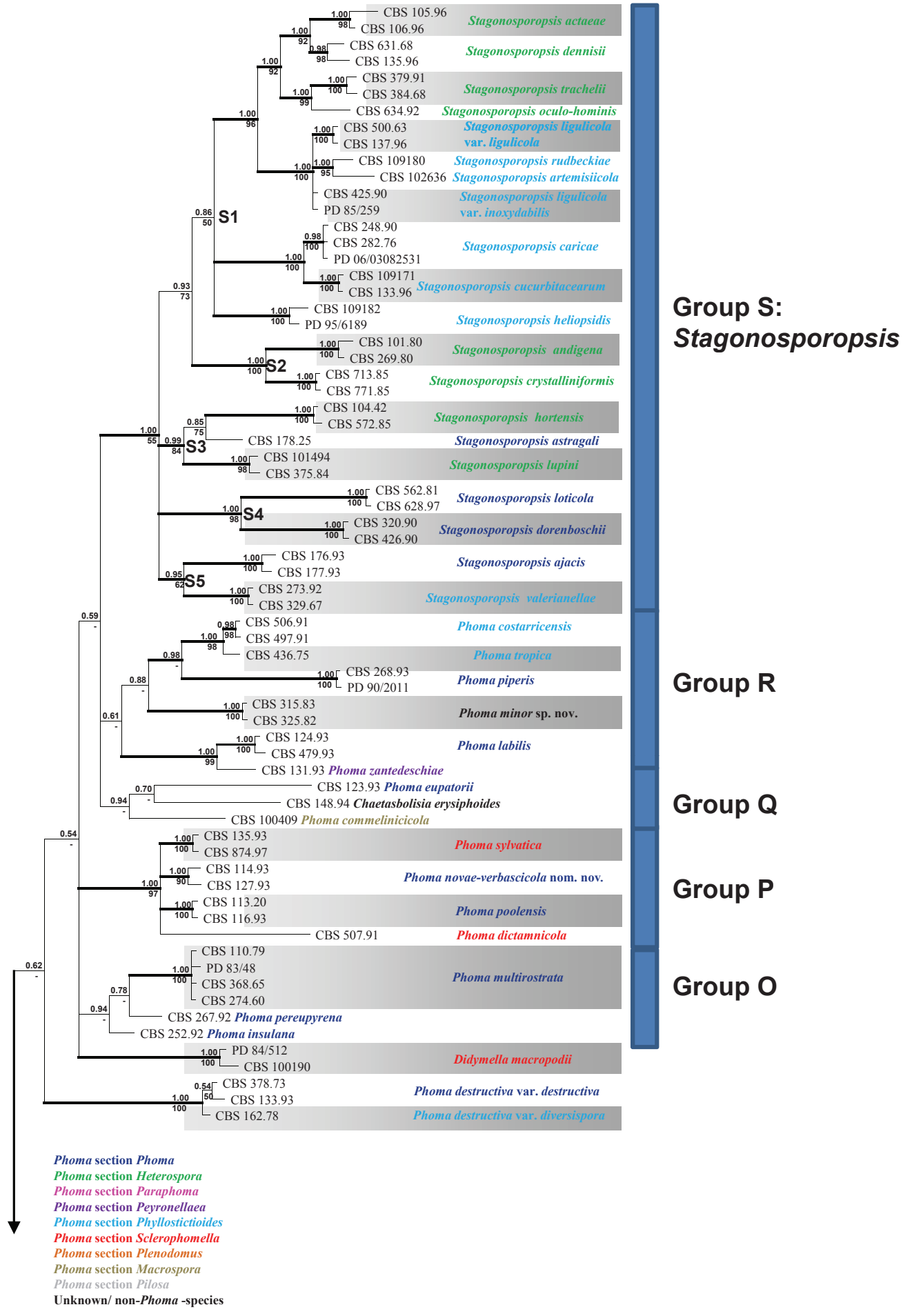


Fig. 2. (Continued).

2004), which is type species of the genus (Boerema 1964). This clade also includes the type species of the *Phoma* sections *Phoma*, *Peyronellaea*, *Phyllostictoides*, *Sclerophomella* and *Macrospora*. Some phytopathologically and medically relevant species of the section *Heterospora* are also associated with this clade, although some species of this section are found in other clades, such as *Ph. samarorum* (clade 6) and *Ph. dimorphospora,* and the sectional type *Ph. heteromorphospora* (clade 7). Finally, a single species of the setose section *Paraphoma*, *Ph. gardeniae*, is found in the *Didymellaceae*. Based on the sequence data obtained in this study, it is estimated that approximately 70 % of the species recognised by Boerema *et al*. (2004) can be associated with the *Didymellaceae*.

Besides the many *Phoma* species, several other anamorph fungi are found within this clade, including *Ampelomyces quercinus, Ascochyta fabae* (teleom. *Didymella fabae*), *Asc. hordei* var. *hordei*, *Asc. pinodes* (teleom. *Didymella pinodes*), *Chaetasbolisia erysiphoides*, *Didymella exigua*, *Epicoccum nigrum* (synanamorph *Ph. epicoccina*) and *Microsphaeropsis olivacea*. Of these species, *Asc. pisi*, *C. erysiphoides* and *M. olivacea* are recognised as type species for their respective genera. De Gruyter *et al*. (2009) already discussed the probability of finding most of these non-*Phoma* taxa in the *Didymellaceae* clade.

It should be noted that not all *Ascochyta* species are found within this clade, indicating that this genus is also polyphyletic. Whereas *A. hordei* var. *hordei* is found to be one of the basal taxa of clade 8, the legume associated pathogens *A. fabae*, *A. pinodes* and the type species *A. pisi* are found in close association with several species of *Phoma*. This result is in congruence with the observations in the study of Peever *et al.* (2007). Also the recently described *Didymella clematidis* has an anamorph state in *Ascochyta* and is closely related to *Phoma* taxa in this major clade (Woudenberg *et al*. 2009). A representative strain *Asc. caulina* and a new *Ascochyta* species that is still due to be published (G.J.M. Verkley, pers. comm.), however, have been found to be only distantly related and are found in clades 7 and 6, respectively.

Where a sexual state is known for the *Phoma* and *Ascochyta* species in clade 8, it is *Didymella*. The type species of this teleomorph genus, *D. exigua*, is also found within this clade, although it is not associated with a *Phoma* anamorph state. The family *Didymellaceae* was introduced for this group by De Gruyter *et al*. (2009). However, type species of two other teleomorph genera have also been found within this clade. DNA sequences of *Leptosphaerulina australensis* resemble a high level of similarity with those of the various *Phoma* and *Didymella* strains, although none are identical. Also sequences of LSU and ITS sequence data obtained from GenBank of *L. americana*, *L. argentinensis*, *L. chartarum*, *L. crassiasca* and *L. trifolii* (GenBank accession no. AY278318, AY849949, EU272493, U79485, AY8315585 respectively) were highly similar or even identical to the *Didymellaceae* sequences obtained in the present study (data not shown). These observations are in congruence with the results obtained by Silva-Hanlin & Hanlin (1999), who found that *D. bryoniae* (anam. *Ph. cucurbitacearum*) was closely related with *L. chartarum* and *L. crassiasca*. Also *Macroventuria anomochaeta*, which represents the genus *Macroventuria* (Van der Aa 1971) groups in *Didymellaceae*. The close genetical resemblance of *Macroventuria* and *Leptosphaerulina* found in the present study is in congruence with the results of Kodsueb *et al.* (2006).

The loci employed here for phylogenetic analysis are sufficient to identify clades at the family level, but for proper resolution at generic level or lower, additional gene regions need to be sequenced. As the majority of *Phoma* species is embedded in the *Didymellaceae* clade, we will define further generic and species boundaries within this recently established family in the subsequent part of this paper.

Systematics of the *Didymellaceae*

DNA phylogenetic analysis

The alignment that was used to delineate the *Didymellaceae* consisted of 274 sequences belonging to 196 species. A list of the species names and numbers, original substrates, geographical origins and GenBank Accession numbers of the strains used in this study is provided in Table 3. The sequence matrix had a total length of 2 188 characters including the alignment gaps (LSU: 1 327; ITS: 508 and TUB: 353). Of those characters, 1 788 (LSU: 1 233; ITS: 374 and TUB: 181) were constant, whereas 400 characters (LSU: 94; ITS: 144 and TUB: 192) were variable.

The analysis run of the LSU-ITS-TUB sequence matrix in MrBayes was aborted after obtaining 20 000 trees, which was well after stationarity in the probability of the trees was reached, whereas the standard deviation of split frequencies was below 0.02. From the obtained tree population, the 25 % burn-in was discarded and the consensus tree and posterior probabilities were calculated. The topology and support values of the BI tree were in congruence with the optimal tree obtained in the ML analysis.

Systematics: treatment of clades

As most other anamorph genera, *Phoma* has largely been used as a convenient form genus, rather than a phylogenetic entity. With the number of *Phoma* species that are being analysed on DNA sequence level rapidly increasing, the question is raised whether form genera should be maintained or that more natural groupings, merging both phylogeny and morphological data, should be erected. Of course, as greater numbers of taxa are collected and analysed, the taxonomic boundaries of more clades will be resolved. However, for the present, only those genera that could be resolved based on available cultures are treated. The groups mentioned below refer to those indicated A–R in Fig. 2. The unresolved clades are left untreated, and are thus not discussed.

The taxa in this part of the study were selected based on genetic and/or morphological similarities with the species that were associated with the *Didymellaceae* in Fig. 1. Although numerous taxa from various genera have been associated with "*Phoma*", the number of genera that could be included in the selection for the *Didymellaceae* was limited. Next to *Phoma*, the only species found were those accommodated on basis of previous morphological studies in either *Ampelomyces*, *Ascochyta*, *Chaetasbolisia*, *Coniothyrium*, *Didymella*, *Diplodina*, *Dothiorella*, *Epicoccum*, *Leptosphaerulina*, *Macroventuria*, or *Microsphaeropsis*. Of three of these generic representatives, viz. *Chaetasbolisia, Diplodina* and *Dothiorella*, we suspect that some cultures have been preserved under an incorrect name. The species representing *Ampelomyces*, *A. quercinus,* was correctly identified, but as suggested earlier, the taxonomic placement in this genus appears to be incorrect (Szentiványi *et al.* 2005).

Strains belonging to a single species proved to be genetically identical or at least highly similar, indicating that the initial identification of these strains had been carried out correctly.

Several well-supported clusters are recognised within this family that are treated here as novel groups of the *Didymellaceae*. In this section these separate groups are treated. However, although multiple genes were employed in this study to generate a phylogenetic reconstruction of the family, high levels of basal polytomy were observed as well (Fig. 2). Application of general nrDNA loci alone did not reduce this high level of polytomy, whilst interspecies variation in several well-supported clades was reduced drastically.

Group A – outgroup and basal lineages:
The tree presented in Fig. 2 is rooted to *Ascochyta hordei* and *Ph. paspali*, which proved to be ancestral to the *Didymellaceae* in Fig. 1. The latter species was described by Johnston (1981) as a species from grasses in New Zealand and Australia, but in recent years, isolates with similar genotypes were isolated from iron-rich volcanic soil from France (C. Gueidan, pers. comm.), and from common reed (*Phragmites australis*) in Germany (Wirsel *et al.* 2001). These isolates were, however, never studied morphologically.

Another species used as outgroup is *Ascochyta hordei* var. *hordei* (CBS 544.74), which was obtained from a South African *Triticum aestivum*, indicating that also within the *Didymellaceae*, species that are ascribed to *Ascochyta* do not form a monophyletic group. Also CBS 259.92, the isotype of *Ph. matteuciicola*, proved to be basal to most other *Phoma* species. *Phoma matteuciicola* is commonly known as a pathogen of many fern species (De Gruyter *et al.* 2002). Within the basal lineages, also a group comprising *Ph. humicola* and the novel species *Ph. saxea* is found, although this group is only supported by BI analysis (BPP = 0.92, RBS < 50 %). Although *Phoma humicola* is known as a saprobic soil fungus, it is sometimes mistaken for the notorious potato pathogen *Ph. foveata* (Group N), due to a similar biochemical reaction to NaOH and the formation of citrine green crystals on MEA (De Gruyter *et al.* 1998). However, conidia of *Ph. humicola* are always eguttulate in contrast to those of *Ph. foveata*. *Phoma saxea* has been found twice in Germany on rock material, and will be further described below.

Phoma humicola J.C. Gilman & E.V. Abbott, Iowa St. Coll. J. Sci. 1(3): 266. 1927.

Specimen examined: **U.S.A.**, Nevada, Death Valley, from a dead leaf of *Franseria* sp., 1971, G.H. Boerema, CBS H-16390, culture CBS 220.85.

Phoma matteuciicola Aderkas, Gruyter, Noordel. & Strongman, Canad. J. Pl. Pathol. 14(3): 227. 1992.

Specimen examined: **Canada**, Nova Scotia, Five Mile River, from leaf base of *Matteuccia struthiopteris*, May 1981, P. von Aderkas, **holotype** DAOM 183092, culture ex-holotype CBS 259.92 = IMI 286996 = PD 91/272.

Notes: Gangrene in ostrich fern was originally attributed to *Ph. exigua* var. *foveata* (von Aderkas & Brewer 1983), which is here recombined as *Boeremia foveata*, but Von Aderkas *et al.* (1992) recognised a new species as causal agent of this disease. The phylogeny presented here supports these observations, as *Ph. matteuciicola* is found rather distinct from *B. foveata*.

Phoma paspali P.R. Johnst., New Zealand J. Bot. 19(2): 181. 1981.

Specimens examined: **New Zealand**, Auckland, Kaikohe, from a dead leaf of *Paspalum dilatatum*, Jan. 1979, P.K. Buchanan, **isotype** CBS H-7623, culture ex-isotype CBS 560.81 = PD 92/1569; Waikato District, Ruakura, from *Lolium perenne*, Jan. 1979, G.H. Boerema, CBS 561.81 = PDDCC 6615.

Phoma saxea Aveskamp, Gruyter & Verkley, **sp. nov.** MycoBank MB515591. Fig. 3.

Conidia dimorpha, intra idem pycnidia formata. Conidia typus 1 (sub)globosa, glabra, hyalina, continua, (3–)3.5–5.5 µm diam., (0–)3–10(–15) guttulis praedita. Conidia typus 2 cylindrica vel ellipsoidea, glabra, hyalina, continua, (3.5–)4.5–7(–7.5) × 2.5–3.5(–4) µm, plerumque eguttulata, vel 1–3 guttulis praedita. Matrix conidiorum salmonea. Chlamydosporae continuae, globosae, viridulae, in catenas usque 35 positae, (8.5–)10–16.5(–17.5) × (6–)8–12.5(–14) µm.

Etymology: Refers to the substratum on which both isolates of this species were found, stone material.

Pycnidia solitary, (sub-)globose, glabrous or covered with hyphal outgrows, (90–)135–280(–310) × (90–)105–260(–275) µm. *Ostioles* single, papillate, with wide openings, *ca*. 40–80 µm diam. *Pycnidial wall* pseudoparenchymatous, composed of oblong to isodiametric cells, 2–3 layers, 10–17 µm thick, outer cell layer brown pigmented. *Conidiogenous cells* phialidic, hyaline, simple, smooth, variable in appearance, flask-shaped, oblong or isodiametric *ca*. 5.5–7.5 × 3–4 µm. *Conidia* of two types, both originating from the same pycnidia. Conidia of type 1: (sub-)globose, thin-walled, smooth, hyaline, aseptate (3–)3.5–5.5 µm diam, with (0–)3–10(–15) guttules. Conidia of type 2: cylindrical to ellipsoidal, thin-walled, smooth, hyaline, aseptate, (3.5–)4.5–7(–7.5) × 2.5–3.5(–4) µm, mainly egutullate or with up to 3 minute guttules. *Conidial matrix* salmon. *Chlamydospores* ubiquitously present in the agar, unicellular, globose, in long chains of up to 35 elements, greenish pigmented, measuring (8.5–)10–16.5(–17.5) × (6–)8–12.5(–14) µm.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular. Immersed mycelium flat, olivaceous to greenish olivaceous, citrine-green or coral near the colony margin. Aerial mycelium absent, but sometimes some grey erect tufts are encountered near the colony centre; reverse concolourous. Colonies on MEA 20–25 mm diam after 7 d, margin regular. Immersed mycelium violet-slate, but saffron near the colony margin. Abundant pycnidia are present on the agar surface; reverse iron-grey, saffron near the colony margin. Colonies on CHA similar as on MEA, but somewhat slower growing, 10–15 mm diam. after 7 d, and some sparse white aerial mycelia hyphae are present in the colony. Application of NaOH results in a greenish yellow discolouration of the agar, best to be observed on OA medium.

Specimens examined: **Germany**, Oldenburg, from corroded Mediterranean marble, June 1992, J. Kuroczkin, **holotype designated here** CBS H-20240, culture ex-holotype CBS 419.92; Oldenburg, from limestone, 1987, J. Kuroczkin, CBS 298.89.

Notes: The pycnidial wall of *Phoma saxea* is extremely thin and almost hyaline when the conidia have exuded. Older pycnidia collapse and remain as a double-layered, disc-like structure on the agar.

Both strains of this species have been isolated from stone material, such as limestone (CBS 298.89) and corroded Mediterranean marble (CBS 419.92). Although the genus is known from all kinds of substrates, the number of rock-inhabiting *Phoma* isolates is relatively low. Selbmann *et al.* (2002) report on *Ph. herbarum* from Antarctic rock, and Boerema *et al.* (2004) list several species from rock-like materials, such as cement (*Ph. herbarum*), wall-plaster (*Ph. heteroderae* – here recombined into *Ph. calorpreferens*) and crockery (*Ph. pomorum*). In addition, multiple species are recorded from rock-inhabiting lichens (Nelson *et al*. 2009, Ruibal *et al.* 2009). These species, listed by Hawksworth & Cole (2004) are, however, unculturable and could therefore not be compared with *Ph. saxea in vitro*. However, the morphological descriptions suggest that the mentioned species and *Ph. saxea* are different taxonomic entities.

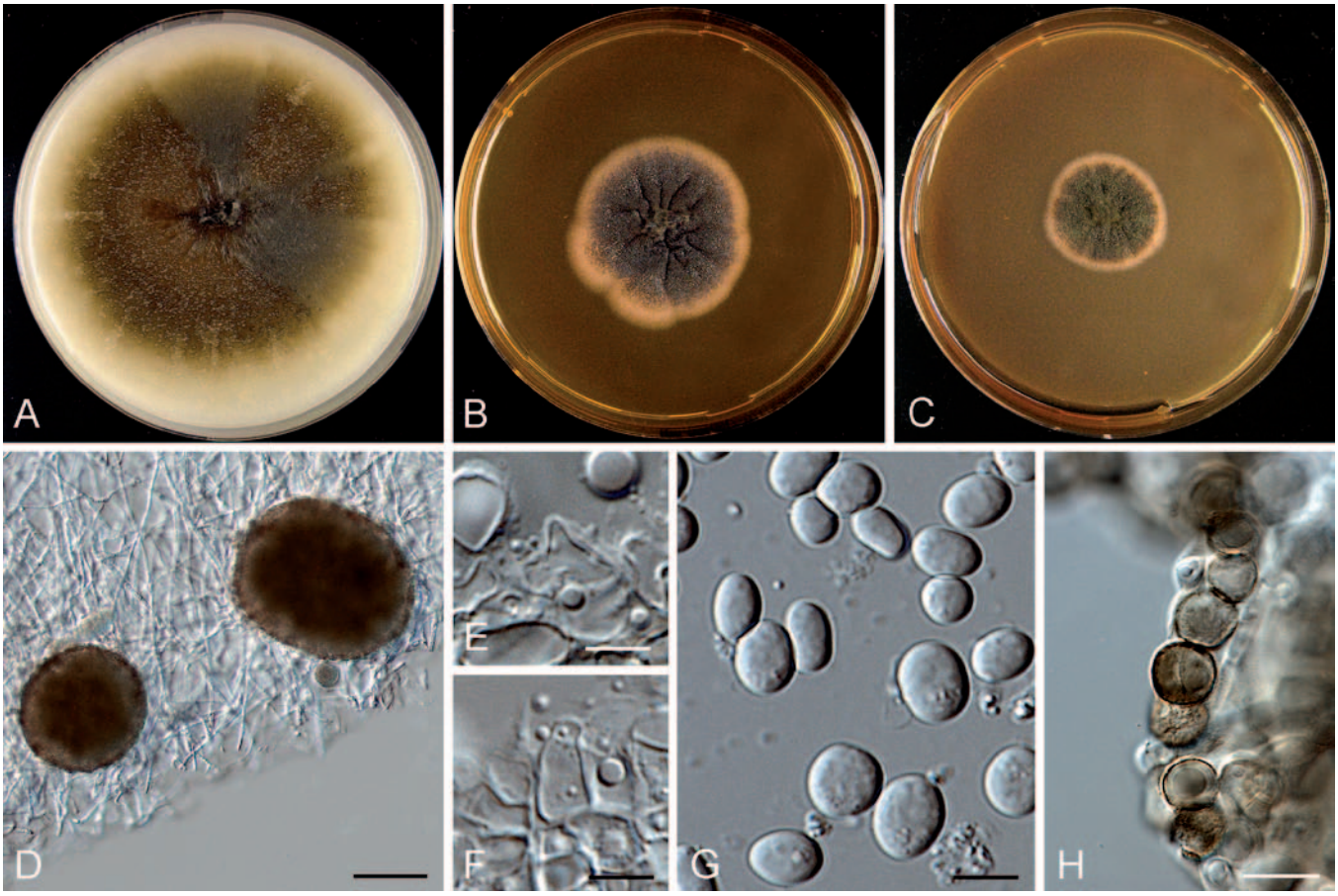


Fig. 3. *Phoma saxea* (CBS 419.92). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D. Pycnidia. E–F. Conidiogenous cells. G. Conidia. H. Chain of unicellular chlamydospores. Scale bars: D = 100 µm; E–G = 5 µm; H = 20 µm.

Group B:

Four of the six species clustering in Group B produce a *Didymella* teleomorph. Only *Ph. polemonii* and *Ph. xanthina* presently have no known sexual state. The species in this clade are collected from a wide variety of dicots, although all individual taxa appear to be host-specific (Boerema *et al.* 2004). Also the micromorphological features of these species are highly variable.

A single strain that was kept in the CBS collection as *Diplodina coloradensis* was found in this clade as well. However, this genus name has been accommodated in the *Gnomoniaceae* (*Diaporthales*), indicating that this strain has been preserved under an incorrect name and should be renamed. However, as this strain proved to be sterile, no proper redescription of the material could be provided.

Didymella applanata (Niessl) Sacc., Syll. Fung. 1: 546. 1882.

Basionym: *Didymosphaeria applanata* Niessl, Oesterr. Bot. Z. 25(4): 129. 1875.

Anamorph: ***Phoma argillacea*** (Bres.) Aa & Boerema, in De Gruyter, Boerema & Van der Aa, Persoonia 18(1): 17. 2002.

Basionym: *Phyllosticta argillacea* (Bres.), Hedwigia 1894: 206. 1894.

Specimens examined: **The Netherlands**, Baarn, from *Rubus idaeus*, Sep. 1963, A. van Dijkman, CBS H-11943, culture CBS 205.63; from *Rubus idaeus*, 1975, G.H. Boerema, CBS 102634 = PD 75/248.

Didymella cannabis (G. Winter) Arx, in Müller & Arx, Beitr. Kryptogamenfl. Schweiz 11(2): 365. 1962.

Basionym: *Sphaerella cannabis* G. Winter, Hedwigia 11(10): 145. 1872.

Anamorph. ***Phoma cannabis*** (L.A. Kirchn.) McPartl., Mycologia 86(6): 871. 1995.

Basionym: *Depazea cannabis* L.A. Kirchn., Lotos 6: 183. 1856.

Specimen examined: Unknown origin, from *Cannabis sativa*, Oct. 1937, K. Röder, CBS 234.37.

Notes: The studied culture (Röder 1937) is now sterile, and could therefore not be described here morphologically.

Didymella catariae (Cooke & Ellis) Sacc., Syll. Fung. 1: 557. 1882.

Basionym: *Sphaeria catariae* Cooke & Ellis, Grevillea 5: 96. 1876.

Anamorph: ***Phoma nepeticola*** (Melnik) Dorenb. & Gruyter, Persoonia 18(1): 18. 2002.

Basionym: *Ascochyta nepeticola* Melnik, Novoste Sist. Nizsh. Rast. 1968: 178. 1968.

Specimen examined: **The Netherlands**, from the stem of *Nepeta catenaria*, 1977, M.M.J Dorenbosch, CBS 102635 = PD 77/1131.

Didymella urticicola Aa & Boerema, in Boerema, Trans. Brit. Mycol. Soc. 67(2): 303. 1976.

Anamorph: ***Phoma urticicola*** Aa & Boerema, in Boerema, Trans. Brit. Mycol. Soc. 67(2): 303. 1976.

Specimens examined: **The Netherlands**, Wageningen, from a dead stem tip of *Urtica dioica*, Mar. 1973, G.H. Boerema, holotype CBS H-11971, culture ex-holotype CBS 121.75 = ATCC 32164 = IHEM 3403 = IMI 194767 = PD 73/584; from *Urtica dioica*, 1973, G.H. Boerema, PD 73/570.

Phoma polemonii Cooke, Grevillea 13(68): 94. 1885.

Specimen examined: **The Netherlands**, from *Polemonium caeruleum*, 1983, J. de Gruyter, CBS 109181 = PD 83/757.

Phoma xanthina Sacc., Michelia 1(4): 359. 1884.

Specimens examined: **The Netherlands**, Baarn, from leaves of *Delphinium* sp., May 1968, H.A. van der Aa, CBS H-8938, culture CBS 383.68; from *Delphinium* sp., 1984, G.H. Boerema, PD 84/407.

Group C:
The species in Group C cluster in two subgroups: One comprising the *Clematis* pathogens *Ph. clematidina* and *Coniothyrium clematidis-rectae*, the other subgroup comprising *Ph. aquilegiicola* and *Ph. glaucii*, two pathogens of *Ranunculaceae* and *Papaveraceae,* respectively. All three *Phoma* species in this group were morphologically linked to the section *Heterospora* (Boerema *et al.* 1997), but are distinct from the species in clade S by the absence of conidia that represent the *Stagonosporopsis* synanamorph in culture, although smaller septate conidia do occur. In these species the *Stagonosporopsis* synanamorph is only known from *in vivo* material (Boerema 1993, Boerema *et al*. 1997).

The several species that were associated with the *Ph. clematidina* morphotype have recently been distinguished in a study of Woudenberg *et al.* (2009). In the same study, the authors showed that *C. clematidis-rectae* is closely related and, based on sequence analysis, a member of the family *Didymellaceae*. The major character on which this species is regarded as distinct from *Ph. clematidina* is by the production of pale brown pigmented conidia. In addition, the conidiogenesis of *Coniothyrium* is annellidic with percurrent proliferation, in contrast to the conidiogenesis in *Phoma*, which is considered to be solely phialidic with periclinal thickening (Boerema & Bollen 1975, Sutton 1980). Evidence for the presence of annellides has, however, not been observed in *C. clematidis-rectae*, while conidial pigmentation is relatively pale in comparison to other *Coniothyrium* species. Pigmented conidia have also been observed in various *Phoma* species before (Dorenbosch 1970, Boerema *et al.* 2004, Aveskamp *et al.* 2009a). These features may indicate that this species is actually a *Phoma* with early conidial pigmentation. Therefore *C. clematidis-rectae* is recombined into *Phoma* below.

Phoma aquilegiicola M. Petrov, Acta Inst. Bot. Acad. Sci. USSR Pl. Crypt. [Trudy Bot. Inst. Akad. Nauk SSSR] Fasc. 1: 281. 1933.

Specimens examined: **The Netherlands**, from a stem of *Aconitum pyramidale*, 1973, G.H. Boerema, CBS 107.96 = PD 73/598; from a stem of *Aquilegia* sp., 1979, G.H. Boerema, CBS 108.96 = PD 79/611.

Phoma clematidina (Thüm.) Boerema, Verslagen Meded. Plziektenk. Dienst Wageningen (Jaarboek 1978) 153: 17. 1979. emend. Woudenberg *et al*., Persoonia 22: 59. 2009.
Basionym: *Ascochyta clematidina* Thüm., Bull. Soc. Imp. Naturalistes Moscou 55: 98. 1880.

Specimens examined: **Russia**, Minussinsk, from leaves of *Clematis glaucae*, N. Martianoff, **isotype** LE 40082; **The Netherlands**, Spaubeek, from the stem of *Clematis* sp., July 1978, *G.H. Boerema*, **epitype** CBS H-16193, culture ex-epitype CBS 108.79 = PD 78/522; from *Clematis* sp., I. de Boer, Nov. 1949, CBS 201.49; Boskoop, from *Clematis jackmanii*, C. Dorsman, Oct. 1962, CBS 195.64; Wageningen, from *Selaginella* sp. M.M.J. Dorenbosch, 1966, CBS 520.66; **U.K.**, England, from *Clematis* sp., Jan. 1966, F.T. Last, CBS 102.66.

Phoma clematidis-rectae (Petr.) Aveskamp, Woudenberg & Gruyter, **comb. nov.** MycoBank MB515592.
Basionym: *Coniothyrium clematidis-rectae* Petr., Fungi Polon. 576. 1921.

Pycnidia solitary or confluent, immersed or produced on the agar surface, globose, glabrous, (80–)85–130(–155) µm diam, in older cultures pycnidia may become larger and grow after maturation to 220–250 µm diam. *Ostioles* 1(–4), wide, non-papillate to papillate or, in older cultures, on a elongated neck. *Pycnidial wall* pseudoparenchymatous, composed of oblong to isodiametric cells, 4–5 layers, (10–)11–19(–19.5) µm thick, outer 1–2 layers pigmented. *Conidiogenous cells* phialidic, hyaline, simple, smooth, ampulliform to doliiform, measuring 3–4.5(–5) × 2.5–4.5 µm. *Conidia* ellipsoidal to cylindrical, thin-walled, smooth, aseptate, (3–)4–7(–8) × 2–3(–3.5) µm, with (2–)5–12 guttules, initially hyaline, but mature conidia become slightly brownish pigmented. *Conidial matrix* sepia.

Culture characteristics: Colonies on OA 42–52 mm diam after 7 d, margin regular. Immersed mycelium dark brick to sepia or iron-grey, but hyaline near the colony margin. Pycnidia in concentric rings give the colony an olivaceous tinge. Aerial mycelium absent; reverse concolourous. Colonies on MEA 27–52 mm diam after 7 d, margin regular. Aerial mycelium incidentally occurs in sectors in some strains, grey to olivaceous. Immersed mycelium rosy-buff to rosy-vinaceous with olivaceous and grey tinges; reverse olivaceous iron-grey to saffron. Application of NaOH did not have any effect.

Specimens examined: **The Netherlands**, Boskoop, from *Clematis* sp., 1963, G.H. Boerema, CBS H-20275, culture CBS 507.63 = PD 07/03486747 = MUCL 9574; from *Clematis* sp., 1995, J. de Gruyter, PD 95/1958.

Notes: In congruence with the studies of Woudenberg *et al.* (2009), this species was found to be closely related to *Ph. clematidina* and other *Didymellaceae* species. In contrast, it is only distantly related to the type species of *Coniothyrium*, *C. palmarum*. Therefore, a recombination into *Phoma* is proposed here. The present species is clearly distinct from *Ph. clematidina* by the production of pigmented conidia, although the level of pigmentation is low, which distinguishes *Ph. clematidis-rectae* from the species remaining in *Coniothyrium* that produce darker, olivaceous conidia.

Phoma glaucii Brunaud, "*Ph. glauci*", Ann. Soc. Sci. Nat. La Rochelle 1892: 97. 1892.

Specimens examined: **The Netherlands**, near Lisse, from *Dicentra* sp., 1979, G.H. Boerema, CBS 112.96; Wageningen, from a leaf of *Chelidonium majus*, 1994, G.H. Boerema, CBS 114.96 = PD 94/888.

Groups D & E – Leptosphaerulina and Macroventuria:
The most remarkable findings in the *Didymellaceae* are the *Leptosphaerulina* and *Macroventuria* (clade E) teleomorph genera. The species belonging to these teleomorphs are found amidst the *Didymellaceae*, causing the genus *Didymella* to be paraphyletic. The species in both genera are closely related to each other, as was already pointed out by Kodsueb *et al.* (2006), who, however, missed the link with *Didymella*. A phomoid anamorph state has, thus far, not been recorded for any of the species in these teleomorph genera.

Leptosphaerulina is morphologically distinct from *Macroventuria* and *Didymella*, although all three genera are known for their hyaline ascospores (Van der Aa 1971, Von Arx 1981). *Leptosphaerulina*

produces large, longitudinally and transversally septated ascospores, resembling those of *Pleospora* and *Cucurbitaria*, although the ascospores of these genera are pigmented. The major difference between *Didymella* and *Macroventuria* is the presence of setae on the pseudothecia of the latter genus, whereas *Didymella* ascomata are commonly glabrous. According to the original description (Van der Aa 1971), *Macroventuria* strains resemble *Venturia* by their setose pycnidia, but differ in their restricted number of the asci.

Leptosphaerulina americana (Ellis & Everh.) J.H. Graham & Luttr., Phytopathology 51: 686. 1961.
Basionym: *Pleospora americana* Ellis & Everh., in North American Pyrenomycetes: 336. 1892, nom. nov. pro *Pleospora hyalospora* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia: 238. 1890, non *Pleospora hyalospora* Speg.

Specimen examined: **U.S.A.**, Georgia, from *Trifolium pratense*, Apr. 1954, E.S. Luttrell, CBS 213.55.

Leptosphaerulina arachidicola W.Y. Yen, M.J. Chen & K.T. Huang, J. Agric. Forest. 10: 167. 1956.

Specimen examined: **Taiwan**, from a leaf of *Arachis hypogaea*, 1956, K.T. Huang, CBS 275.59 = ATCC 13446.

Note: CBS 275.59 is degenerated and forms only very tiny sclerotia *in vitro.*

Leptosphaerulina australis McAlpine, Fungus Diseases of stone-fruit trees in Australia: 103. 1902.

Specimens examined: **Indonesia**, Lampung, from *Eugenia aromatica*, Dec. 1982, H. Vermeulen, CBS 317.83. **The Netherlands**, Baarn, from soil, Sep. 1969, J.A. Stalpers, CBS 939.69.

Leptosphaerulina trifolii (Rostr.) Petr., Sydowia 13: 76. 1959.
Basionym: *Sphaerulina trifolii* Rostr., Bot. Tidsskr. 22: 265. 1899.

Specimen examined: **The Netherlands**, from *Trifolium* sp., 1958, CBS 235.58.

Macroventuria anamochaeta Aa, Persoonia 6(3): 362. 1971.

Specimens examined: **South Africa**, Karroo Desert, from decayed canvas, Aug. 1971, M.C. Papendorf, **holotype** CBS H-14192, ex-holotype culture CBS 525.71; Cape Province, from a trunk of *Medicago sativa*, June 1972, W.F.O. Marasas, CBS 502.72.

Macroventuria wentii Aa, Persoonia 6(3): 361. 1971.

Specimen examined: **U.S.A.**, Nevada, Death Valley, from plant litter, Aug. 1971, F.W. Went, **holotype** CBS H-14195, ex-holotype culture CBS 526.71.

Group F:
As a sister group to *Leptosphaerulina*, several host-specific *Phoma* species are found that induce leaf spots on a variety of plant species, including *Ph. infossa*, *Ph. anigozanthi*, *Ph. arachidis-hypogaeae* and *Ph. gossypiicola*. The latter species causes leaf spots and stem canker on cotton plants (*Gossypium* spp.). However, other plant species may also become symptomatic when deliberately infected (Holliday & Punithalingam 1970). *Phoma infossa* has originally been reported from stems of ash trees (*Fraxinus* sp.) in New York State (Ellis & Everhart 1888), but has recently been associated with a severe foliar disease of green ash (*F. pennsylvanica*) in Argentina (Aveskamp *et al.* 2009a). All species produce aseptate conidia in culture, although *Ph. gossypiicola* is known to also produce 2- to multi-celled conidia *in vivo*, hence the *Ascochyta gossypii* synonym (De Gruyter 2002).

In contrast to these plant pathogens, a fungicolous species also occurs in the present clade. Species from the genera *Phoma* and *Ampelomyces* have been "frequently confused with each other" (Sullivan & White 2000), which explains why *Ph. fungicola* is found here. This species was previously known as *Amp. quercinus* and is recombined in the subsequent taxonomical section. The finding of this species in the *Didymellaceae* is in congruence with sequence results obtained by Sullivan & White (2000) and Szentiványi *et al.* (2005). Also *Amp. humuli*, another fast-growing species, proved to be phylogenetically similar to species that currently represent the *Didymellaceae* (Kiss & Nakasone 1998). Additionally, it has been suggested that the fast growing species *Amp. artemisiae* and *Amp. uncinulae* (Rudakov 1979, Kiss 1997) actually do, in fact, not represent *Ampelomyces*, but belong to the genus *Phoma*; these species were incorrectly identified based on their host-association (Kiss *et al.* 2004). The species in *Ampelomyces* are all recognised as parasites of fungi that cause powdery mildew (Kiss 1997). However, it is suggested that also the ubiquitous species *Ph. glomerata* has fungicolous capacities, and may be suited as mycoparasitic control agent of powdery mildew (Sullivan & White 2000).

Only one of the *Phoma* species embedded in this clade has been associated with a teleomorph. In the description of *Ph. anigozanthi*, the sexual state is recorded as *Sphaerella millepunctata* (apud Gruyter & Noordeloos 1992). *Sphaerella* is practically synonymised with *Mycosphaerella* (*e.g.* Aptroot 2006), but as described above, several of the *Mycosphaeralla* species have subsequently been recombined into *Didymella*. In the present study no evidence of teleomorph formation *in vitro* has been observed, which is in congruence with the results of Gruyter & Noordeloos (1992). As also type material of *Ph. anigozanthi* and *S. multipunctata* could not be obtained, this taxonomic link is still to be confirmed.

Phoma anigozanthi Tassi, Boll. Reale Orto Bot. Siena 3 (2 – 1899): 148. 1900.

Specimen examined: **The Netherlands**, from a leaf of *Anigozanthus maugleisii*, 1979, H. Cevat CBS H-5199, culture CBS 381.91 = PD 79/1110.

Phoma arachidis-hypogaeae (V.G. Rao) Aa & Boerema, Persoonia 15(3): 388. 1993.
Basionym: *Phyllosticta arachidis-hypogaeae* V.G. Rao, Sydowia 16 (1962): 275. 1963.

Specimen examined: **India**, Madras, from a leaf of *Arachis hypogaea*, 1977, CBS 125.93 = PD 77/1029.

Phoma fungicola Aveskamp, Gruyter & Verkley, **nom. nov.** pro *Cicinobolus quercinus* Syd. Ann. Mycol. 13: 42. 1915. MycoBank MB515593.
Basionym: *Cicinobolus quercinus* Syd., Ann. Mycol. 13: 42. 1915.
≡ *Ampelomyces quercinus* (Syd.) Rudakov, Mikol. Fitopatol. 13(2): 109. 1979. not *Phoma quercina* Sacc & Roum. Syll. fung. 3: 96. 1881, = *Phomopsis quercina* Sacc.) Höhn., not *Phoma quercina (*Peck) Sacc. Syll. fung. 3: 96. 1884.

Etymology: Epithet refers to the fungicolous lifestyle of this species.

Pycnidia always solitary, produced on the agar surface, globose, peroblate to suboblate, glabrous, measuring (50–)65–130(–150) ×

(65–)95–200(–220) µm with a single, conspicuous, non-papillate ostiole. *Pycnidial wall* pale brown, pseudoparenchymatous, composed of isodiametric cells, 3–5 layers, (6–)8.5–14.5(–16) µm thick, outer 1–2 layers slightly pigmented. *Conidiogenous cells* phialidic, hyaline, simple, smooth, doliiform to ampulliform, variable in size, *ca*. (3–)3.5–5 × 3–4(–5) µm. *Conidia* variable in shape and size, subglobose to oval or obtuse, thin-walled, smooth, aseptate, measuring (5–)5.5–7.5(–8.5) × 3–4.5(–5) µm, with 0–2(–3) minute guttules, initially hyaline, but brown at maturity. Conidial exudates not recorded.

Culture characteristics: Colonies on OA 55–68 mm diam after 7 d, margin regular. Aerial mycelium white, floccose to woolly. Immersed mycelium greenish olivaceous to olivaceous near the colony centre. Abundant black pycnidia are scattered over the medium; reverse concolourous. Colonies on MEA 65–75 mm diam after 7 d, margin regular. Aerial mycelium covering the whole colony, compact, white to pale grey, with olivaceous tinges near the colony centre; reverse olivaceous-black.

Specimen examined: **Ukraine**, Crimea, in the vicinity of Feodosiya, on *Microsphaera alphitoides* from *Quercus* sp., 1979, O.L. Rudakov, CBS H-20276, culture CBS 633.92 = ATCC 36786, VKM MF-325.

Notes: The epithet used for the description of this species in the genera *Cicinobolus* and *Ampelomyces* could not be transferred to the genus *Phoma* as *Ph. quercina* is already occupied. This name, however, refers to a *Phyllosticta* species (Van der Aa & Vanev 2002). Therefore, a new name is proposed here for the present species.

Kiss & Nakasone (1998) already found that several fast-growing *Ampelomyces* species were phylogenetically distinct from the type species, which is characterised by a rather slow growth rate, and suggested that *A. quercinus* belonged to *Phoma*. This finding was supported by results obtained in later studies (Sullivan & White 2000, Szentiványi *et al.* 2005).

Phoma gossypiicola Gruyter, Persoonia 18(1): 96. 2002.

Specimen examined: **U.S.A.**, Texas, from a leaf of *Gossypium* sp., 1963, L.S. Bird CBS H-9006, culture CBS 377.67.

Phoma infossa Ellis & Everh., J. Mycol. 4(10): 102. 1888, emend. Aveskamp *et al.*, Mycologia 101. 373. 2009.

Specimens examined: **Argentina**, Buenos Aires Province, La Plata, from leafs of *Fraxinus pennsylvanica*, 2008, M. Murace, **neotype** CBS H-20145, culture ex-neotype CBS 123395; Buenos Aires Province, La Plata, from leafs of *Fraxinus pennsylvanica*, 2008, M. Murace, CBS 123394.

Group G:

This group (BPP = 1.00, RBS = 99 %) consists of *Ph. subherbarum* and *Ph. pedeiae* sp. nov. Although the first species name suggests a close resemblance with the type species *Ph. herbarum*, it is phylogenetically distinct. Both *Ph. herbarum* and *Ph. subherbarum* are accommodated in section *Phoma*, but are distinct in colony characters: in contrast to *Ph. herbarum, Ph. subherbarum* does not react to the application of a droplet of NAOH (De Gruyter *et al.* 1993). The growth rate of *Ph. subherbarum* is also considerably faster, as a colony can cover the plate surface within 1 wk.

Boerema *et al.* (2004) hypothesised that *Ph. subherbarum* is from American origin. In contrast, both strains of *Ph. pedeiae* were found in the Netherlands. Both species in this clade appear to have a plurivorous nature. The novel species *Ph. pedeiae* is described below.

Phoma pedeiae Aveskamp, Gruyter & Verkley, **sp. nov.** MycoBank MB515594. Fig. 4.

Conidia ellipsoidea vel cylindrica, glabra, hyalina, continua, 3–4.5 × 1.5–2.5 µm, 0–2(–3) guttulis praedita. Matrix conidiorum cremeo-alba.

Etymology: Named after the institute that has facilitated most of the research on the taxonomy of the genus *Phoma* and affiliated genera in the past decade, the PD (Plantenziektenkundige Dienst – Dutch Plant Protection Service). Both isolates of this species were collected and preserved by employees of this institute.

Pycnidia solitary or confluent, produced on the agar surface, globose to ellipsoidal, glabrous, (90–)100–230(–255) × (75–)90–155(–165) µm with 1–2 conspicuous, non-papillate ostioles. *Pycnidial wall* pseudoparenchymatous, composed of oblong to isodiametric cells, 3–5 layers, 11–17 µm thick. *Conidiogenous cells* phialidic, hyaline, simple, smooth, flask-shaped, relatively small, *ca.* 3.5–4(–4.5) × 3–4 µm. *Conidia* ellipsoidal to cylindrical, thin-walled, smooth, hyaline, aseptate 3–4.5 × 1.5–2.5 µm, with 0–2(–3) guttules. *Conidial matrix* creme-white.

Culture characteristics: Colonies on OA, 65–75 mm diam after 7 d, margin regular. Immersed mycelium olivaceous. Aerial mycelium floccose, white or smoke-grey to greenish olivaceous. Abundant black pycnidia are scattered over the medium; reverse concolourous with some reddish tinges. Colonies on MEA 55–65 mm diam after 7 d, margin regular. Aerial mycelium covering the whole colony, floccose, smoke-grey to greenish olivaceous, white near the centre of the colony; reverse olivaceous-black or bay. Agar colour changes to bay due to diffusible pigments produced by the fungus. Colonies on CHA similar as on MEA, but somewhat faster growing, 70–80 mm diam after 7 d. Application of NaOH did not have any effect.

Specimens examined: **The Netherlands**, Aalsmeer region, on *Schefflera elegantissima*, 1992, J. de Gruyter, **holotype designated here** CBS H-20239, culture ex-holotype CBS 124517 = PD 92/612A; on *Orchidaceae* sp., 1984, J. de Gruyter, CBS 124516 = PD 84/453.

Notes: *Phoma pedeiae* has been found in association with several tropical ornamental pot plants in Dutch greenhouses. Only mild disease symptoms were recorded from this species, and therefore the fungus was not further studied. Phylogenetically, this species is found in close relation to *Ph. subherbarum* (BPP= 1.00; RBS = 99 %), which is probably a weak pathogen and saprobe of different plant substrates occurring on the American continent (De Gruyter *et al.* 1993).

Phoma subherbarum Gruyter, Noordel. & Boerema, Persoonia 15(3): 387. 1993.

Specimens examined: **Canada**, from *Zea mays*, **holotype** L 992.177.439, culture ex-holotype CBS 250.9292 = DAOM 171914 = PD 92/371; from *Zea mays*, May 1978, G.A. Neish, CBS 305.79A = DAOM 170848; **Peru**, from *Solanum* sp., CBS 249.92 = PD 78/1088.

Group H:

Phoma bellidis and *Ph. senecionis* are found in association with two plant genera from the *Compositae* family: *Bellis* spp. and *Senecio* spp. respectively (De Gruyter *et al.* 1993). The distantly related *Ph. digitalis* is a pathogen of *Digitalis* spp. (*Scrophulariaceae*), but shares the feature with *Ph. bellidis* that it is also recorded as a seed-pathogen (Boerema & Dorenbosch 1979). In contrast, *Ph. senecionis* is only known as a necrophyte.

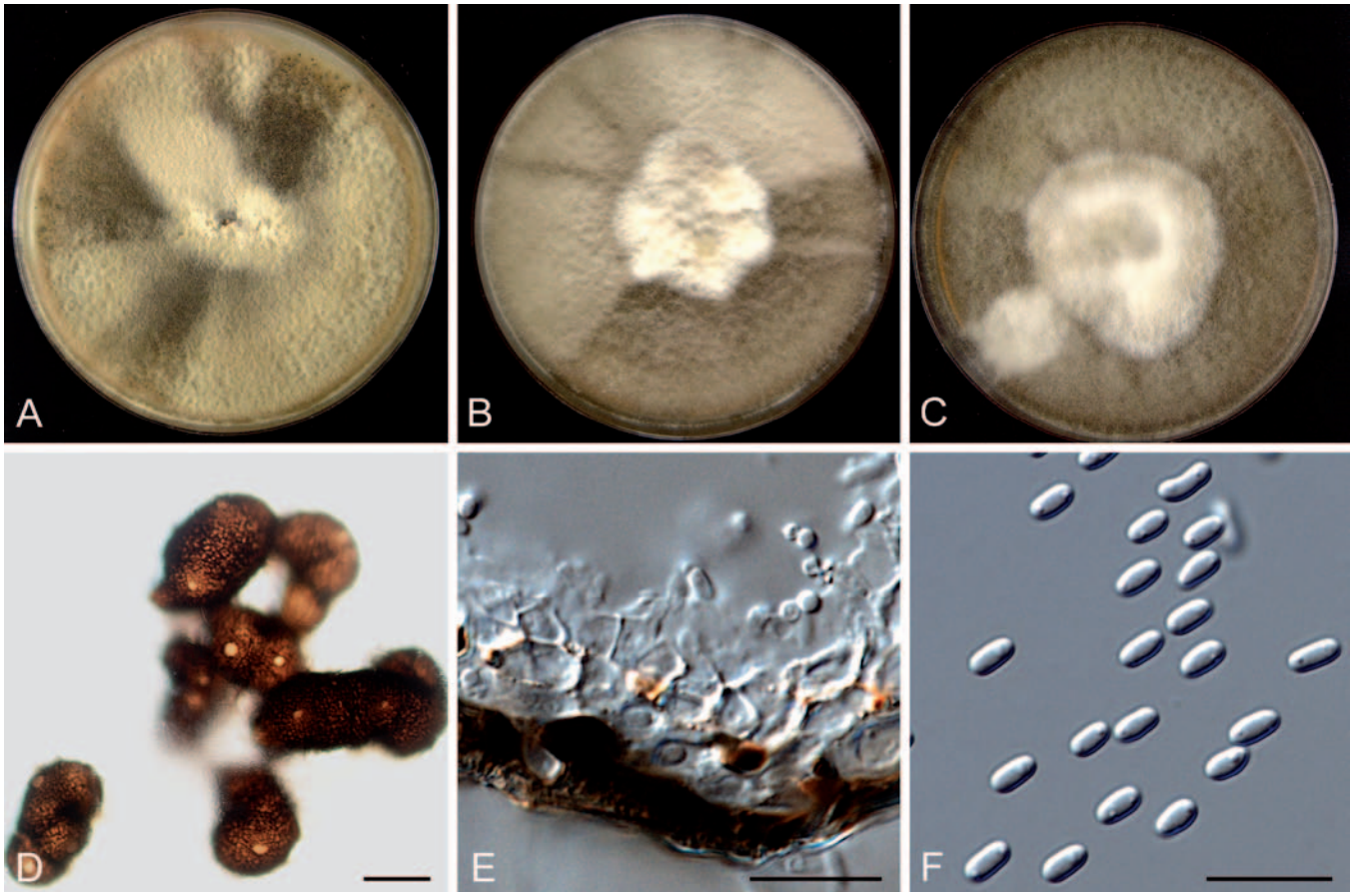


Fig. 4. *Phoma pedeiae* (CBS 124517). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D. Pycnidia. E. Section of the pycnidial wall. F. Conidia. Scale bars: D = 100 µm; E–F = 10 µm.

Phoma bellidis Neerg., Friesia 4: 74. 1950.

Specimens examined: **The Netherlands**, from seed of *Bellis perennis*, 1985, G.H. Boerema, CBS H-5200, culture CBS 714.85 = PD 74/265; from *Bellis* sp., 1994, J. de Gruyter, PD 94/886.

Phoma digitalis Boerema apud Boerema & Dorenbosch, Verslagen Meded. Plziektenk. Dienst Wageningen 153: 19. 1979.

Specimen examined: **The Netherlands**, Ommen, from *Digitalis* sp., 1990, J. de Gruyter, CBS 109179 = PD 90/835-1.

Phoma senecionis P. Syd., Hedwigia, Beibl. 38: 136. 1899.

Specimen examined: **New Zealand**, Raetihi, from a stem of *Senecio jacobaea*, Feb. 1977, S. Ward, CBS 160.78 = LEV 11451.

Group I:

Group I comprises three *Phoma* taxa (*Ph. acetosellae*, *Ph. macrostoma* var. *macrostoma* and var. *incolorata*) that were placed in the section *Phyllostictoides* on the basis of the presence of septate conidia (Gruyter *et al.* 2002), but also accommodates *Ph. viburnicola.* The placement of this species in section *Phoma* can be debated, as a single septate conidium has been observed in strain CBS 500.91, one of the strains that was designated as reference strain (De Gruyter & Noordeloos 1992). Also *D. exigua* (CBS 183.55 - Neotype) is found in this clade, the type species of the genus *Didymella* (De Gruyter *et al.* 2009), which does however not produce an anamorph state. The four species do not exhibit a shared pathological feature or geographic origin. The variety *incolorata* differs from var. *macrostoma* in lacking a red to violet pigment in the hyphae and any reaction to NaOH.

Phoma acetosellae (A.L. Sm. & Ramsb.) Aa & Boerema, in De Gruyter, Boerema & Van der Aa, Persoonia 18(1): 16. 2002.

Basionym: *Phyllosticta acetosellae* A.L. Sm. & Ramsb., Trans. Brit. Mycol. Soc. 4: 173. 1912.

Specimens examined: **France**, Corrèze, Monteil sur Bois, from a leaf of *Rumex acetosella*, 1976, H.A. van der Aa, CBS H-16138, culture 631.76. **The Netherlands**, Baarn, from a stem of *Rumex hydrolapathum*, March 1996, H.A. van der Aa, CBS 179.97.

Phoma macrostoma var. ***incolorata*** (A.S. Horne) Boerema & Dorenb., Persoonia 6(1): 55. 1970.

Basionym: *Polyopeus purpureus* var. *incolorata* A.S. Horne, J. Bot. 58: 240. 1920.

Specimens examined: **Switzerland**, Vierwaldstättersee, near Brunnen, from a leaf of *Acer pseudoplatanus*, Oct. 1968, J. Gemmen, CBS H-20240, culture CBS 223.69. **The Netherlands**, from *Malus sylvestris*, 1983, J. de Gruyter, CBS 109173 = PD 83/908.

Phoma macrostoma var. ***macrostoma*** Mont., Annls Sci. Nat., Bot. III 11: 52. 1849.

Specimens examined: **Germany**, near München, from the bark of *Larix decidua*, 1995, G.J. Verkley, CBS 482.95. **The Netherlands**, Wageningen, from wood of *Malus sylvestris*, Sep. 1969, G.H. Boerema, CBS H-16431, culture CBS 529.66 = PD 66/521.

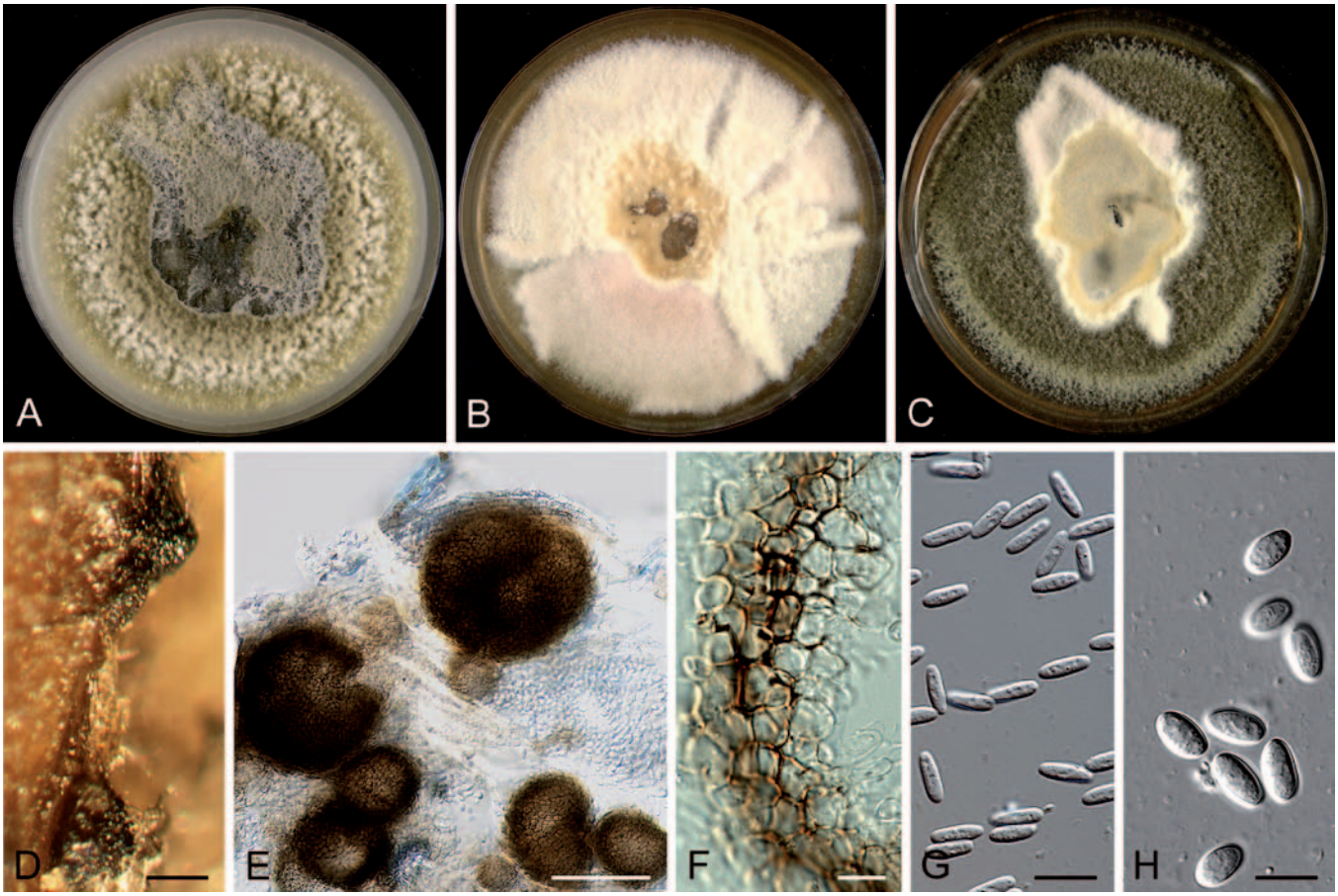


Fig. 5. *Phoma dimorpha* (CBS 346.82). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D. Pycnidia on stem of *Urtica dioica*. E. Pycnidia. F. Pycnidial wall. G–H. Conidia *in vitro* (G) and *in vivo* (H). Scale bars: D–E = 100 µm; F = 20 µm; G–H = 10 µm.

Phoma viburnicola Oudem., Contr. Flora Mycol. d. Pays-Bas 17: 247. 1901.

Specimens examined: **The Netherlands**, Wageningen, Aboretum, from *Viburnum cassioides*, 1969, G.H. Boerema, CBS H-16605, culture CBS 523.73 = PD 69/800; from *Chamaecyparis lawsoniana*, 1981, G.H. Boerema, CBS 371.91 = PD 81/413; Baarn, from a leaf of *Ilex aquifolium*, 1993, J. de Gruyter, CBS 500.91 = PD 83/222.

Group J:

This small group (BPP = 1.00, RBS = 96 %) comprises only two species. Because of the production of dictyochlamydospores, *Phoma boeremae* was suggested to belong to the section *Peyronellaea* (Group K, Aveskamp *et al*. 2009a), to which the present group is closely related. No such structures were, however, observed in its sister species, *Ph. dimorpha* sp. nov. This species is known from a single strain, which sporulates poorly and may be degenerated.

Phoma boeremae Gruyter, Persoonia 18 (1): 91. 2002.

Specimen examined: **Australia**, Victoria, Burnley Gardens, from seed of *Medicago littoralis* cv. Harbinger, Febr. 1982, M. Mebalds, **neotype** L 996.294.536, ex-neotype culture CBS 109942 = PD 84/402.

Phoma dimorpha Aveskamp, Gruyter & Verkley, **sp. nov.** MycoBank MB515595. Fig. 5.

Conidia dimorpha, in vitro cylindrica, glabra, hyalina, continua, 8–9.5(–10.5) × (2–)2.5–3(–3.5) µm, (5–)6–8(–10) guttulis minutis apolaribus praedita, in vivo eguttulata, (8–)9–12(–12.5) × (4.5–)5–5.5(–6.5) µm.

Etymology: The epithet refers to the two different conidial types that are observed.

Pycnidia produced only scarcely *in vitro*, in clusters of *ca*. 4–10 elements, globose, glabrous, non-papillate, produced on the agar surface, relatively small, measuring (65–)85–170(–190) µm diam. *Ostioles* single, non-pappillate. *Pycnidial wall* pseudoparenchymatous, composed of isodiametric cells, 4–7 layers, 14–20 µm thick. *Conidiogenous cells* phialidic, hyaline, simple, smooth, flask-shaped, *ca.* 5.5–7 × 4.5–6.5 µm. *Conidia* cylindrical, thin-walled, smooth, hyaline, aseptate 8– 9.5(–10.5) × (2–)2.5–3(–3.5) µm, with (5–)6–8(–10) minute apolar guttules. *In vivo* eguttulate and somewhat broader, measuring (8–)9–12(–12.5) × (4.5–)5–5.5(–6.5) µm. Conidial exudates not observed.

Culture characteristics: Colonies on OA 45–50 mm diam after 7 d, margin regular. Immersed mycelium olivaceous-black, in some sectors covered by a low mat of floccose white to grey aerial mycelium, towards colony margin the aerial mycelium is gradually becoming more felted and white; reverse olivaceous buff to dark mouse-grey. Colonies on MEA 50–55 mm diam after 7 d, margin regular. Immersed mycelium hyaline, amber or iron-grey. Only sparsely small white tufts of whitish aerial mycelium are produced in older cultures; reverse concolourous. Colonies on CHA 55–60 mm diam after 7 d, margin regular. Immersed mycelium hyaline, honey to isabelline or dark mouse-grey. Aerial mycelium more proliferent near colony margin initially white, later developing to iron-grey with olivaceous-grey tinges; reverse black, but hyaline near colony centre. Application of NaOH did not have any effect. In older cultures white dendritic crystals are formed both in the aerial mycelium and in immersed in the agar.

Specimen examined: **Spain**, Canary Isles, Gran Canaria, from phyllocladium of *Opuntiae* sp., June 1982, H.A. Van der Aa, **holotype designated here** CBS H-20234, culture ex-holotype CBS 346.82.

Notes: Although sufficient pycnidial primordia are formed on OA, maturation of pycnidia is only incidentally observed *in vitro*. Therefore the characters of the pycnidia and the pycnidial wall described here are based on only three samples. Formation of mature pycnidia can be induced by addition of a sterilised stem piece of stinging nettle (*Urtica dioica*). The conidia that were described from *in vivo* material were obtained using this technique.

Several other *Phoma* species are known from *Opuntiae*, including *Ph. opuntiae* (*Phoma sensu lato*) and *Ph. longicolla* sp. nov. (see below). The conidia of *Ph. opuntiae* are, however, considerably smaller, measuring 2.5–3.5 × 1–1.5 µm (De Gruyter & Noordeloos 1992), whereas the main difference with *Ph. longicolla* are the pycnidia, which are uniostiolate and significantly larger in the latter species.

Group K – Peyronellaea:

This group (BPP = 1.00, RBS = 58 %) comprises many of the chlamydospore forming species, including the majority of the species that were accommodated in *Phoma* section *Peyronellaea* (Boerema *et al.* 1965a, 1968, 1971, 1973, 1977). Also *Ph. glomerata*, type species of this section is accommodated here (Boerema 1997). However, as section, *Peyronellaea* has a polyphyletic nature (Aveskamp *et al.* 2009a). *Phoma chrysanthemicola*, *Ph. violicola* and the recently established species *Ph. schachtii* (Aveskamp *et al.* 2009a) have been found to be basal to the *Didymellaceae* (Fig. 1), whilst several species producing botryoid chlamydospores, representing the genus *Epicoccum* as emended below, are clustered in group M. Also *Ph. infossa* and *Ph. omnivirens*, which have proven to produce dictyochlamydospores in culture (Aveskamp *et al.* 2009a), are not situated in this part of the phylogenetic tree. *Peyronellaea calidophila* and *Ph. microchlamydospora* reside in the basal lineages of this clade.

Also several *Phoma* species that were not included in *Peyronellaea* in the Boeremaean taxonomical system, but that do produce either uni- or multicellular chlamydospores, are included in this clade. In *Ph. gardeniae*, *Ph. narcissi*, and *Ph. zeae-maydis* multicellular chlamydospores have been observed, whereas *Ph. pinodella*, *Ph. arachidicola*, and *Ph. heteroderae* are species that form unicellular chlamydospores. Several species in this clade, however, have never been recorded to produce any unicellular or multicellular chlamydospores. These species are *Ph. alectorolophi*, *Ph. obtusa* and *Ph. protuberans*, which will be treated in a subsequent section of this paragraph, and *Ph. anserina*, *Ph. aurea*, *Ph. nigricans* and *Ph. eucalyptica*. However, two of these species, *Ph. anserina* and *Ph. eucalyptica* are well-known for the formation of swollen cells and anastomosis in culture (De Gruyter & Noordeloos 1992), which may be regarded as a precursor to chlamydospore formation. The ancestral location of *Ph. anserina* in this clade may also be an indication that chlamydospore production has not completely been developed yet in this group. The high posterior probabillity for this group justifies the recognition of a separate genus in the *Didymellaceae*. Therefore the genus name *Peyronellaea* Goid. is re-established, and the associated species are recombined into this genus below.

The plurivorous species *Ph. calorpreferens* and *Ph. heteroderae* share identical LSU, ITS and TUB genes. Also morphologically the representative strains of these species are highly similar. A synonymisation of these species is therefore proposed in this paper.

Another notable subgroup within this clade is a cluster formed by *Didymella pinodes*, *D. lethalis*, *D. arachidicola* and *Ph. pinodella*. Recently, Irinyi *et al.* (2009) synonymised *Ph. sojicola* with *Ph. pinodella*, based on morphological observations and sequence data of ITS, β-tubulin and translation elongation factor 1-α. This indicates that the notorious pathogen of green pea (*Pisum sativum*) is also capable of infecting soybean (*Glycine max*). These observations are supported by the results obtained in the present study. As reported in previous studies (Faris-Mokaiesh *et al.* 1996, Onfroy *et al.* 1999, Fatehi *et al.* 2003, Peever *et al.* 2007), *Ph. pinodella* appears to be very closely related to *D. pinodes* (anam. *Ascochyta pinodes*) and because these species share the same host range they are often confused. Both species can however easily be differentiated on basis of the amount of septate conidia formed *in vitro*, abundantly in *D. pinodes*, and in very small numbers in *Ph. pinodella*.

Because *Ph. pinodella* is morphologically so similar to *Ph. medicaginis*, it was once regarded as a variety of this species by Boerema *et al.* (1965b). The variety was elevated to species rank after careful observation (White & Morgan-Jones 1987), but the varietal name is however currently still in common use (*e.g.* Onfroy *et al*. 1999, Fatehi *et al*. 2003, Taylor & Ford 2007). The results obtained in this study however, illustrate a substantial phylogenetical distance to *Ph. medicaginis*, and warrant recognition at species level, in the in the re-instated genus *Peyronellaea*.

The close association of *Ph. arachidicola* with *Ph. pinodella* and *D. pinodes* is reflected by the morphology of these species, which all produce, next to septate and aseptate conidia, also globose to ellipsoidal unicellular chlamydospores, which may be formed in chains. These chlamydospores measure 5–20 µm diam, which is somewhat larger than the species in group N. The close relationship of these three species has been hypothesised before, and was based on chemical analysis of the crystals produced by these taxa (Noordeloos *et al.* 1993).

Didymella arachidicola is a specific pathogen of groundnut (*Arachis hypogaea*), another host plant of the family *Fabaceae* with which the other species in this subclade are also associated.

In the *Ph. pinodella* / *D. pinodes* subcluster (BPP = 1.00, RBS = 94 %), four teleomorph species are found with a coelomycete anamorph state. Next to *D. pinodes*, these are *D. alectorolophi*, *D. arachidicola,* and *D. lethalis*. A fifth teleomorph is the sexual state of *Ph. pinodella* (as *Ph. medicaginis* var. *pinodella*) that is reported and described by Bowen *et al.* (1997), but that has not been named thus far. From a phylogenetic point of view, this record is very plausible as all species in the subclade in which *Ph. pinodella* is embedded, do form a *Didymella*-like teleomorph (Fig. 2). However, as we did not include mating type tests in our studies, and as the species is probably heterothallic (Bowen *et al.* 1997), pseudothecia were not observed in the present study. A formal name for the teleomorph of *Ph. pinodella* could therefore not be proposed here either.

A fifth species in group K that has a known teleomorph is *Ph. zeae-maydis*. This species is however only distantly related to the four species mentioned above. Nevertheless, it can be concluded that the sole teleomorph genus that is associated with group K is *Didymella*-like. This would further support the suggestion (Peever *et al.* 2007) that the teleomorph name for *A. pinodes* that is often referred to by plant pathologists, *Mycosphaerella pinodes,* should be omitted.

Remarkably, three species are found in this clade that are identical based on sequence analyses, but that are morphologically rather distinct. Also sequence comparisons of parts of the actin and

calmodulin genes did not reveal any differences between those four strains (Aveskamp & Woudenberg, unpubl. data). *Phoma alectorolophi* and *Ph. protuberans* are associated with *Phoma* section *Sclerophomella* (Boerema *et al.* 1997, De Gruyter *et al.* 2002), because of the thick-walled pycnidia formed in culture and *in vivo*. However, because of the production of relatively large secondary conidia, a link with sections *Heterospora* or *Phyllostictoides* can also be advocated. Colony characters, microscopic features and ecology indicate that the two species should actually be rather distinct. A third taxon found in this group is *Ph. obtusa*, a saprobic species that has a thin pycnidial wall and lacks septate conidia. Nevertheless, these three species are recovered in a clade in which solely chlamydospore-forming species reside, a character that never has been recorded in any of these taxa. The explanation of the contrast between the level of genetic and morphological similarity will be one of the main challenges in *Phoma* taxonomy.

Peyronellaea Goid. ex Togliani, Ann. Sperim. Agrar. II 6: 93. 1952, **emend.** Aveskamp, Gruyter & Verkley

Conidiomata pycnidial, globose to subglobose, measuring 50–380 µm diam, on agar surface or immersed, solitary or confluent, ostiolate or poroid. *Pycnidial wall* pseudoparenchymatous, counting 2–8 cell layers of which the outer 1–3 are brown or olivaceous pigmented. *Conidiogenous cells* phialidic, hyaline, simple, smooth, ampulliform or doliiform, *ca*. 3.5–7 × 3.5–6 µm. *Conidia* generally aseptate, ellipsoidal to subglobose, thin-walled, smooth, hyaline, but in older cultures conidia may become pigmented, generally measuring 4–15 × 2–4 µm, but larger or septated conidia may occur in at least one species. *Unicellular chlamydospores* often abundantly formed in and on the agar and in the aerial mycelium, globose, intercalary, brown or olivaceous pigmented, measuring 5–22 µm diam. *Multicellular chlamydospores* mainly alternarioid, terminal or intercalary, often in chains, brown or olivaceous pigmented, 10–50 × 7–25 µm. *Pseudothecia* only present in a few species, (sub-)globose, up to 200 µm diam, but in one species also flattened pseudothecia occur. *Asci* cylindrical to clavate, measuring 35–65 × 11–17 µm, always 8-spored, biseriate. *Ascospores* ellipsoid, measuring 12–24 × 4–8 µm, uniseptate, upper cell usually larger than the lower cells.

Type species: *Peyronellaea glomerata* (Corda) Goid. ex Togliani

Peyronellaea alectorolophi (Rehm.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515597.
Basionym: *Didymella alectorolophi* Rehm, apud Ade, Hedwigia 64: 294. 1923.

≡ *Phoma alecotorolophi* Boerema, Gruyter & Noordel., Persoonia 16(3): 366. 1997.

Specimen examined: **The Netherlands**, from seed of *Rhinanthus major*, 1993, L 992.167.515, culture CBS 132.96 = PD 93/853.

Peyronellaea americana (Morgan-Jones & J.F. White) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515596.
Basionym: *Phoma americana* Morgan-Jones & J.F. White, Mycotaxon 16(2): 406. 1983.

Specimens examined: **Argentina**, Buenos Aires Province, Olavarria, from leaves of *Triticum aestivum* cv. Buck Diamante, Aug. 2002, A. Perelló, CBS 112525. **Denmark**, Copenhagen, from seed of *Phaseolus vulgaris*, May 1965, S.B. Mathur, CBS 256.65. **Nigeria**, from *Sorghum vulgare*, 1979, PD 79/58. **South Africa**, from *Zea mays*, 1978, PD 78/1059. **U.S.A.**, Arkansas, from pod lesions of *Glycine max*, 1981, H.J. Walters, CBS 568.9797 = ATCC 44494 = PD 94/1544; Georgia, from *Zea mays*, 1985, G.H. Boerema, CBS H-16144, culture CBS 185.85 = PD 80/1191; from *Zea mays*, 1980, PD 80/1143. Unknown origin, from a nematode cyst, 1982, G.H. Boerema, PD 82/1059.

Peyronellaea anserina **(**Marchal) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515598.
Basionym: *Phoma anserina* Marchal, Champignon Copr. 11: 1891.

Specimens examined: **The Netherlands**, from *Pisum sativum*, 1979, CBS 363.91 = PD 79/712; Ter Apel, from potato flour, 1983, CBS 360.84.

Peyronellaea arachidicola (Khokhr.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515599.
Basionym: *Mycosphaerella arachidicola* Khokhr., Bolezni i vrediteli maslichnykh kul'tur 1(2): 29. 1934.

≡ *Didymella arachidicola* (Khokhr.) Tomilin, Opredelitel' gribov roda Mycosphaerella Johans: 285. 1979.

Anamorph: *Phoma arachidicola* Marasas, Pauer & Boerema, Phytophylactica 6(3): 200. 1974.

Specimens examined: **South Africa**, Cape Province, Jan Kempdorp, Vaalharts Research Station, from a leaf of *Arachis hypogaea*, Mar. 1972, G.D. Pauer, **isotype** of *Ph. arachidicola* CBS H-7601, ex-isotype culture CBS 333.75 = ATCC 28333 = IMI 386092 = PREM 44889; **Zimbabwe**, from *Arachis hypogaea*, 1980, CBS 315.90 = PD 80/1190.

Peyronellaea aurea (Gruyter, Noordel. & Boerema) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515600.
Basionym: *Phoma aurea* Gruyter, Noordel. & Boerema, Persoonia 15(3): 394. 1993.

Specimen examined: **New Zealand**, Auckland, from a stem of *Medicago polymorpha*, 1978, **holotype** L 992.177.422, ex-holotype culture CBS 269.93 = PD 78/1087.

Peyronellaea australis Aveskamp, Gruyter & Verkley, **nom. nov.** pro *Phoma nigricans* P.R. Johnst. & Boerema, MycoBank MB515601.

≡ *Phoma nigricans* P.R. Johnst. & Boerema, New Zealand J. Bot. 19(4): 394. 1982.

Etymology: Epithet refers to the Southern Hemisphere, where this fungus is mainly found.

Specimens examined: **New Zealand**, from *Actinidea chinensis*, 1977, P.R. Johnston, PD 77/919; Auckland, Mt. Albert, from a leaf of *Actinidia chinensis*, Apr. 1979, P.R. Johnston, **isotype** CBS H-7619, ex-isotype culture CBS 444.81 = PDDCC 6546.

Note: A new name was sought for this species, as the epithet "*nigricans*" already was occupied in *Peyronellaea*, referring to a species which is now synonymised with *Pey. pomorum* var. *circinata* (see below).

Peyronellaea calorpreferens (Boerema, Gruyter & Noordel.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515602.
Basionym: *Phoma pomorum* var. *calorpreferens* Boerema, Gruyter & Noordel. apud Boerema, Persoonia 15: 207. 1993.

≡ *Phoma calorpreferens* (Boerema, Gruyter & Noordel.) Aveskamp, Gruyter & Verkley, Mycologia 101: 370. 2009.

= *Phoma heteroderae* Sen Y. Chen, D.W. Dicks. & Kimbr., Mycologia 88: 885.1996.

Conidiomata pycnidial, solitary or confluent, partially or completely immersed in the agar, (sub-)globose or irregular due to the presence

of 1(–4) slightly papillate ostioles, measuring (70–)100–200(–250) µm diam. *Pycnidial wall* pseudoparenchymatous, composed of isodiametric cells, 2–5 layers thick, with many hyphal outgrows, some setae-like. *Conidiogenous cells* phialidic, hyaline, simple, smooth, flask-shaped, *ca*. 3–5.5 × 3–6.5 µm. *Conidia* broadly ellipsoidal to ovoid to cylindrical, thin-walled, smooth, hyaline, (3.5–)4–8.5(–12) × 2–3.5(–4.5) µm, aseptate, with (1–)2–5(–8) polar guttules. Conidial matrix pale pink. *Chlamydospores* highly variable in shape and size, mostly unicellular but also multicellular. Where unicellular, pale brown to brown, guttulate, intercalary, solitary or in chains, globose, 7.5–19(–26) µm, thick-walled and often with a distinct "envelope". Where multicellular dictyosporous alternarioid or botryoid, brown to black, terminal or occasionally intercalary in chains of unicellular chlamydospores, measuring *ca.* (16–)21–55 × (7–)12–30(–33) µm.

Specimens examined: **The Netherlands**, from undefined food material, 1973, G.H. Boerema, **holotype** L 990.290.418, ex-holotype culture CBS 109.92 = PD 73/1405. **U.S.A.**, Florida, Gainesville, from eggs of *Heterodera glycines* from greenhouse soil, CBS 630.97 = ATCC 96683 = IMI 361196 = PD 96/2022; from indoor environment, 1993, CBS 875.97 = PD 93/1503.

Notes: *Peyronellaea calorpreferens* is a taxon that was recently elevated from variety level to species rank, as *Phoma calorpreferens* (Aveskamp *et al.* 2009a). Due to its morphological and genetical similarity with *Ph. heteroderae*, it is concluded that both taxa are actually one and the same species. According to the International code of Botanical Nomenclature (McNeal *et al.* 2006) the epithet *calorpreferens* has priority, as its basionym *Ph. pomorum* var. *calorpreferens* was published earlier.

The type of *Peyronellaea calorpreferens* has been recovered from food materials, but Boerema (1993) hypothesises about the plurivorous nature of this taxon, and mainly records it as a world-wide occurring soil- and seedborne opportunist, whereas Chen *et al.* (1996) record this species (as *Ph. heteroderae*) from eggs of a cyst nematode, *Heterodera glycines*.

Peyronellaea coffeae-arabicae (Aveskamp, Verkley & Gruyter) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515603.
Basionym: *Phoma coffeae-arabicae* Aveskamp, Verkley & Gruyter, Mycologia 101(3): 371. 2009.

Specimens examined: **Ethiopia**, from *Coffea arabica*, 1984, M.M.J. Dorenbosch, **holotype** CBS H-20143, ex-holotype culture CBS 123380 = PD 84/1013; from *Coffea arabica*, 1984, M.M.J. Dorenbosch, CBS 123398 = PD 84/1014.

Peyronellaea curtisii (Berk.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515604.
Basionym: *Hendersonia curtisii* Berk., in Cooke, Nuovo Giorn. Bot. Ital. 10: 19. 1878.
≡ *Stagonosporopsis curtisii* (Berk.) Boerema, in Boerema & Dorenbosch, Verslagen Meded. Plziektenk. Dienst Wageningen 157: 20. 1981.
= *Phyllosticta narcissi* Aderh., Centralbl. Bakteriol., 2 Abth. 6: 632. 1900.
≡ *Phoma narcissi* (Aderh.) Boerema, Gruyter & Noordel., Persoonia 15(2): 215. 1993.

Specimens examined: **The Netherlands**, from *Nerine* sp., May 1992, J. de Gruyter, culture 251.92 = PD 86/1145; from *Sprekelia* sp., PD 92/1460. Unknown origin, from *Ismene* sp., 1971, PD 71/6. Unknown origin, from *Hippeastrum* sp., 1976, PD 76/61.

Peyronellaea eucalyptica (Sacc.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515605.
Basionym: *Phoma eucalyptica* Sacc., Syll. Fung. 3: 78. 1884.

Specimens examined: **Australia**, Western Australia, from a leaf of *Eucalyptus* sp., 1979, CBS 377.91 = PD 79/210. **Croatia**, Adriatic Sea, from seawater, 1973, CBS 508.91 = PD 73/1413. **Indonesia**, Sumatra, Sulavesi, from *Eugenia aromatica,* 1982, CBS 378.91 = PD 82/107.

Peyronellaea gardeniae (S. Chandra & Tandon) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515606.
Basionym: *Pyrenochaeta gardeniae* S. Chandra & Tandon, Mycopathol. Mycol. Appl. 29: 274. 1966.
≡ *Phoma gardeniae* (S. Chandra & Tandon) Boerema, in Boerema & Dorenbosch, Verslagen Meded. Plziektenk. Dienst Wageningen 156: 27. 1980.

Specimens examined: **India**, Allahabad, from the leaf of *Gardenia jasminoides*, 1966, S. Chandra and R.N. Tandon, **isotype** CBS H-7605, ex-isotype culture CBS 626.68 = IMI 108771. **Netherlands Antilles**, Curacao, from air sample, 1978, A. Kikstra, CBS 302.79 = PD 79/1156.

Peyronellaea glomerata (Corda) Goid. ex Togliani, Ann. Sperim. Agrar. III 6: 93. 1952.
Basionym: *Coniothyrium glomeratum* Corda, Icon. Fung. (Prague) 4: 39. 1840.
≡ *Phoma glomerata* (Corda) Wollenw. & Hochapfel, Z. Parasitenk. 3(5): 592. 1936.

Specimens examined: **Germany**, Berlin-Zehlendorf, Domäne Düppel, from a tuber of *Solanum tuberosum*, 1936, H.W. Wollenweber, CBS 293.36 = MUCL 9882; Monheim, from *Hordeum sativum*, 1984, M. Hossfeld, CBS 834.84; from indoor environment, 2003, C. Rudolph, CBS 112448. **Romania**, Bukarest, from a church wall-fresco, Nov. 1971, I. Ionita, CBS 133.96 = PD 79/127. **Russia**, Novosibirsk, Hortus Botanicus, from a leaf of *Populus nigra*, 1963, T.T. Kuznetsova, CBS 284.76 = ATCC 26238 = IMI 176748 = VKM F-1842; Novosibirsk, Hortus Botanicus, from a leaf of *Rubus idaeus*, 1963, T.T. Kuznetsova, CBS 287.76 = ATCC 26240 = IMI 176746 = VKM F-1847; Novosibirsk, Hortus Botanicus, from a leaf of *Populus alba*, 1963, T.T. Kuznetsova, CBS 288.76 = ATCC 26243 = VKM F-1845; Novosibirsk, Hortus Botanicus, from a leaf of *Allium nutans*, 1963, T.T. Kuznetsova, CBS 289. 76 = ATCC 26239 = IMI 176745 = VKM F-1846; Novosibirsk, Hortus Botanicus, from a leaf of *Ribes nigrum*, 1963, T.T. Kuznetsova, CBS 290.76 = ATCC 26244 = IMI 176747 = VKM F-1848; from *Heracleum* sp., 1973, PD 73/1415. **The Netherlands**, from a root of *Lycopersicon esculentum*, 1949, D. Verleur, CBS 304.49 = MUCL 9884; from *Chrysanthemum* sp., 1963, CBS 528.66 = PD 63/590; from indoor bathroom environment, 1997, M. Komen, CBS 464.97; from *Medicago sativa*, PD 77/47. **U.K.**, from air, PD 74/1023. **U.S.A.**, Virginia, from *Juniperus* sp., Jan. 2002, A.Y, Rossman, CBS 120109. Unknown origin, from *Cucumis sativus*, PD 81/767; from *Capsicum* sp., PD 83/782.

Peyronellaea lethalis (Ellis & Bartholomew) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515607.
Basionym: *Ascochyta lethalis* Ellis & Bartholomew, Fungi Columb. 1808. 1903.
= *Mycosphaerella lethalis* R. Stone, Ann. Mycol. 10: 587. 1912.
≡ *Didymella lethalis* (R. Stone) Sivan., Bitunicate Ascomycetes and their Anamorphs: 424. 1984.

Specimen examined: Unknown origin and substrate, 1925, A.W. Archer, CBS 103.25.

Peyronellaea musae P. Joly, *Revue Mycol*. **26**: 97. 1961.
≡ *Phoma jolyana* Piroz. & Morgan-Jones, Trans. Brit. Mycol. Soc. 51: 200. 1968.

Specimens examined: **India**, from fruit of *Mangifera indica*, May 1969, CBS 463.69; from *Malus sylvestris*, PD 83/326.

Notes: *Phoma jolyana* was originally described in the genus *Peyronellaea*, as *Pey. musae*. The epithet "*jolyana*" was later proposed for this species, as the epithet *musae* was already occupied in *Phoma* (Pirozynski & Morgan-Jones 1968). Here, we reinstate this fungus under its original name.

Peyronellaea obtusa (Fuckel) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515608.
Basionym: *Phoma obtusa* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 378. 1870.

Specimens examined: **The Netherlands**, from a root of *Daucus carota*, July 1993, J. de Gruyter, CBS 377.93 = PD 80/976; from *Spinacia oleracea*, July 1993, J. de Gruyter, CBS 391.93 = PD 80/87.

Peyronellaea pinodella (L.K. Jones) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515609.
Basionym: *Ascochyta pinodella* L.K. Jones, Bull. New York State Agric. Exp. Sta. 547: 10. 1927.
≡ *Phoma medicaginis* var. *pinodella* (L. K. Jones) Boerema apud Boerema, Dorenbosch & Leffring, Netherlands J. Pl. Pathol. 71**:** 88. 1965.
≡ *Phoma pinodella* **(**L.K. Jones) Morgan-Jones & K.B. Burch, Mycotaxon 29: 485. 1987.

Specimens examined: **Hungary**, from *Glycine max,* 1996, G. Kövics, CBS 567.97 = PD 97/2160; from seed of *Glycine max*, 1997, G. Kövics, CBS 100580 = PD 98/1135. **The Netherlands**, from *Pisum sativum*, 1981, CBS 318.90 = PD 81/729. **U.S.A.**, Minnesota, from *Trifolium pretense*, 1966, CBS 531.66.

Notes: *Phoma sojicola*, which was erected in 1999 (Kövics *et al.* 1999), has recently been synonymised with the present species, based on morphological and genetical similarities (Irinyi *et al.* 2009). The present study supports these findings.

Peyronellaea pinodes (Berk. & A. Bloxam) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515610.
Basionym: *Sphaeria pinodes* Berk. & A. Bloxam, Ann. Mag. Nat. Hist., Ser. III 7: 454. 1861.
≡ *Didymella pinodes* (Berk. & A. Bloxam) Petr., Ann. Mycol. 22(1/2): 16. 1924.
≡ *Mycosphaerella pinodes* (Berk. & A. Bloxam) Vestergr., Ann. Mycol. 10(5): 581. 1912.
= *Ascochyta pinodes* L.K. Jones, Bull. New York State Agric. Exp. Sta. 547: 4. 1927.

Specimens examined: **Belgium**, Gembloux, from *Pisum sativum*, 1977, G. Sommereyns, CBS 525.77. **Iraq**, Basrah province, from *Pisum sativum*, 1977, CBS 159.78. **Switzerland**, Glarus Kanton, Filzbach, from a leaf of *Primula auricula*, June 1949, E. Müller, CBS 285.49. **The Netherlands**, from an unknown substrate, 1955, M.H. van Raalte, CBS 235.55.

Peyronellaea pomorum var. ***circinata*** (Kusnezowa) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515612.
Basionym: *Peyronellaea circinata* Kusnezowa, Novoste Sist. Nizsh. Rast. 8: 189. 1971.
≡ *Phoma jolyana* var. *circinata* (Kusnezowa) Boerema, Dorenb. & Kesteren, Kew Bull. 31: 535. 1977 [1976].
≡ *Phoma pomorum* var. *circinata* (Kusnezowa) Aveskamp, Gruyter & Verkley, Mycologia 101(3): 377. 2009.
= *Peyronellaea nigricans* Kusnezowa, Novoste Sist. Nizsh. Rast. 8: 191. 1971.

Specimens examined: **Russia**, Siberia, Novosibirsk, from *Heracleum dissectum*, 1963, T.T. Kusnezowa, **isotype** CBS H-3747, ex-isotype culture CBS 285.76 = ATCC 26241 = IMI 176742 = VKM F-1843; Siberia, Novosibirsk, from a leaf of *Allium nutans*, 1963, T.T. Kusnezowa, CBS 286.76 = ATCC 26242 = IMI 176743 = VKM F-1844.

Peyronellaea pomorum var. ***cyanea*** (Jooste & Papendorf) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515614.
Basionym: *Phoma cyanea* Jooste & Papendorf, Mycotaxon 12: 444. 1981.
≡ *Phoma pomorum* var. *cyanea* (Jooste & Papendorf) Aveskamp, Gruyter & Verkley, Mycologia 101(3): 377. 2009.

Specimen examined: **South Africa**, Heilbron, from straw of *Triticum* sp., 1972, W.J. Jooste, **holotype** PREM 45736, ex-holotype culture CBS 388.80.

Peyronellaea pomorum var. ***pomorum*** (Thüm.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515611.
Basionym: *Phoma pomorum* var. *pomorum* Thüm., Fungi Pomicoli: 105. 1879.

Specimen examined: **The Netherlands**, Wageningen, from *Polygonum tataricum*, 1964, M.M.J. Dorenbosch, CBS H-16540, culture CBS 539.66 = ATCC 16791 = IMI 122266 = PD 64/914.

Peyronellaea protuberans (Lév.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515613.
Basionym: *Phoma protuberans* Lév., Ann. Sci. Nat. Bot. III 5: 281. 1846.

Specimen examined: **The Netherlands**, from a leaf of *Lycium halifolium*, 1971, CBS 381.96 = PD 71/706.

Peyronellaea sancta **(**Aveskamp, Gruyter & Verkley) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515615.
Basionym: *Phoma sancta* Aveskamp, Gruyter & Verkley, Mycologia 101(3): 377. 2009.

Specimens examined: **Argentina**, from *Opuntia ficus-indica*, 1997, CBS 644.97. **South Africa**, from dead branches of *Ailanthus altissima*, Oct. 1982, C. Jansen CBS H-16332, ex-holotype culture CBS 281.83. Unknown origin, from *Gleditsia triancantha* culture LEV 15292.

Peyronellaea subglomerata (Boerema, Gruyter & Noordel.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515616.
Basionym: *Phoma subglomerata* Boerema, Gruyter & Noordel., Persoonia 15(2): 204. 1993.

Specimens examined: **U.S.A.**, North Dakota, from *Triticum* sp., 1976, CBS 110.92 = PD 76/1010. Unknown origin, from *Zea mays*, 1978, PD 78/1090.

Peyronellaea zeae-maydis (Mukunya & Boothr.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515617.
Basionym: *Mycosphaerella zeae-maydis* Mukunya & Boothr., Phytopathology 63: 530. 1973.
≡ *Didymella zeae-maydis* (Mukunya & Boothr.) Arx, Beih. Nova Hedwigia 87: 288. 1987.
Anamorph: *Phyllosticta maydis* Arny & R.R. Nelson, Phytopathology 61: 1171. 1971.
≡ *Phoma zeae-maydis* Punith., Mycopathologia 112(1): 50. 1990.

Specimen examined: **U.S.A.**, Wisconsin, Hancock, from *Zea mays*, June 1969, D.C. Arny, ex-holotype culture CBS 588.69.

Group L:
Phoma draconis, *Ph. henningsii*, *Ph. plurivora* and the novel species *Ph. brasiliensis* cluster basally to the *Epicoccum* species in group M. The species clustered here, however, all lack chlamydospores. These species do, like the chlamydospore-forming species mentioned above, solely produce unicellular conidia, and have glabrous, thin-walled, pseudoparenchymatous pycnidial walls composed of isodiametric cells.

Phoma brasiliensis Aveskamp, Gruyter & Verkley, **sp. nov.** MycoBank MB515618. Fig. 6.

Conidia cylindrica, glabra, hyalina, continua, 6–9(–10) × 2–3(–3.5) µm, (3–)4–6(–8) guttulis parvis praedita. Matrix conidiorum alba.

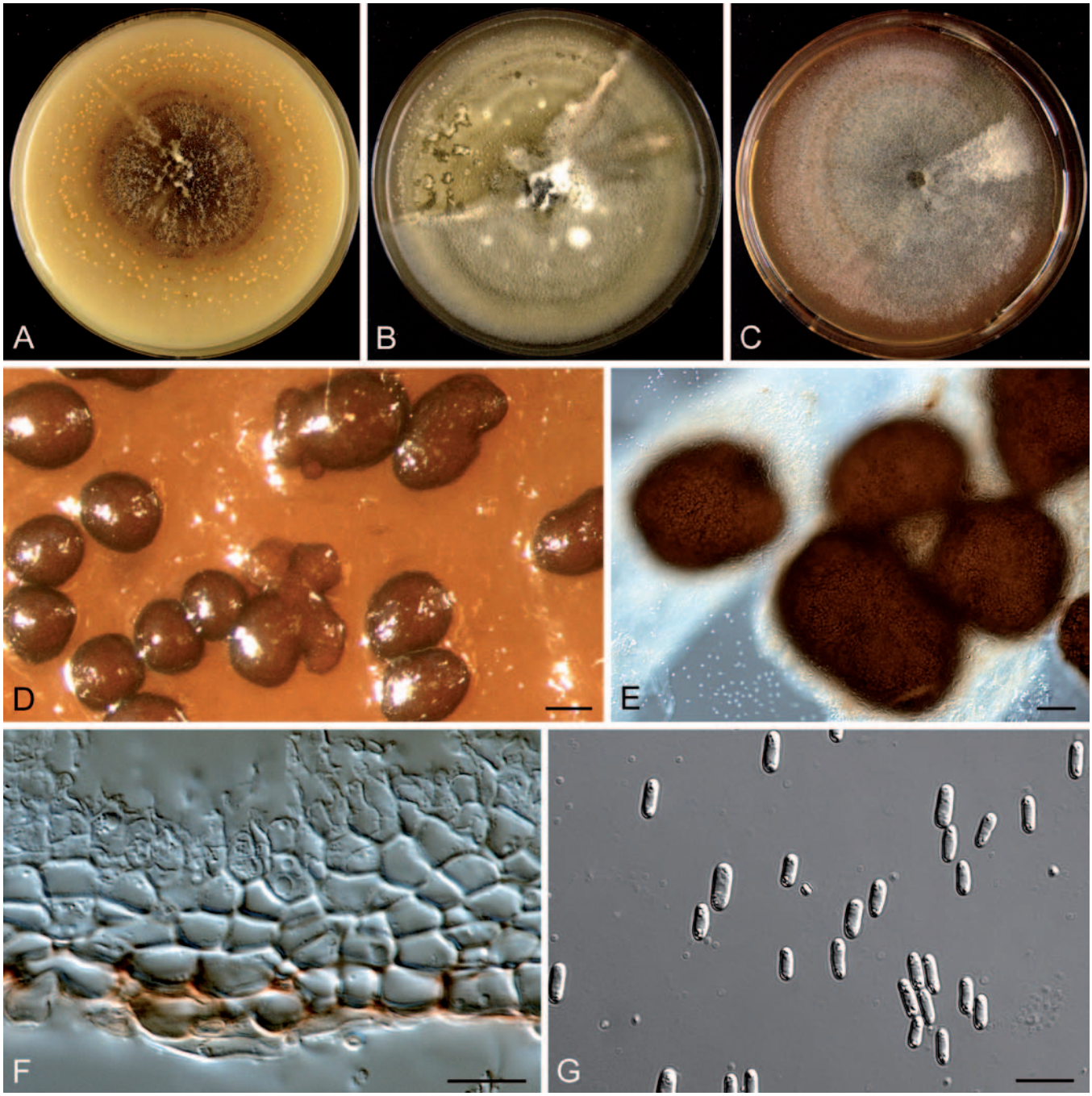


Fig. 6. *Phoma brasiliensis* (CBS 120105a). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D–E. Pycnidia. F. Section of the pycnidial wall. G. Conidia. Scale bars: D = 200 µm; E = 100 µm; F–G = 10 µm.

Etymology: Epithet refers to the country of origin, Brazil.

Conidiomata pycnidial, mainly solitary but also confluent, globose to irregularly shaped, glabrous, on the agar surface and immersed, (220–)250–370(–550) × (150–)190–290(–320) µm. Usually with a single inconspicuous non-papillate ostiole. *Pycnidial wall* pseudoparenchymatous, composed of 5–9 layers of oblong to isodiametric cells, 18–27 µm thick. *Conidiogenous cells* phialidic, hyaline, simple, smooth, globose to flask-shaped, *ca*. 4–5 × 3.5–4 µm. *Conidia* variable in size, cylindrical, thin-walled, smooth, hyaline, aseptate 6–9(–10) × 2–3(–3.5) µm, with (3–)4–6(–8) small polar guttules. Conidial matrix white.

Culture characteristics: Colonies on OA 50–53 mm diam after 7 d, margin regular. Aerial mycelium sparse, tufted near the centre of the colony, white. Immersed mycelium hyaline. Abundant pycnidia produced semi-immersed in concentric rings. Pycnidia in the outer rings pale luteous, darkening towards the centre of the colony via buff, honey, hazel to brown-vinaceous; reverse concolourous. Colonies on MEA 59–63 mm diam after 7 d, margin regular. Immersed mycelium completely covered by a mycelial mat, which is densely floccose, greenish olivaceous to greenish grey, with elements of citrine, olivaceous black and white; reverse concolourous. Hyphae locally containing red amorphous chrystaline material. Colonies on CHA 62–67 mm diam after 7 d, margin regular. Aerial mycelium floccose, white. Abundant dark pycnidia are formed on the agar surface. Application of NaOH results in a luteous discolouration of the agar, later changing to reddish, best to be observed on OA medium.

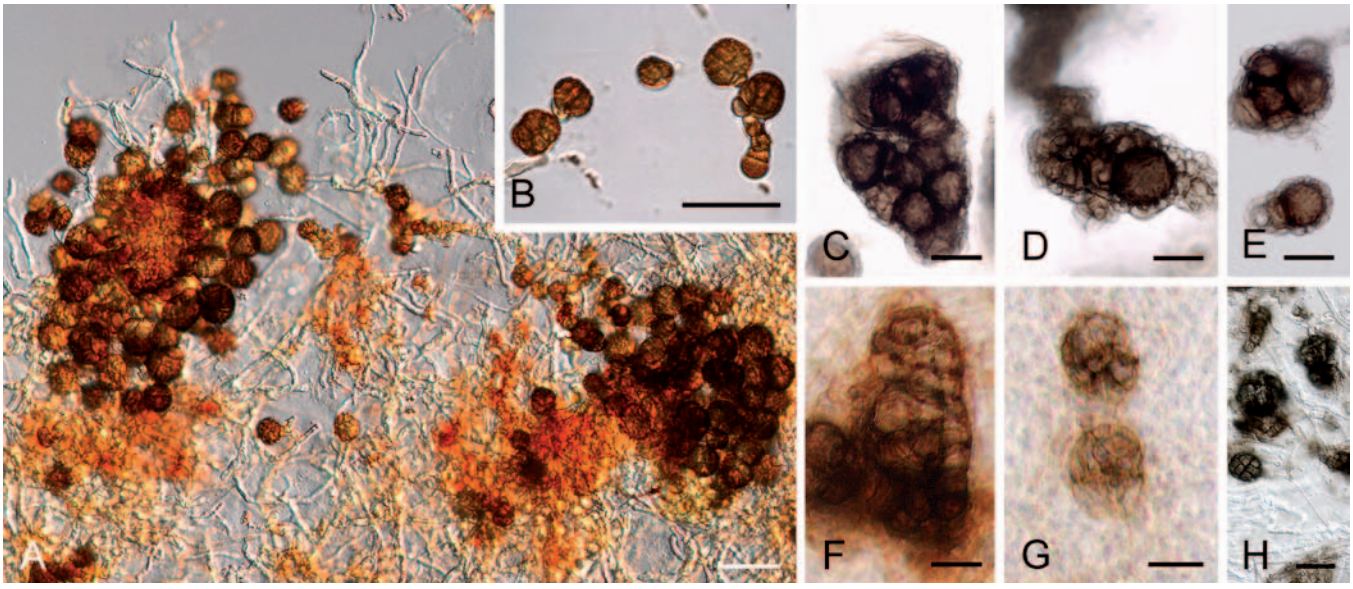


Fig. 7. Globose chlamydospores of *Epicoccum* spp. A–B. *E. nigrum* (CBS 173.73). C–E. *E. sorghi* (CBS 246.60). F–H. *E. pimprinum* (CBS 179.80). Scale bars: A–B = 50 µm; C–H = 20 µm.

Specimen examined: **Brazil**, from *Amaranthus* sp., Nov. 2007, E. Rosskopf, **holotype designated here** CBS H-20235, ex-holotype culture CBS 120105.

Notes: This species is thus far only known from a single isolate from a wild *Amaranthus* sp. in Brazil. According to Boerema *et al.* (2004), no other *Phoma* species have been recorded from the same host.

Phoma draconis (Berk. ex Cooke) Boerema, Verslagen Meded. Plziektenk. Dienst Wageningen 159 (Jaarboek 1982): 24. 1983.
Basionym: *Phyllosticta draconis* Berk. ex Cooke, Grevillea 19: 8. 1891.

Specimen examined: **Rwanda**, from a leaf of *Dracaena* sp., Jan. 1982, G.H. Boerema, CBS H-16207, culture CBS 186.83 = PD 82/47.

Phoma henningsii Sacc., Syll. Fung. 10: 139. 1892.

Specimen examined: **Kenya**, Maguga, from the bark of *Acacia mearnsii*, June 1992, T.W. Olembo, CBS H-16354, culture CBS 104.80 = PD 74/1017.

Phoma plurivora P.R. Johnst., New Zealand J. Bot. 19(2): 181. 1981.

Specimens examined: **Australia**, from *Medicago sativa*, 1975, CBS 248.93 = PD 95/907. **New Zealand**, Auckland, Mt Albert, from a leaf of *Setaria sp.*, Feb. 1979, P.R. Johnston, CBS H-7624, ex-isotype culture CBS 558.81 = PDDCC 6873.

Group M – Epicoccum:
This group (BPP = 1.00, RBS = 66 %) comprises three species that are accommodated in the section *Peyronellaea*. The *Peyronellaea* species in this group, *Ph. sorghina*, *Ph. pimprina* and *Epicoccum nigrum* (chlamydospore-based synanamorph of *Ph. epicoccina*; Arenal *et al.* 2000, 2004) are characterised by the production of botryoid or epicoccoid chlamydospores, in contrast to the species in group K, which produce alternarioid dictyochlamydospores. The distinct morphology and phylogenetic position justify the recombination into a separate genus. As the oldest generic name in this clade is *Epicoccum*, new combinations for *Ph. pimprina* and *Ph. sorghina* are proposed below.

Epicoccum Link, Mag. Gesell. Naturf. Freunde Berlin 7: 32. 1815, **emend.** Aveskamp, Gruyter & Verkley. Fig. 7.

Conidiomata pycnidial, globose to subglobose, measuring 50–250 µm diam, on agar surface or immersed, mostly solitary but incidentally confluent. *Ostioles* papillate or on pronounced necks. *Pycnidial wall* pseudoparenchymatous, counting 2–8 cell layers of which the outer 1–3 are brown-olivaceous pigmented. *Conidiogenous cells* phialidic, hyaline, simple, smooth, ampulliform, *ca.* 3–7 × 3–7 µm. *Conidia* variable in shape, initially hyaline but in later stages a slight brownish pigmentation may be found, thin-walled, smooth, always aseptate 3–8.5(–10) × 1.5–4(–4.5) µm. *Chlamydospores* unicellular or multicellular, intercalary or terminal, smooth, verrucose or incidentally tuberculate, subhyaline to dark brown, where unicellular globose, measuring 5–15 µm diam, where multicellular globose or irregular shaped, smooth, verrucose or incidentally tuberculate, measuring 8–35 µm.

Type species: *Epicoccum nigrum* Link.

Epicoccum nigrum Link, Mag. Gesell. Naturf. Freunde Berlin 7: 32. 1815.
≡ *Phoma epicoccina* Punith., M.C. Tulloch & C.M. Leach, Trans. Brit. Mycol. Soc. 59(2): 341 (1972).

Specimens examined: **Germany**, Berlin, from soil, 1985, H.J. Halfmann, CBS 505.85. **The Netherlands**, Geleen, from human toe nail, Dec. 1981, CBS 125.82 = IMI 331914 = CECT 20044; Randwijk, from *Malus* sp., J. Köhl, 2003, CBS 115825. **U.S.A.**, Oregon, from seeds of *Dactylis glomerata*, 1967, CBS 173.73 = ATCC 24428 = IMI 164070.

Epicoccum pimprinum (P.N. Mathur, S.K. Menon & Thirum.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515619.
Basionym: *Phoma pimprina* P.N. Mathur, S.K. Menon & Thirum., Sydowia 13: 146. 1959.

Specimens examined: **India**, Poona, Pimpri, from soil, Mar. 1959, S.K. Menon, ex-isotype culture CBS 246.60 = ATCC 22237 = ATCC 16652 = IMI 81601; from soil, 1977, PD 77/1028.

Epicoccum sorghi (Sacc.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515620.

Basionym: *Phyllosticta sorghina* Sacc., *Michelia* **1** (2): 140. 1878.

≡ *Phoma sorghina* (Sacc.) Boerema, Dorenb. & Kesteren, Persoonia 7(2): 139. 1972.

For a complete synonymy see Boerema *et al.* (1977).

Specimens examined: **France**, Antibes, from a twig of *Citrus* sp., 1966, CBS 627.68 = PD 66/926. **Guinea-Bissau**, Gacheu Région, from *Oryza sativa*, Oct. 1978, CBS 181.81. **India**, from a fruit of *Coffea* sp., July 1968, C.V. Subramanian, CBS 846.68; Jabalpur, from *Panicum miliare*, Jan. 1972, D. Sharma, CBS 293.72. **Martinique**, from a leaf of *Lycopersicon esculentum*, June 1989, B. Hostachy, CBS 301.89. **Papua New Guinea**, from *Stellaria* sp., A. Aptroot, Oct. 1995, CBS 886.95; Central Province, Varirata National Park near Port Moresby, from soil, A. Aptroot, Oct. 1995, CBS 986.95. **Puerto Rico**, Mayaguez, from *Sorghum vulgare*, Apr. 1976, R. Alconera, CBS 179.80= PD 76/1018. **South Africa**, Potchefstroom, from a leaf of *Zea mays*, Nov. 1978, W.J. Jooste, CBS 180.80 = PD 78/1100.

Notes: The strains that were previously accommodated in *Ph. sorghina* are morphologically and phylogenetically highly diverse (Aveskamp *et al.* 2009a, Pažoutová 2009), and probably represent multiple species. These species were, however, not treated in the present study.

Group N – Boeremia gen. nov.:

This group represents species that are morphologically similar to what is currently known as *Ph. exigua*. Group N is a well-defined clade (BPP = 1.00, RBS = 100 %) and comprises all taxa that were previously recognised as separate *Ph. exigua* varieties by Abeln *et al.* (2002). *Phoma foveata* and *Ph. sambuci-nigrae* are embedded here as well, two species that previously were known as varieties of *Ph. exigua*, but were elevated to species rank due to their phytopathological relevance (*Ph. foveata*, Boerema *et al.* 1987) or distinct physiological characters (*Ph. sambuci-nigrae*, Monte *et al.* 1991). As already noted by Aveskamp *et al.* (2009b) also *Ph. telephii*, *Ph. strasseri* and *Ph. lycopersici* are closely related. This study also reveals the close relationship with *Ph. tarda*, a pathogen of coffee. *Phoma hedericola*, a frequently occurring causal agent of leaf spots on poison ivy (*Hedera helix*) and *Ph. crinicola*, a pathogen of *Amaryllidaceae* are embedded in this clade. In contrast to the other species in this clade, which are linked to *Phoma* section *Phyllostictoides*, *Ph. hedericola* and *Ph. crinicola* are associated with *Phoma* section *Phoma*, due to the absence of septate conidia (De Gruyter & Noordeloos 1992, De Gruyter *et al.* 1993). The sequence data of CBS 172.34, a strain recorded as *Dothiorella ulmi*, appeared to be genetically identical to *Ph. exigua*, as was already noted by De Gruyter *et al.* (2009). Based on morphological studies of other strains, *Dothiorella ulmi* was suggested to be recombined into *Plectophomella* (Redfern & Sutton 1981), a genus that is linked to the Pezizomycotina. Morphological features of the present strain appeared to be similar to *Ph. exigua*, suggesting that this strain was probably preserved under an incorrect name, and actually belongs to *Ph. exigua* var. *populi*.

Of the species within this clade, a teleomorph is only named in *Ph. lycopersici* (*Didymella lycopersici*), although Stewart (1957) has reported the existence of pseudothecia of *Ph. tarda* in nature, a finding that also has been reported by Salgado *et al.* (2007). This contradicts with the fact that none of the varieties embedded in the *Ph. exigua* has been found in association with a teleomorph thus far.

For further delineation of this clade, a comparison of actin gene sequences is proposed (Aveskamp *et al*. 2009b), although not all species and varieties in this complex can be recognised using this gene only. Thus far the varieties of *Ph. exigua* could only be delineated using two fingerprint techniques: Amplified Fragment Length Polymorphism (AFLP, Abeln *et al.* 2002) and DAF (DNA Amplification Fingerprinting) using mini-hairpin primers (Aveskamp *et al.* 2009b). Based on this latter technique Aveskamp *et al.* (2009b) recognised two varieties within *Ph. exigua* that had not been described before. These two infraspecific taxa, var. *gilvescens* and var. *pseudolilacis* are treated and described below.

Based on the phylogenetic reconstruction obtained here, the taxa previously known as *Ph. exigua* var. *noackiana* and *Ph. exigua* var. *diversispora* cluster in a distinct clade from the other varieties in this complex, and are elevated to species level here. Also actin sequence data and DAF analysis (Aveskamp *et al*. 2009b), AFLP data (Abeln *et al.* 2002) reveal a basal topology of these species compared to *Ph. exigua*. Morphological data obtained by Van der Aa (2000) also suggest that these species are not completely fitting in the *Ph. exigua* concept.

The species and varieties in this clade differ from other *Phoma* taxa based on their ostiole morphology. In contrast to other species, which have a smoothly lined ostiole, the taxa present in this clade have distinct hyaline cells lining their ostiolar openings (Fig. 8A). In addition, these species, with the exception of *Ph. hedericola*, produce septate conidia in addition to the regular aseptate ones, although in general the septate conidia are produced in smaller numbers in culture than on the host. These conidia are mostly 1-septate, as only in *Ph. exigua* incidentally multiseptate conidia occur, and are often only slightly larger than the regular aseptate ones (Fig. 8C). Due to the morphological and genetic distinctiveness, we propose a new generic name for the taxa in this clade.

Boeremia Aveskamp, Gruyter & Verkley, **gen. nov.** MycoBank MB515621. Fig. 8.

Conidiomata pycnidialia, plerumque globosa vel subglobosa, glabra vel eminentiis sparsis hypharum vestita, superficialia vel in agaro immersa, solitaria vel confluentia, 75–370 µm diam. Ostiola papillata vel epapillata, tempore maturitatis interne cellulis hyalinis papillatis. Paries pycnidii pseudoparenchymatus, e 2–8 stratis cellularum compositus, extima 1–3 strata brunnea. Cellulae conidiogenae phialidicae, hyalinae, glabrae, ampulliformes vel dolliiformes, *ca.* 3–7.5 × 3–6.5 µm. Conidia hyalina, tenuitunicata, glabra, plerumque continua, 2.5–12 × 2–4 µm, et interdum uni- vel biseptata, usque 15 × 5 µm.

Conidiomata pycnidial conidiomata variable in shape and size, mostly globose to subglobose, glabrous or with few mycelial outgrowths, on agar surface or immersed, solitary or confluent, measuring 75–370 µm diam. *Ostioles* 1–2(–3), non-pappillate or pappillate, lined internally with a pappillate hyaline cells when mature. *Pycnidial wall* pseudoparenchymatous, counting 2–8 cell layers of which the outer 1–3 are brown pigmented. *Conidiogenous cells* phialidic, hyaline, simple, smooth, ampulliform to doliiform, *ca*. 3–7.5 × 3–6.5 µm. *Conidia* variable in shape, hyaline, thin-walled, smooth, mainly aseptate, 2.5–12 × 2–4 µm, but regularly 1(–2)-septate conidia may be found which measure up to 15 × 5 µm. *Pseudothecia*, only rarely recorded in one species *in vivo*, subglobose, up to 300 µm diam. *Asci* cylindrical or subclavate, measuring 50–95 × 6–10 µm, always 8-spored, biseriate. *Ascospores* ellipsoid, measuring 12–18 × 5–6 µm, uniseptate.

Type species: *Boeremia exigua* (Desm.) Aveskamp, Gruyter & Verkley

Etymology: Named after Gerhard H. Boerema, who made great contributions to our understanding of the taxonomy of phomoid fungi.

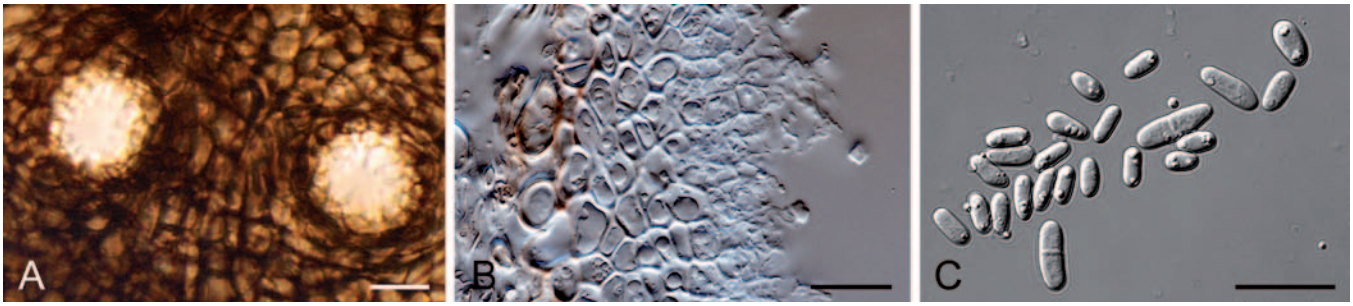


Fig. 8. *Boeremia* gen. nov. A. Ostiole configuration of *B. exigua* var. *exigua* (CBS 431.74). B. Pycnidial wall and conidiogenous cells of *B. telephii* (CBS 760.73) C. Aseptate and septate conidia of *B. lycopersici* (CBS 378.67). Scale bars: A = 20 µm; B–C = 10 µm.

Boeremia crinicola (Siemasko) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515622.
Basionym: *Phyllosticta crinicola* Siemasko, Acta Soc. Bot. Poloniae 1: 22. 1923.
≡ *Phoma crinicola* (Siemasko) Boerema apud Boerema & Dorenbosch, Verslagen Meded. Plziektenk. Dienst Wageningen 153: 18.1979.

Specimens examined: **The Netherlands**, Haarlem, from a bulb of *Crinum powellii*, Mar. 1976, G.H. Boerema, CBS H-16198, CBS 109.79 = PD 77/747; Alkmaar, from a bulb of *Crinum* sp., 1970, G.H. Boerema, CBS 118.93 = PD 70/195.

Boeremia diversispora (Bubák) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515623.
Basionym: *Phoma diversispora* Bubák, Oest. Bot. Z. 55: 78. 1905
≡ *Phoma exigua* var. *diversispora* (Bubák) Boerema apud Boerema & van Kesteren, Gewasbescherming 11: 122. 1980

For a complete description see Boerema *et al.* (1981a, 2004), and Van der Aa *et al.* (2000).

Specimens examined: **Brazil**, leaf of *Phaseolus*, F. Noack, **holotype** B. **Kenya**, from a pod of *Phaseolus vulgaris*, 1979, G.H. Boerema, **epitype designated here** CBS H-16308, ex-epitype culture CBS 102.80 = CECT 20049 = IMI 331907 = PD 79/61. **The Netherlands**, near Tilburg, from *Phaseolus vulgaris*, 1979, J. de Gruyter, CBS 101194 = PD 79/687 = IMI 373349.

Notes: *Phoma diversispora* was originally described by Bubák as a pathogen of cowpea (*Vigna unguiculata*) causing Black Node Disease (Van der Aa *et al.* 2000), but was later classified as a variety of *Ph. exigua* by Boerema & Van Kesteren (1980) and Boerema *et al.* (1981a), on basis of its morphology. The present study, however, revealed the *B. exigua* varieties to be phylogenetically distinct from the present species, which justifies re-establishment of the taxon as separate species in the genus *Boeremia*. The present species is closely related to *B. noackiana*, formerly known as *Ph. exigua* var. *noackiana* (see below).

Boeremia exigua var. ***coffeae*** (Henn.) Aveskamp, Gruyter & Verkley, **stat. et comb. nov.** MB515632.
Basionym: *Ascochyta coffeae* Henn., Hedwigia 41: 307. 1902; not *Phoma coffeae* Delacr., Bull. Soc. Mycol. France 13: 122. 1897.
= *Ascochyta tarda* R.B. Stewart, Mycologia 49: 430. 1957.
≡ *Phoma tarda* (R.B. Stewart) H. Verm., Coffee Berry Dis. Kenya: 14. 1979.
For a complete description see De Gruyter *et al.* (2002).

Specimens examined: **Brazil**, Patrocínio, from leaf of *Coffea arabica*, L.H. Pfenning, CBS 119730. **Cameroon**, Bemenda, from *Coffea arabica*, CBS 109183 = PD 2000/10506 = IMI 300060.

Notes: *Boeremia exigua* var. *coffeae* was originally described from leaves of coffee plants (*Coffea arabica*, Stewart 1957) as *Ascochyta coffeae* and *A. tarda*. The observed late euseptation in this species proved to be a character common for *Phoma* species accommodated in section *Phyllostictoides*, leading to a recombination into *Phoma*, as *Ph. tarda*. Phylogenetic results obtained in the present study reveal genetic similarity between the present species and the *B. exigua* species complex. The cultures of *B. exigua* varieties are somewhat slower growing than those of the present species, which completely covers the agar surface (90 mm diam) within 7 d. The pycnidia of *B. exigua* var. *tarda* may grown to up to 255 µm (De Gruyter *et al.* 2002), but other micromorphological characters fit within the scope of *B. exigua* as described for Ph. exigua by Van der Aa *et al.* (2000) and De Gruyter *et al.* (2002). It is concluded, therefore, that *Ph. tarda* should be reduced to a variety of the *B. exigua*. Multiple *Phoma* species have been found in association with *Coffea arabica*, such as *Ph. coffeae-arabicae*, *Ph. coffeicola*, *Ph. coffeiphila*, *Ph. costarricensis*, *Ph. excelsa*, and *Ph. pereupyrena* (Saccas 1981, Aveskamp *et al.* 2009a). None of these species however matches the description that is applied to taxa in the *B. exigua* complex.

Boeremia exigua var. ***exigua*** (Desm.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515624.
Basionym: *Phoma exigua* Desm., Ann. Sci. Nat. Bot. III 11: 282. 1849.

Specimens examined: **Germany**, Artern, from *Foeniculum vulgare*, Apr. 1984, S. Petzoldt, CBS 391.84. **The Netherlands**, from a tuber of *Solanum tuberosum*, 1928, CBS 236.28; Emmeloord, from a tuber of *Solanum tuberosum*, 1974, G.H. Boerema, CBS 431.74 = PD 74/2447; Emmeloord, from *Cichorium intybus*, 1979, G.H. Boerema, CBS 101150 = PD 79/118; Ommen, from *Digitalis* sp., 1990, J. de Gruyter, CBS 101152 = PD 90/835-3.

Boeremia exigua var. ***forsythiae*** (Sacc.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515625.
Basionym: *Phyllosticta forsythiae* Sacc., Michelia 1(1): 93. 1997.
≡ *Phoma exigua* var. *forsythiae* (Sacc.) Aa, Boerema & Gruyter, Persoonia 17: 452. 2000.

Specimens examined: **The Netherlands**, from *Forsythia* sp., 1992, J. de Gruyter, CBS 101213 = PD 92/959; from *Forsythia* sp., 1995, J. de Gruyter, CBS 101197= PD 95/721.

Boeremia exigua var. ***gilvescens*** Aveskamp, Gruyter & Verkley, **var. nov.** MycoBank MB515626. Fig. 9.

Varietas Phomae exiguae similis, sed matrix conidiorum flavida vel luteola. In agaro et in mycelio aereo catenis cellularum inflatarum (11.5–)12.5–27.5(–31) × (5.5–)7.5–14.5(–18) µm.

Etymology: Varietal name refers to the yellow conidial matrix, which distinguishes this variety.

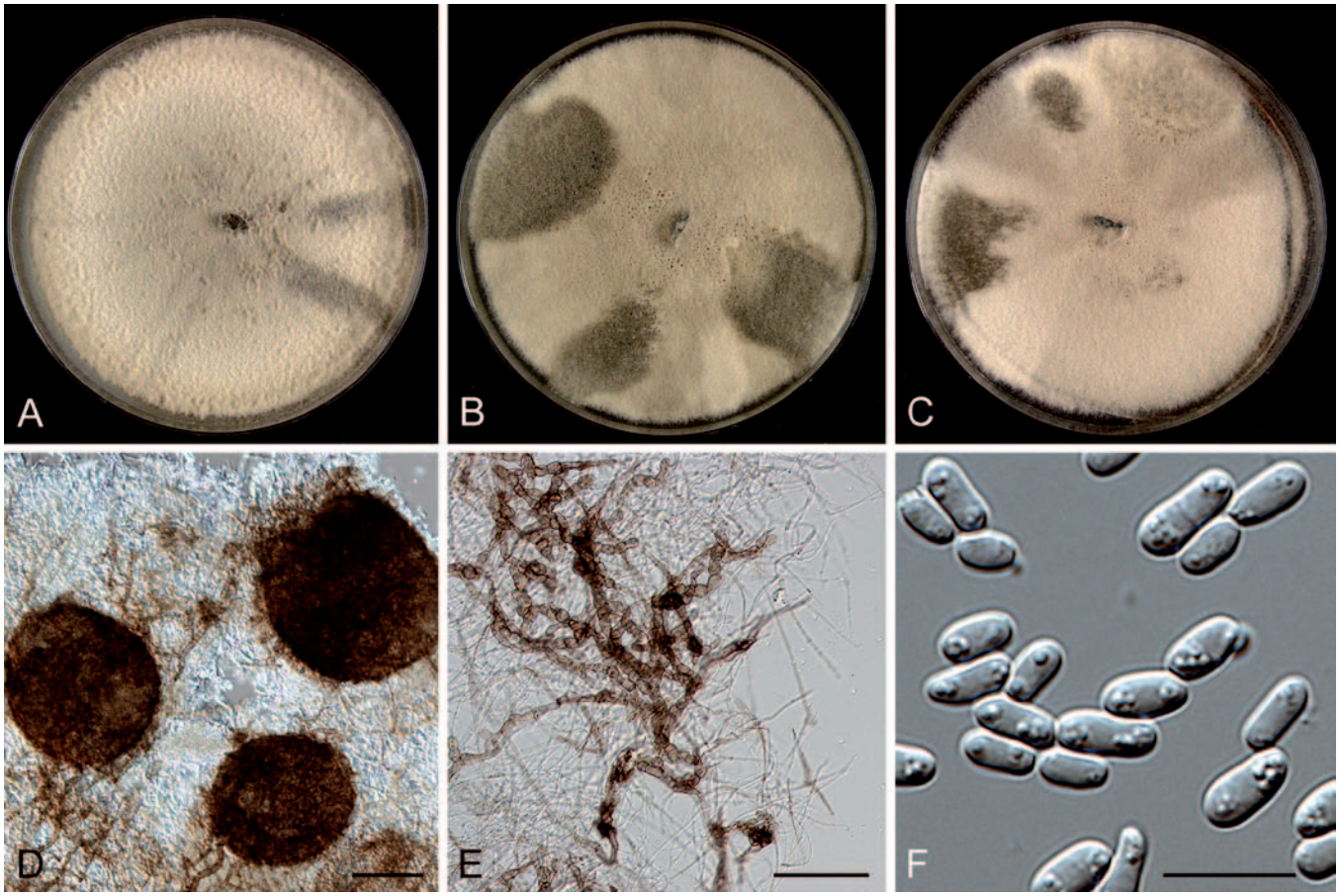


Fig. 9. *Boeremia exigua* var. *gilvescens* (CBS 101150). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D. Pycnidia. E. Chains of wollen cells. F. Conidia. Scale bars: D = 100 µm; E = 100 µm; F = 10 µm.

Culture characteristics: Colonies on OA 75–80 mm diam after 7 d, margin regular or irregular. Immersed mycelium sparsely visible due to coverage by the aerial mycelium, hyaline or black to greenish olivaceous, with many pycnidia; reverse mouse-grey to olivaceous. Colonies on MEA 70–75 mm diam after 7 d, margin regular or irregular. Immersed mycelium completely covered by a compact aerial mat, which is smoke-grey with some mouse-grey zones; reverse black. Colonies on CHA at least (75–)80 mm diam after 7 d, but often the agar surface is completely covered, margin regular or somewhat crenate. Immersed mycelium completely covered by a compact smoke-grey mat of aerial mycelium, or, in some zones floccose, olivaceous with white tufts; reverse shows a dendritic leaden-black zone around the colony centre, with black zones near the colony border. Application of NaOH did not have any effect.

Pycnidial and conidial shapes and sizes fit within the *Ph. exigua* species concept. Conidial matrix yellowish or pale luteous. Brown pigmented swollen cells occur in chains in the agar and in the aerial mycelium, measuring (11.5–)12.5–27.5(–31) × (5.5–)7.5–14.5(–18) µm.

Specimens examined: **Philippines**, from *Solanum tuberosum*,1990, L.J. Turkensteen, CBS 101156 = PD 90/731; **The Netherlands**; from a graft of *Ulmus*, 1961, H.M. Heybroek, CBS 373.61; Baarn, from leaves of *Dactylis purpurea*, 1970, H.A. van der Aa, **holotype designated here** CBS H-16281, culture ex-holotype CBS 761.70; Lisse, from *Dahlia*, 1982, J. de Gruyter, CBS 101151 = PD 82/1022.

Notes: This novel variety of *B. exigua*, distinguished from other *B. exigua* varieties on basis of DAF analysis (Aveskamp *et al.* 2009b), is closely related to *B. exigua* var. *exigua*, but different in the colour of its conidial matrix (yellowish) and absence of a positive reaction to NaOH. This variety may be identical to *Ph. exigua* var. *inoxydabilis* Boerema & Vegh, but as the type culture has been lost (Van der Aa *et al.* 2000) a proper comparison of the varieties cannot be made. Additionally, *Ph. exigua* var. *inoxydabilis* was originally only known from periwinkle (*Vinca minor*, Vegh *et al.* 1974), whereas the strains associated to the present taxon are isolated from a wide range of host plants.

Boeremia exigua var. ***heteromorpha*** (Schulzer & Sacc.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515627.

Basionym: *Phoma heteromorpha* Schulzer & Sacc., Hedwigia 23: 107. 1884.

≡ *Phoma exigua* var. *heteromorpha* (Schulzer & Sacc.) Noordel. & Boerema, Verslagen Meded. Plziektenk. Dienst Wageningen 166: 109.1989.

Specimens examined: **France**, Antibes, from *Nerium oleander*, 1979, CBS 101196 = PD 79/176. **Italy**, Perugia, from *Nerium oleander*, 1994, A. Zazzerini, CBS 443.94.

Boeremia exigua var. ***lilacis*** (Sacc.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515628.

Basionym: *Phoma herbarum* f. *lilacis* Sacc., Michelia 2(1): 93. 1880.

Specimen examined: **The Netherlands**, Wageningen, from a twig of *Syringa vulgaris*, June 1976, G.H. Boerema, CBS H-163131, culture CBS 569.79 = PD 72/741.

Notes: Although in the present study this variety clusters outside the *B. exigua* cluster, it is phylogenetic affiliation is ambiguous. In previous studies in which fingerprint markers and actin sequences were applied to delineate this species complex (Abeln *et al.*

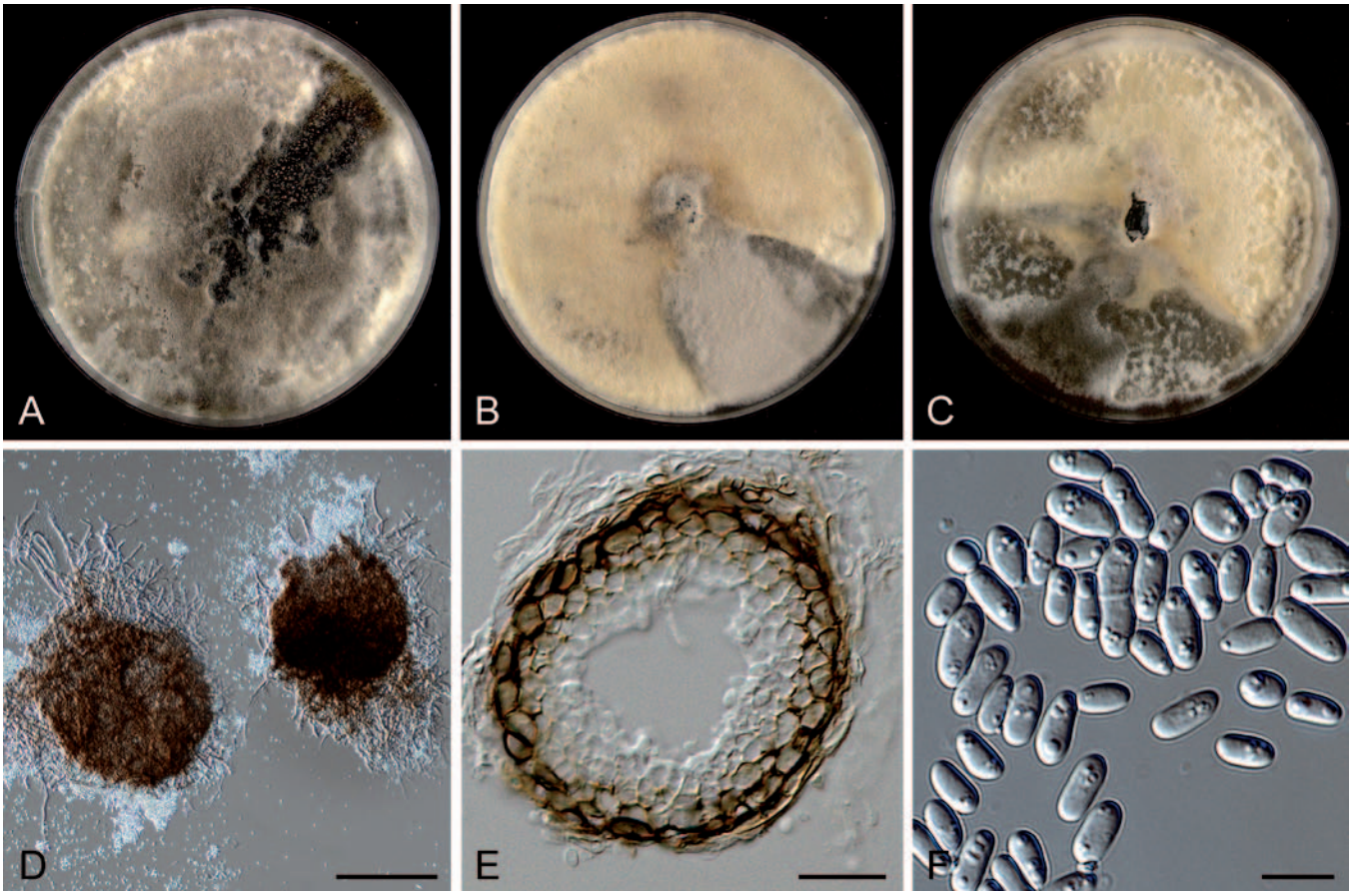


Fig. 10. *Boeremia exigua* var. *pseudolilacis* (CBS 101207). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D. Pycnidia. E. section of young pycnidium. F. Conidia. Scale bars: D = 100 µm; E = 20 µm; F = 5 µm.

2002, Aveskamp *et al.* 2009b) the present taxon clusters within *Ph. exigua*, and is therefore recombined as *B. exigua* var. *lilacis*. Further analysis of this complex is, however, advocated.

Boeremia exigua var. ***linicola*** (Naumov & Vassiljevsky) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515629.

Basionym: *Ascochyta linicola* Naumov & Vassiljevsky, Mater. Micol. Fitopatol. 5: 3. 1926.

Specimens examined: **The Netherlands**, Zierikzee, from *Linum usitatissimum*, 1928, H.A. Diddens, CBS 114.28; Flevoland, from a stem of *Linum usitatissimum*, 1976, G.H. Boerema, CBS 116.76 = ATCC 32332 = CECT 20022 = CECT 20023 = IMI 197074 = PD 75/544.

Boeremia exigua var. ***populi*** (Gruyter & P. Scheer) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515630

Basionym: *Phoma exigua* var. *populi* Gruyter & P. Scheer, J. Phytopathol. 146(8–9): 413. 1998.

Specimens examined: **The Netherlands**, Deil, from a twig of *Populus* X *euramericana* cv. Robusta, Feb. 1993, A.J.P. Oort, **holotype** L 995.263.325, ex-holotype culture CBS 100167 = PD 93/217; Rotterdam, from *Salix* sp., 1982, J. de Gruyter, CBS 101202 = PD 82/942.

Boeremia exigua var. ***pseudolilacis*** Aveskamp, Gruyter & Verkley, **var. nov.** MycoBank MB515631. Fig. 10.

Varietas haec in cultura habitu Phomae exiguae var. exiguae et var. gilvescentis similis, sed matrix conidiorum roseo-bubalina et citius crescens.

Etymology: Refers to the former placement in and close resemblance to *Ph. exigua* var. *lilacis*.

Colonies on OA 70–75 mm diam after 7 d, margin regular. Immersed mycelium black to greenish olivaceous, sparsely visible due to coverage by a mat of mouse-grey woolly to compact aerial mycelium; reverse mouse-grey to olivaceous. Colonies on MEA 70–75 mm diam. after 7 d, margin regular. Immersed mycelium completely covered by a compact aerial mat, which is smoke-grey with some mouse-grey to white zones; reverse black. Colonies on CHA slower growing, 70–80 mm diam after 7 d, margin regular, appearance similar as on MEA. Application of NaOH did not have any effect. Pycnidial and conidial shapes and sizes fit within the *B. exigua* species concept. Conidial matrix rosy-buff.

Specimen examined: **The Netherlands**, near Boskoop, from *Syringa vulgaris*, 1994, J. de Gruyter, **holotype** CBS H-20371, culture ex-holotype CBS 101207 = PD 94/614.

Notes: This novel variety of *B. exigua*, distinguished from other *B. exigua* varieties on basis of DAF analysis (Aveskamp *et al.* 2009b) and AFLP (Abeln *et al.* 2002), is closely related to *B. exigua* var. *exigua* and *B. exigua* var. *gilvescens*. Upon collection, the strain representing *B. exigua* var. *pseudolilacis* has probably erroneously been identified as var. *lilacis* due to its host association.

Boeremia exigua var. ***viburni*** (Roum. ex. Sacc.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515633.

Basionym: *Ascochyta viburni* Roum. ex Sacc., Syll. Fung. 3: 387. 1884.

≡ *Phoma exigua* var. *viburni* (Roum. ex. Sacc.) Boerema apud De Gruyter & P. Scheer, J. Phytopathol. 146: 414. 1998.

Specimens examined: **The Netherlands**, Boskoop, from *Viburnum opulus*, 1984, G.H. Boerema, CBS 100354 = PD 83/448; from *Lonicera* sp., 1993, J. de Gruyter, CBS 101211 = PD 93/838.

Boeremia foveata (Foister) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515653.
Basionym: *Phoma foveata* Foister, Trans. & Proc. Bot. Soc. Edinburgh 33: 66. 1940.

Specimens examined: **Bulgaria**, from a tuber of *Solanum tuberosum*, 1994, J. de Gruyter, CBS 109176 = CECT 2828 = PD 94/1394. **U.K.**, from a tuber of *Solanum tuberosum*, Mar. 1937, C.E. Foister, ex-isotype culture CBS 200.37; Northern Ireland, Belfast, from a tuber of *Solanum tuberosum*, 1966, C. Logan, CBS 341.67 = CECT 20055 = IMI 331912.

Boeremia hedericola (Durieu & Mont.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515634.
Basionym: *Phyllosticta hedericola* Durieu & Mont., Flore d'Algérie Cryptog. 1: 611. 1849.
≡ *Phoma hedericola* (Durieu & Mont.) Boerema, Trans. Brit. Mycol. Soc. 67: 295. 1976.

Specimens examined: **The Netherlands**, Meppel, from a leaf of *Hedera helix*, 1970, CBS 366.91 = PD 70/811; from *Hedera helix*, 1987, J. de Gruyter, CBS 367.91 = PD 87/229.

Note: Strain CBS 367.91 is sterile.

Boeremia lycopersici (Cooke) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515635.
Basionym: *Phoma lycopersici* Cooke, Grevelia 13: 94. 1885.
Teleomorph: *Didymella lycopersici* Kleb., Z. Pflanzenkrankh. 31: 9. 1921.

Specimens examined: **The Netherlands**, Heerde, from fruit of *Lycopersicon esculentum*, Aug. 1967, G.H. Boerema, CBS 378.67 = PD 76/276; from *Lycopersicon esculentum*, 1984, J. de Gruyter, CBS 109172 = PD 84/143.

Boeremia noackiana (Allesch.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515636.
Basionym: *Phyllosticta noackiana* Allesch., Bol. Inst. Agron. Campinas 9: 85. 1898.
≡ *Phoma exigua* var. *noackiana* (Allesch.) Aa, Boerema & Gruyter, Persoonia 17: 450. 2000.
For a complete description see Van der Aa *et al.* (2000).

Specimens examined: **Colombia**, from *Phaseolus vulgaris*, 1979, J. de Gruyter, CBS 101203 = PD 79/1114. **Guatemala**, from *Phaseolus vulgaris*, 1987, IPO Wageningen, CBS 100353 = PD 87/718.

Notes: *Boeremia noackiana* is genetically a sister species to *B. diversispora*, and was also noted by Boerema *et al*. (2004) as "the American cousin". Just like *B. diversispora*, the present species is known from beans, although the main host appears to be *Phaseolus vulgaris.* The two species have many characters in common with *B. exigua* (Van der Aa *et al.* 2000, Boerema *et al.* 2004) and with each other, but are distinguished based on enzyme analysis (Obando-Rojas, 1989) and molecular fingerprinting methods such as AFLP (Abeln *et al.* 2002) and DAF (Aveskamp *et al.* 2009b). Additionally, *B. noackiana* is characterised by a relative fast growth rate on MEA: (6–)6.5–7.5 mm diam after 7 d, and is further distinguished from *B. diversispora* by its relatively uniform conidia. Due to the relatively large genetical distance to the *B. exigua* complex, this taxon is elevated to species level.

Boeremia sambuci-nigrae (Sacc.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515637.
Basionym: *Phoma herbarum* f. *sambuci-nigrae* Sacc., Syll. Fung. 3: 133. 1884.
≡ *Phoma exigua* var. *sambuci-nigrae* (Sacc.) Boerema & Höweler, Persoonia 5(1): 26. 1967.
≡ *Phoma sambuci-nigrae* (Sacc.) E. Monte, Bridge & B. Sutton, Mycopathologia 115: 102. 1991.

Specimens examined: **The Netherlands**, Wageningen, from a leaf of *Sambucus nigra*, 1967, **lectotype** CBS H-16314, ex-lectotype culture CBS 629.68 = CECT 20048 = IMI 331913 = PD 67/753; Baarn, Maarschalksbos, from a leaf of *Sambucus nigra*, Nov. 1967, H.A. van der Aa, CBS 104.68= CECT 20010; from *Sambucus nigra*, 1975, G.H. Boerema, CBS 109170 = PD 75/796.

Boeremia strasseri (Moesz) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515638.
Basionym: *Phoma strasseri* Moesz, *Bot. Közlem.* 22: 45. 1924. nom. nov. pro *Phoma menthae* Strasser, Verh. zool. Bot. Ges. Wien 60: 317. 1910 [non *Phoma menthae* Roum. (date of publication unknown)].

Specimens examined: **The Netherlands**, Arnhem, from a stem of *Mentha* sp., 1973, CBS 126.93 = PD 73/642. **U.S.A.**, Oregon, from *Mentha piperita*, 1970, H.A. van der Aa, CBS 261.92 = ATCC 244146 = PD 92/318.

Note: As the older name *Ph. menthae* is illegitimate, the epithet "*strasseri*" prevails.

Boeremia telephii (Vestergr.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515639.
Basionym: *Ascochyta telephii* Vestergr., Öfvers. Förh. Kongl. Svenska Vetenska.-Akad. 54: 41. 1897.
≡ *Phoma telephii* (Vestergr.) Kesteren, Netherlands J. Pl. Pathol. 78: 117.1972.

Specimens examined: **The Netherlands**, Utrecht, from a stem of *Sedum telephium*, 1971, G.H. Boerema, CBS 760.73 = PD 71/1616; from *Sedum spectabile*, 1975, G.H. Boerema, CBS 109175 = PD 79/524.

Group O:
Three species are clustered in group O, which all were accommodated in the Boeremaean section *Phoma*. These species, *Ph. multirostrata*, *Ph. pereupyrena* and *Ph. insulana* are characterised by the production of small (5–15 µm diam), unicellular chlamydospores, comparable to those formed by some species in group K. The absence of septate conidia and a thin pycnidial wall are further characters of the species accommodated in group O.

The strains accommodated in *Ph. multirostrata* reveal a high variation in spore size. Boerema *et al.* (1986) introduced three varieties within this species, but based on morphological observations and DNA sequence analyses, these varieties were not recognised by later researchers and thus the varieties were merged again (Morgan-Jones 1988, Aveskamp *et al.* 2009a).

Phoma insulana (Mont.) Boerema & Malathr., in Boerema, Verslagen Meded. Plziektenk. Dienst Wageningen 158 (Jaarboek 1981): 28. 1982.
Basionym: *Phyllosticta insulana* Mont., Ann. Sci. Nat. Bot. IV 5: 343.1856.

Specimen examined: **Greece**, from the berries of *Olea europaea*, 1980, G.H. Boerema, CBS 252.92 = PD 80/1144.

Phoma multirostrata (P.N. Mathur, S.K. Menon & Thirum.) Dorenb. & Boerema, Mycopathol. Mycol. Appl. 50(3): 256. 1973, emend. Aveskamp *et al.* Mycologia 101: 375. 2009.

Basionym: *Sphaeronaema multirostratum* P.N. Mathur, S.K. Menon & Thirum., Sydowia 13: 146. 1959. (as "*Sphaeronema*").

Specimens examined: **India**, Maharashtra, Poona, Talegaon, from poultry farm soil, Mar. 1959, M.J. Thirumalachar, **isotype** CBS H-7616, culture CBS 274.60 = IMI 081598; Maharashtra, Poona, Talegaon, from soil, Mar. 1959, M.J. Thirumalachar, CBS H-16499, culture CBS 368.65 = PD 92/1757. **The Netherlands**, Hoorn, greenhouse, from the stem of *Cucumis sativus*, Aug. 1967, G.H. Boerema, CBS H-16502, culture CBS 110.79 = PD 65/8875. Unknown origin, from *Cucumis sativus*, 1983, PD 83/48.

Phoma pereupyrena Gruyter, Noordel. & Boerema, Persoonia 15(3): 390. 1993.

Specimen examined: **India**, from a leaf of *Coffea arabica,* 1976, CBS 267.92 = PD 76/1014.

Group P:

This well-supported clade (BPP = 1.00, RBS = 97 %) comprises *Ph. dictamnicola* and *Ph. sylvatica*, which are both associated with the section *Sclerophomella* (Boerema *et al.* 1998). In addition, both varieties of *Ph. poolensis* are recovered here. As in the *Sclerophomella* species, an ostiole is commonly absent in *Ph. poolensis* var. *poolensis*, a character which supports the sequence data found in the present study. In contrast, the second variety of this species, *Ph. poolensis* var. *verbascicola*, always produces ostiolate pycnidia (De Gruyter *et al.* 1993). Both *Ph. poolensis* varieties can further be differentiated on the basis of the β-tubulin sequence, and are morphologically distinguishable in the colour of the conidial matrix. The conidia of the type variety are on average somewhat smaller, measuring *ca*. 3.5–5 × 1.5–2 µm, than those of var. *verbasicola*, which measure 3.5–5.5 × 1.5–2.5 µm. Both varieties are known from plant hosts belonging to the *Scophulariaceae*, but whereas var. *poolensis* is recorded as causal agent of leaf spots and basal stem rot in snapdragon (*Antirrhinum majus*), var. *verbascicola* is only known as saprobe of *Verbascum* spp., although inoculation trials indicated that it may also have a role as pathogen (Boerema *et al.* 2004). Given all these differences, it is considered to be justified to erect a separate species for *Ph. poolensis* var. *verbascicola* as *Ph. novae-verbascicola*.

Although none of the species in this group has been confirmed to have a teleomorph (Boerema *et al.* 1998), it has been suggested that *Didymella winteriana* is the teleomorph of *Phoma sylvatica* (Munk 1957). Given the topology of the tree, this association with a *Didymella* species is plausible, although a sexual structure was not observed in the present study, nor in the previous studies of Boerema & De Gruyter (1998).

Phoma dictamnicola Boerema, Gruyter & Noordel., Persoonia 15(1): 90. 1992.

Specimen examined: **The Netherlands**, Arnhem, from a stem of *Dictamnus albus*, 1974, J. de Gruyter, CBS 507.91 = PD 74/148.

Phoma novae-verbascicola Aveskamp, Gruyter & Verkley, **nom. nov.** pro *Phyllosticta verbascicola* Ellis & Kellerm. MycoBank MB515640.

Basionym: *Phyllosticta verbascicola* Ellis & Kellerm., Bull. Torrey Bot. Club 11: 115. 1884.

≡ *Phoma poolensis* var. *verbascicola* (Ellis & Kellerm.) Aa & Boerema, in De Gruyter, Noordeloos & Boerema, Persoonia 15(3): 385. 1993. Not *Phoma verbascicola* (Schwein.) Cooke, in Ravenel. 1878.

Etymology: The epithet refers to the host plant, *Verbascum* spp.

For a full description see De Gruyter *et al.* (1993).

Specimens examined: **The Netherlands**, Zeist, Abburg nursery, **holotype** L 9893.00.134; Haarlem, from dead stem material of *Verbascum densiflorum*, 1992, J. de Gruyter, CBS 127.93 = PD 92/347; from stem of *Verbascum* sp., 1974, G.H. Boerema, CBS 114.93 = PD 74/228.

Notes: This species is distinguishable from *Ph. poolensis* by to the presence of 1–2(–5) ostioles, the colourless to whitish matrix and the smaller conidia. On MEA, the aerial mycelium is more compact or woolly than that of *Ph. poolensis*.

The variety epithet could not be elevated to species level, as *Phoma verbascicola* is already occupied. This basionym, however, probably refers to immature pseudothecia of a *Pleospora* species (Boerema *et al.* 1996). Therefore, a new name is proposed here for the present species.

Phoma poolensis Taubenh., Dis. Greenhouse Crops 203. 1919.

Specimens examined: **Denmark**, from a stem of *Antirrhinum majus*, July 1938, P. Neergaard, CBS 253.38. **The Netherlands**, Wageningen, from a stem of *Scrophularia nodosa*, 1974, G.H. Boerema, CBS 115.93 = PD 74/206; Bennekom, from a stem of *Antirrhinum majus*, 1973, G.H. Boerema, CBS 116.93= PD 71/884. Unknown origin and substrate, 1920, E.M. Smiley, CBS 113.20 = PD 92/774.

Phoma sylvatica Sacc. Michelia 2(2): 337. 1881.

Specimens examined: **The Netherlands**, Wageningen, from *Melampyrum pratense*, 1983, J. de Gruyter, CBS 135.93 = PD 83/87; Wageningen, from a stem of *Melampyrum pratense*, 1993, J. de Gruyter, CBS 874.97 = PD 93/764.

Group Q:

The *Phoma* species embedded in this group, *Ph. commelinicicola* and *Ph. eupatorii* are morphologically distinct, hence their accommodation in the sections *Phoma* and *Macrospora* respectively. The accommodation of *Chaetasbolisia erysiphoides* in this clade, the type of its genus, is unexpected. Attempted morphological studies revealed that this strain was sterile, and therefore recombination of the species could not be supported by morphological data. The descriptions provided in literature (Sutton 1980, Patel *et al.* 1997, Reynolds 1999) suggest, however, that this genus could very well represent a group of setose *Phoma* species, although this cannot be resolved due to a lack of isolates. The presence of setae is not recorded in other species in group Q, and moreover, is within the *Didymellaceae* only known from *Peyronellaea gardeniae* (Group K), and from pycnidia in some older cultures from *Epicoccum sorghi* (Group M), *Peyronellaea glomerata* (Group K) and *Phoma herbarum* (Boerema *et al*. 2004). The topology and the clustering of these species cannot be further explained by the morphology or ecology, nor by their geographical distribution.

Phoma commelinicola (E. Young) Gruyter, Persoonia 18(1): 93. 2002.

Basionym: *Phyllosticta commelinicola* E. Young, Mycologia 7: 144. 1915.

Specimen examined: **New Zealand**, South Auckland, Alfriston, from *Tradescantia* sp., 1997, K. Ramsay, CBS 100409.

Phoma eupatorii Died., Ann. Mycol. 10(5): 447. 1912.

Specimen examined: **The Netherlands**, Arnhem, from *Eupatorium cannabinum*, 1977, G.H. Boerema, CBS 123.93 = PD 77/1148.

Group R:
This group comprises five species that previously were accommodated in the sections *Phoma*, *Peyronellaea* and *Phyllostictoides*. As the name of *Ph. tropica* already suggests, it concerns a thermotolerant species, which is mainly found in European greenhouses on a wide range of hosts, but which probably has a tropical origin (Schneider & Boerema 1975), as do most other species found in the present clade. The sole host of *Ph. costarricensis* is coffee bean (*Coffea arabica*), while *Ph. piperis* is associated with Indian Long Pepper (*Piper longus*), and the novel species *Ph. minor* has been isolated twice from clove (*Syzygium aromaticum*) in Indonesia. In addition, *Ph. labilis* is a warmth-preferring plurivorous species that has been isolated in European greenhouses and from nature in the Middle East, Turkey and Indonesia (Boerema *et al.* 2004). *Phoma zantedeschiae* is widespread throughout the Western Hemisphere, but always in association with arum or calla (*Zantedeschia* sp.), a genus that is indigenous in southern Africa (Boerema & Hamers 1990). Thus far, however, no data of temperature-growth studies are available for these species except for *Ph. tropica*. Several other thermotolerant species, such as *Ph. calidophila*, *Ph. calorpreferens* and *Ph. multirostrata*, are, however, not accommodated in this group. These three species are soil-borne, in contrast to *Ph. tropica* and *Ph. costarricensis*, which are associated with leaf-spots.

Phoma tropica and *Ph. costarricensis* are both closely related, and colony characters are highly similar. However, the strains available revealed a significant difference in conidial and pycnidial sizes, consistent with the data obtained in previous studies (Schneider & Boerema 1975, De Gruyter & Noordeloos 1992).

Phoma costarricencis Echandi, Rev. Biol. Trop. 5: 83. 1957.

Specimens examined: **Nicaragua**, from a twig of *Coffea* sp., 1991, CBS 506.91 = PD 91/876 = IMI 215229. Unknown origin, from *Coffea arabica*, 1979, CBS 497.91 = PD 79/209.

Notes: Strain CBS 497.91 was initially identified as *Ph. tropica*. The close phylogenetic association between this species and *Ph. costarricensis* concurs with their overlapping morphological characters (see Schneider & Boerema 1975, De Gruyter & Noordeloos 1992).

Phoma labilis Sacc., Michelia 2(7): 341. 1881.

Specimens examined: **Israel**, from a stem of *Rosa* sp., 1970, G.H. Boerema, CBS 479.93 = PD 70/93. **The Netherlands**, Barendrecht, from a stem of *Lycopersicon esculentum*, 1987, J. de Gruyter, CBS 124.93 = PD 87/269.

Phoma minor Aveskamp, Gruyter & Verkley, **sp. nov.** MycoBank MB515641. Fig. 11.

Conidia ellipsoidea, ovoidea vel leniter allantoidea, glabra, hyalina, continua, (3–)3.5–4.5(–5) × 1.8–2.5(–3) µm, (0–)1–3(–4) guttulis minutis praedita. Matrix conidiorum alba.

Etymology: Epithet derived from the small-sized conidia.

Conidiomata pycnidial, solitary, (sub-)globose to broadly ellipsoidal, glabrous or with some hyphal outgrows, on the agar surface and immersed, (125–)150–280(–330) × (125–)150–220(–245) µm. *Ostioles* (1–5), slightly papillate or non-papillate. *Pycnidial wall* pseudoparenchymatous, composed of oblong to isodiametric cells, outer cell layer pigmented, 2–4 layers, 8–15 µm thick. *Conidiogenous cells* phialidic, hyaline, simple, smooth, flask-shaped or somewhat isodiametric, *ca*. 4–5.5(–6.2) × 3–4.5(–4.7) µm. *Conidia* ellipsoidal to ovoid or slightly allantoid, thin-walled, smooth, hyaline, aseptate (3–)3.5–4.5(–5) × 1.8–2.5(–3) µm, with (0–)1–3(–4) minute guttules. Conidial matrix white.

Culture characteristics: Colonies on OA (44–)45–50(–54) mm diam after 7 d, margin regular. Aerial mycelium flat, grey, but locally well-developed in densely floccose white tufts. Immersed mycelium olivaceous with rosy-buff tinges near the colony margin; reverse concolourous. Colonies on MEA 46-48 mm diam after 7 d, margin regular. Immersed mycelium hyaline, with abundant semi-immersed pycnidia, but almost completely covered by an aerial mycelial mat. Aerial mycelium pluriform, with a compact white mat and some felty glaucous grey or dull green zones, near colony margin white; reverse black to grey-olivaceous. Colonies on CHA 50–54 mm diam. after 7 d, margin regular. Aerial mycelium similar as on MEA, although the felty white and glaucous grey zones are less abundant; reverse slate blue to leaden-black. Application of NaOH results in a greenish yellow discolouration of the agar, best to be observed on OA medium.

Specimens examined: **Indonesia**, Sumatra, from *Syzygium aromaticum*, Apr. 1982, R. Kasim, **holotype designated here** CBS H-20236, ex-holotype culture CBS 325.82; Lampung, from *Syzygium aromaticum*, Dec. 1982, H. Vermeulen, CBS 315.83.

Notes: As for *Ph. eucalyptica*, this species has been recorded in association with clove trees (*Syzygium aromaticum*, Boerema *et al.* 2004). Both species, although genetically distinct, have many characters in common, notably the colony characters on OA, the high variation in ostiole number and a similar reaction to application of NaOH. Although *Phoma minor* produces relatively small conidia, the conidia of *Ph. eucalyptica* are even smaller, measuring only 2–4 × 1–2 µm (De Gruyter & Noordeloos 1992).

Phoma piperis (Tassi) Aa & Boerema, Persoonia 15(3): 398. 1993.
Basionym: *Phyllosticta piperis* Tassi, Boll. Reale Orto Bot. Siena 3(2): 28. 1900.

Specimens examined: **The Netherlands**, Tiel, from a leaf of *Peperomia pereskiifolia*, 1988, J. de Gruyter, CBS 268.93 = CBS 108.93 = PD 88/720; Tiel, from *Peperomia* sp., 1990, J. de Gruyter, PD 90/2011

Phoma tropica R. Schneid. & Boerema, Phytopathol. Z. 83 (4): 361. 1975.

Specimen examined: **Germany**, Horrheim, from *Saintpaulia ionantha*, 1973, R. Schneider, **isotype** CBS H-7629, ex-isotype culture CBS 436.75.

Phoma zantedeschiae Dippen., S. African J. Sci. 28: 284. 1931.

Specimen examined: **The Netherlands**, from a bulb of *Zantedeschiae* sp., 1969, G.H. Boerema, CBS 131.93 = PD 69/140.

Group S – Stagonosporopsis:
This large group (BPP = 1.00, RBS = 55 %) comprises mainly species with *Stagonosporopsis* synanamorphs. In the Boeremaean classification system, these species were embedded in *Phoma* section *Heterospora* (Boerema *et al.* 1997). As with the other sections, this group also appeared to be artificial. Based on LSU and SSU sequences, the type species of the section *Heterospora*, *Ph. heteromorphospora*, clusters outside the *Didymellaceae* (De Gruyter *et al*. 2009), as do *Ph. samarorum* and *Ph. dimorphospora*.

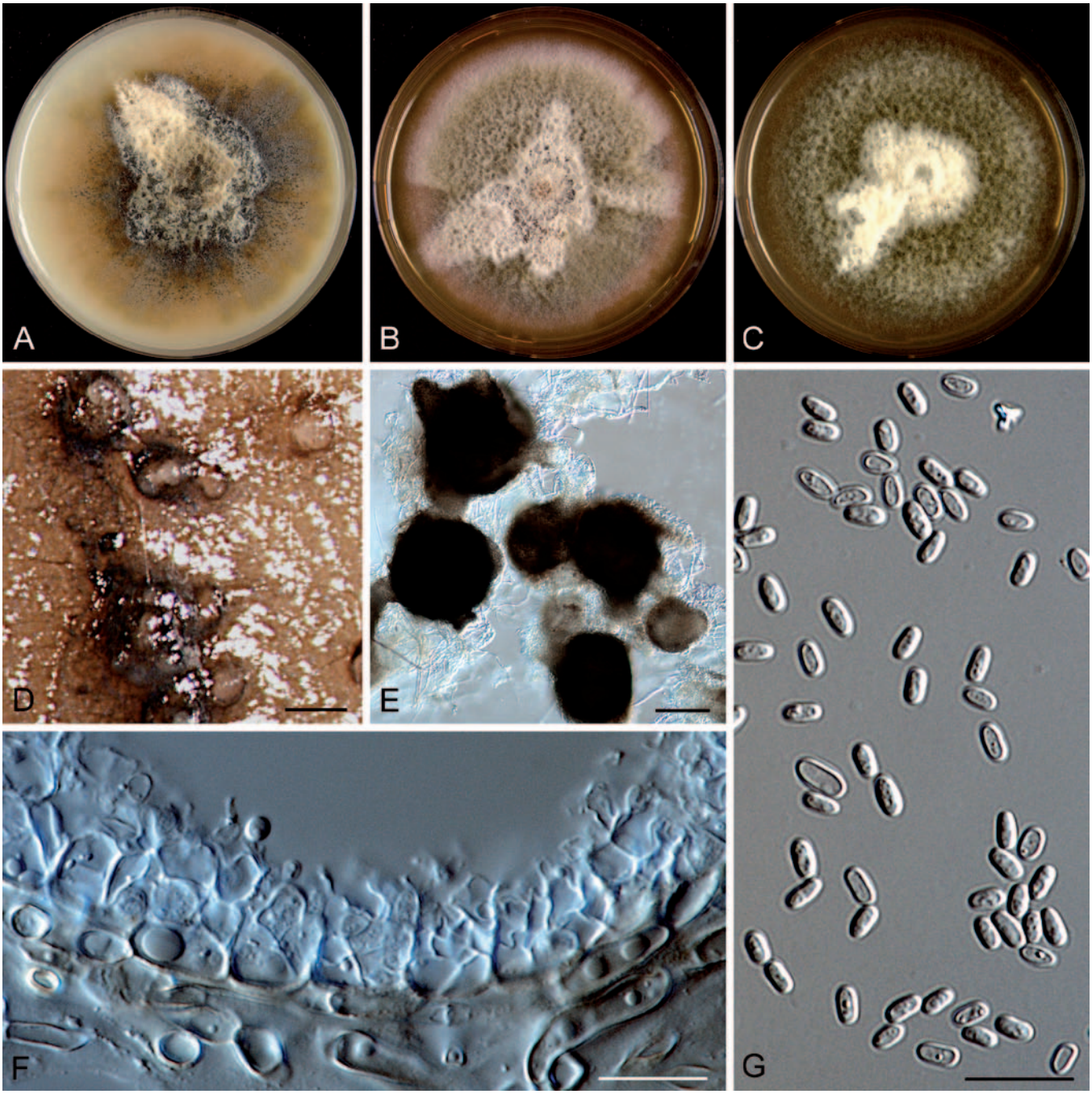


Fig. 11. *Phoma minor* (CBS 325.82). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D–E. Pycnidia. F. Section of the pycnidial wall. G. Conidia. Scale bars: D = 200 µm; E = 100 µm; F–G = 10 µm.

Three species, *Ph. clematidina*, *Ph. glaucii* and *Ph. aquilegiicola* form a separate clade (Group C) within the *Didymellaceae*, and are treated above. Also *Ph. nigripycnidia* and *Ph. narcissi* are not accommodated here.

In contrast to the *Heterospora* species that are absent in this clade, several current *Phoma* taxa recovered here have been associated with the section *Phyllostictoides*, such as *Ph. artemisiicola*, *Ph. caricae-papayae*, *Ph. cucurbitacearum*, *Ph. heliopsidis*, *Ph. rudbeckiae*, and the quarantine-organisms *Ph. ligulicola* var. *ligulicola* and var. *inoxydabilis* (De Gruyter 2002). These are all included in subclade S1 (BPP = 0.93, RBS = 73 %). These species do produce a percentage of multicellular conidia in culture that are often considerably larger than the regular aseptate ones. However, Boerema *et al.* (1997) decided to exclude the *Ph. ligulicola* varieties and *Ph. cucurbitacearum* from section *Heterospora*, as the sizes of the *Stagonosporopsis*-like conidia do not always exceed that of the aseptate conidia in these species. A sister clade to subclade S1 is S2, which hosts the potato pathogens *Ph. andigena* and *Ph. crystalliniformis* – formerly known as *Ph. andina* var. *crystalliniformis*. Both species originate from the Andes region, and are regarded as serious quarantine pathogens in large parts of the world (Smith *et al*. 1992).

In addition, three other subclades can be recognised in this clade. One (S3) comprises the species *Ph. schneiderae* and *Ph. subboltshauserii* (both of the section *Heterospora*) as well as *Ph. astragali*. This species is known as a pathogen of *Astragalus* spp., and is characterised by a high percentage of "distorted" conidia, but thus far, no records have been made of a *Stagonosporopsis*-like synanamorph. Whereas records of *Ph. astragali* and *Ph. schneiderae* are mainly limited to the American continent, *Ph.*

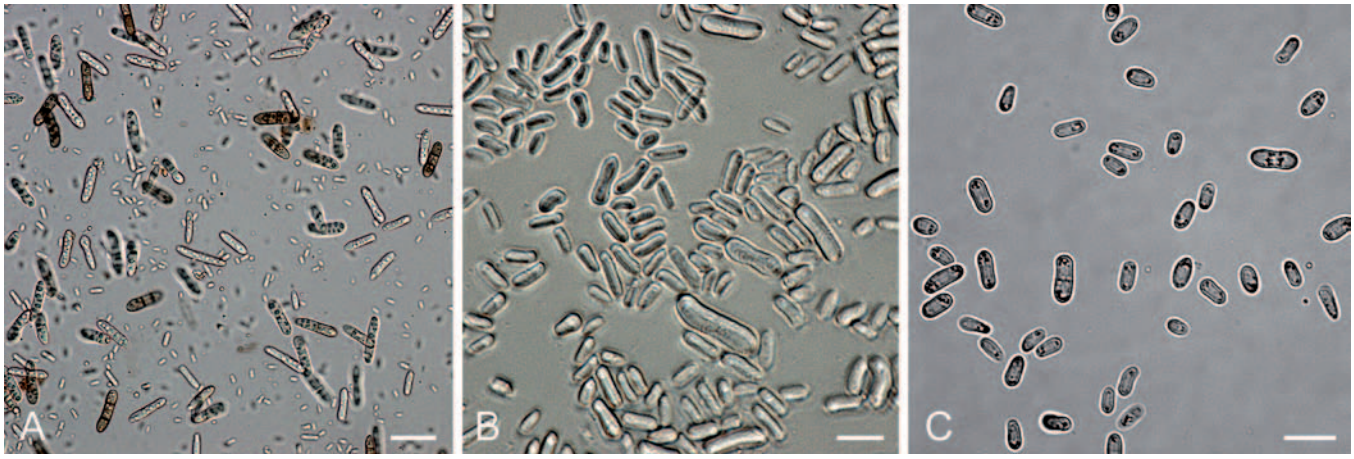


Fig. 12. Conidial dimorphism in three species of *Stagonosporopsis*. A. *S. actaeae* (CBS 106.96). B. *S. lupini* (CBS 101494). C. *S. cucurbitacearum* (CBS 109171). Scale bars: A = 20 µm; B–C = 10 µm.

subboltshauseri appears to occur worldwide on *Fabaceae*. However, Boerema *et al.* (2004) suggested that the original host of this species may have been *Phaseolus*, which is native to the Americas.

A fourth and fifth (S4, S5) subclade in this group comprise species that are accommodated in section *Phoma*, and therefore lack any further features than a plain, globose pycnidium and aseptate, hyaline conidia. The species found here are *Ph. dorenboschiae*, *Ph. loticola* (both S4), *Ph. ajacis* and *Ph. valerianellae* (both S5).

In group S several taxa have been found with a teleomorph in *Didymella*, such as *Ph. ligulicola* var. *ligulicola* (teleomorph *D. ligulicola* var. *ligulicola*), *Ph. ligulicola* var. *inoxydabilis* (*D. ligulicola* var. *inoxydabilis*), and *Ph. cucurbitacearum* (*D. bryoniae*). Also the teleomorph of *Ph. caricae-papayae* has been recovered in this study, and found to be a *Didymella*, which is in line with the other teleomorph observations in this clade. The current teleomorph state of this species is accommodated in *Mycosphaerella* as *M. caricae* (Sivanesan 1990).

As the species in the present clade form a well-defined group within the *Didymellaceae*, the taxa are recombined into the genus *Stagonosporopsis*. This further implies that the names of the *Stagonosporopsis* synanamorphs of *Ph. samarorum* and *Ph. narcissi* (*S. fraxini* and *S. curtisii* respectively) should no longer be used.

Stagonosporopsis Died., Ann. Mycol. 10(2): 142. 1912. **emend.** Aveskamp, Gruyter & Verkley. Fig. 12.

Conidiomata pycnidial, globose to subglobose, measuring 70–300 µm diam, on agar surface or immersed, solitary or confluent, ostiolate or poroid. *Pycnidial wall* pseudoparenchymatous, counting 2–6 cell layers of which the outer 1–3 are brown/olivaceous pigmented. *Conidiogenous cells* phialidic, hyaline, simple, smooth, ampulliform or doliiform, *ca*. 4–7.5 × 3–6 µm. *Conidia* often in two types: majority aseptate, hyaline, ellipsoidal to subglobose, thin-walled, smooth, measuring (3–)3.5–10 × 1.5–3(–3.5) µm. Conidia of the second type can be produced both *in vivo* and *in vitro* in the same pycnidia as the smaller spores, unicellular or with up to 3 septa, measuring up to 30 × 8 µm. *Pseudothecia*, if present, occurring only *in vivo*, globose to subglobose, sometimes with a somewhat conical neck, measuring 90–230 µm diam. *Asci* cylindrical or subclavate, measuring 50–90 × 9–13 µm, always 8-spored, biseriate. *Ascospores* ellipsoid, fusiform or obovoid, measuring 12–18 × 4–7 µm, uniseptate, guttulate.

Stagonosporopsis actaeae (Allesch.) Died., Ann. Mycol. 10: 141. 1912.

Basionym: *Actinonema actaeae* Allesch., Ber. bayer. bot. Ges. 5: 7. 1897.

= *Phoma actaeae* Boerema, Gruyter & Noordeloos, Persoonia 16(3): 347. 1997.

Specimens examined: **The Netherlands**, Zeist, from a stem of *Cimicifuga simplex*, 1974, G.H. Boerema, CBS 105.96 = PD 74/230; Limburg, Schaersbergerbos, from a leaf of *Actaea spicata*, 1994, J. de Gruyter, L 992.167.501, culture CBS 106.96 = PD 94/1318.

Notes: In contrast to the earlier description of the *Phoma* anamorph of this species (Boerema *et al.* 1997), the larger conidia regularly produces up to 3-septate conidia (see Fig. 12A). In the study mentioned above and in the present one the same strains were examined morphologically.

Stagonosporopsis ajacis (Thüm.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515653.

Basionym: *Phyllosticta ajacis* Thüm., apud Bolle & von Thümen, Boll. Soc. Adriat. Sci. Nat. Trieste 6: 329. 1880.

= *Phoma ajacis* Aa & Boerema, apud De Gruyter, Noordeloos & Boerema, Persoonia 15(3): 383. 1993.

Specimens examined: **Kenya**, from *Delphinium* sp., 1990, Hopman, L 993.034.225, culture CBS 177.93 = PD 90/115. **The Netherlands**, Ter Aar, from *Delphinium* sp., 1986, CBS 176.93 = PD 86/547.

Stagonosporopsis andigena (Turkenst.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515655.

Basionym: *Phoma andigena* Turkenst., apud Boerema, Gruyter & Noordeloos, Persoonia 16(1): 131. 1995.

Specimens examined: **Peru**, Dep. Junin, Huancayo, near Vallis Mantaro, from a leaf of *Solanum* sp., 1975, L.J. Turkensteen, CBS 101.80 = PD 75/909 = IMI 386090; Dep. Junin, Huancayo, near Vallis Mantaro, from a leaf of *Solanum* sp., 1975, L.J. Turkensteen, CBS 269.80 = PD 75/914.

Stagonosporopsis artemisiicola (Hollós) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515656.

Basionym: *Phoma artemisiicola* Hollós, Mat. Természettud. Közlem. 35: 40. 1926. (as "*artemisaecola*")

Specimen examined: **France**, from a stem base of *Artemisia dracunculus*, 1973, CBS 102636 = PD 73/1409.

Stagonosporopsis astragali (Cooke & Harkn.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515657.
Basionym: *Phoma astragali* Cooke & Harkn., Grevillea 13: 111. 1885.

Specimen examined: Unknown origin, from *Astragalus* sp., 1925, A.W. Archer, CBS 178.25 = MUCL 9915.

Stagonosporopsis caricae (Sydow & P. Sydow) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515658.
Basionym: *Mycosphaerella caricae* Sydow & P. Sydow, Ann.. Mycol. 11: 403. 1913.
≡ *Phoma caricae-papayae* (Tarr.) Punith., Trans Brit. Mycol. Soc. 75: 340. 1980.
≡ *Ascochyta caricae-papayae* Tarr., The fungi and plant diseases of Sudan: 53. 1955.
= *Ascochyta caricae* Pat., Bull. Soc. Mycol. France 7: 178. 1891.
≡ *Phoma caricae* Punith., CMI Descriptions of Pathogenic Fungi and Bacteria 634: 1. 1979.
For description of the teleomorph see Sivanesan (1990). Punithalingam (1979b) provides an extensive description, *Ph. caricae* is a synonym of the anamorph.

Specimens examined: **Brazil**, from *Carica papaya*, 2006, J. de Gruyter, PD 06/03082531. **Chile**, from fruit of *Carica papaya*, Feb. 1990, H.A. van der Aa, CBS 248.90. **Indonesia**, Java, Segunung, from *Brassica* sp., Feb. 1976, H. Vermeulen, CBS 282.76.

Notes: *Phoma caricae-papayae* has been associated with an undescribed teleomorph state in *Mycosphaerella* or *Didymella* (Boerema *et al.* 2004). Sivanesan (1990) synonymised *Ph. caricae* with *M. caricae*, apparently not noting that *Ph. caricae* already was synonymised with *Ph. caricae-papayae* by Punithalingam (1980). As *Mycosphaerella* is phylogenetically unrelated to *Phoma* (De Gruyter *et al.* 2009), this taxonomic association is unlikely, and the observed sexual state observed was probably *Didymella*-like.

This species has solely been associated with pawpaw (*Carica papaya*, *Caricaceae*), but a single strain, deposited at CBS as *D. exigua* and that was isolated from *Brassica* leaves from Java, Indonesia (CBS 282.76), was genetically identical to the reference strain of *Ph. caricae-papayae*. Herbarium material of this strain consisted of an inoculated lupine stem on cornmeal agar (CBS H-11960) and represented a conidial state similar to this of *Ph. caricae-papayae*. This indicated that probably the *Didymella* teleomorph had been observed, but that it was preserved under an incorrect name as it was only distantly related to the ex-type strain of *Didymella exigua* (CBS 183.55). This finding provides evidence that *S. caricae* is not restricted to pawpaw.

Stagonosporopsis crystalliniformis (Loer., R. Navarro, M. Lôbo & Turkenst.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515659.
Basionym: *Phoma andina* var. *crystalliniformis* Loer., R. Navarro, M. Lôbo & Turkenst., Fitopatología 21(2): 100. 1986.
≡ *Phoma crystalliniformis* (Loer., R. Navarro, M. Lôbo & Turkenst.) Noordel. & Gruyter, apud Noordeloos, de Gruyter, van Eijk & Roeijmans, Mycol. Res. 97: 1344. 1993.

Specimens examined: **Colombia**, Antioquia, Rionegro, from a stem base of *Lycopersicon esculentum*, 1983, R. Navarro, **holotype** CBS H-3926, ex-holotype culture CBS 713.85 = ATCC 76027 = PD 83/826; Guachacal, from a leaf of *Solanum tuberosum*, Nov. 1985, W.M. Loerakker, CBS 771.85 = IMI 386091 = PD 85/772.

Stagonosporopsis cucurbitacearum (Fr.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515660.
Basionym: *Sphaeria cucurbitacearum* Fr., Syst. Mycol. 2(2): 502. 1823.
≡ *Phoma cucurbitacearum* (Fr.) Sacc., Syll. Fung. 3: 148. 1884.
= *Sphaeria bryoniae* Fuck., Jahrb. Nassauischen Vereins Naturk. 23–24: 112. 1870.
≡ *Didymella bryoniae* (Fuckel) Rehm, Ber. Naturhist. Vereins Augsburg 26: 27. 1881.

Specimens examined: **New Zealand**, from *Cucumis* sp., 1979, CBS 133.96= PD 79/127. **The Netherlands**, Horst, from *Cucumis* sp., 1991, J. de Gruyter, CBS 109171 = PD 91/310.

Note: Strain CBS 133.96 could not be identified morphologically, as it proved to be sterile.

Stagonosporopsis dennisii Boerema, Gruyter & Noordel., Persoonia 16(3): 350. 1997.
= *Phoma dennisii* Boerema, Trans. Brit. Mycol. Soc. 67(2): 307. 1976.

Specimens examined: **Canada**, Ontario, from a stem of *Solidago canadensis*, 1995, G.P. White, CBS 135.96 = IMI 19337 = PD 94/4756. **The Netherlands**, Arnhem, from a stem of *Solidago floribunda*, 1968, CBS 631.68 = PD 68/147.

Stagonosporopsis dorenboschii (Noordel. & Gruyter) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515661.
Basionym: *Phoma dorenboschii* Noordel. & Gruyter, Persoonia 15(1): 83. 1992.

Specimens examined: **The Netherlands**, Rijnsburg, from *Physostegia virginiana*, 1986, D. Kruger, **holotype** L 988.202.121, **isotype** CBS H-7604, ex-holotype culture CBS 426. 90 = IMI 386093 = PD 86/551; from *Physostegia virginiana*, 1986, CBS 320.90 = PD 86/932.

Stagonosporopsis heliopsidis (H.C. Greene) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515662.
Basionym: *Phyllosticta heliopsidis* H.C. Greene, Trans. Wisconsin Acad. Sci. 50: 158. 1961.
≡ *Phoma heliopsidis* (H.C. Greene), Aa & Boerema apud De Gruyter Boerema & van der Aa, Persoonia 18(1): 40. 2002.

Specimens examined: **Canada**, Island of Montréal, from *Ambrosia artemisiifolia*, PD 95/6189 = DAOM 221138. **The Netherlands**, from *Heliopsis patula*, 1974, CBS 109182 = PD 74/231.

Stagonosporopsis hortensis (Sacc. & Malbr.) Petr., Ann. Mycol. 19(1/2): 21. 1921.
Basionym: *Hendersonia hortensis* Sacc. & Malbr., in Saccardo, Michelia 2(8): 629. 1882.
= *Phoma subboltshauserii* Boerema, Gruyter & Noordel., Persoonia 16(3): 360. 1997.

Specimens examined: **The Netherlands**, from an unknown substrate, Mar. 1942, N. Hubbeling, CBS 104.42; from *Phaseolus vulgaris*, 1979, G.H. Boerema, CBS 572.85 = PD 79/269.

Stagonosporopsis ligulicola var. ***inoxydabilis*** (Boerema) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515664.
Basionym: *Didymella ligulicola* var. *inoxydabilis* Boerema, Stud. Mycol. 32: 10. 1990.
Anamorph: *Phoma ligulicola* var. *inoxydabilis* Boerema, Stud. Mycol. 32: 10. 1990.

Specimens examined: **The Netherlands**, from *Chrysanthemum parthenii*, 1981, G.H. Boerema, **holotype** CBS H-7611, culture ex-holotype CBS 425.90 = PD 81/520; from *Matricaria* sp. 1985, J. de Gruyter, PD 85/259.

Stagonosporopsis ligulicola var. ***ligulicola*** (K.F. Baker, Dimock & L.H. Davis) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515663.
Basionym: *Mycosphaerella ligulicola* K.F. Baker, Dimock & L.H. Davis, Phytopathology 39: 799. 1949.
Anamorph: *Phoma ligulicola* var. *ligulicola* Boerema, Stud. Mycol. 32: 9. 1990.

Specimens examined: **Germany**, Berlin, from *Chrysanthemum indicum*, 1963, R. Schneider, CBS H-11952, culture CBS 500.63 = MUCL 8090. **The Netherlands**, near Lisse, from a leaf of *Chrysanthemum indicum*, 1984, CBS 137.96 = PD 84/75.

Stagonosporopsis loticola (Died.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515665.
Basionym: *Phoma loticola* Died., Kryptog.-Fl. Mark Brandenburg. 9, Pilze 7(1): 152. 1912.

Specimens examined: **New Zealand**, Auckland, Mt. Albert, from *Lotus pedunculatus*, 1981, P.R. Johnston, **isotype** CBS H-7612, ex-isotype culture CBS 562.81 = PDDCC 6884; Auckland, from the stem of *Lotus tenuis*, 1979, P.R. Johnston, CBS 628.97 = PD 79/72.

Stagonosporopsis lupini (Boerema & R. Schneid.) Boerema, Gruyter & P. Graaf, Persoonia 17(2): 283. 1999.
Basionym: *Ascochyta lupini* Boerema & R. Schneid., apud Boerema, Verslagen Meded. Plziektenk. Dienst Wageningen 162: 28. 1984.
≡ *Phoma schneiderae* (Boerema & R. Schneid.) Boerema, Gruyter & P. Graaf, Persoonia 17(2): 282. 1999.

Specimens examined: **Peru**, Puno, from *Lupinus mutabilis*, 1980, CBS H-9061, culture CBS 375.84= PD 80/1250. **U.K.**, Cambridgeshire, Mepal, from *Lupinus albus*, Apr. 1998, P. van de Graaf, **holotype** L 998.099.105, ex-holotype culture CBS 101494 = PD 98/5247.

Stagonosporopsis oculo-hominis (Punith.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515666.
Basionym: *Phoma oculi-hominis* Punith., Trans Brit. Mycol. Soc. 67: 142. 1976.
≡ *Phoma dennisii* var. *oculo-hominis* (Punith.) Boerema, Gruyter & Noordel., Persoonia 16: 351. 1997.

Specimen examined: **U.S.A.**, Tennessee, Nashville, from a man's corneal ulcer, 23 Apr. 1975, Y.M. Clayton, ex-holotype culture CBS 634.92 = IMI 193307.

For a complete description see Punithalingam (1976) and Boerema *et al.* (1997).

Notes: *Stagonosporopsis oculo-hominis* is a species that thus far has been reported only once in a clinical case in Tennessee, U.S.A., when it was isolated from a man's corneal ulcer (Punithalingam 1976). Due to morphological similarities it has been recombined into a variety of *Ph. dennisii* by Boerema *et al.* (1997), but the genetical data presented here suggest that this entity should be recognised at species level in *Stagonosporopsis*. It is distinguishable from *S. dennisii* by the absence of a diffusible pigment in the agar, and by the absence of a discolouration after application of NaOH to the culture. Further, the septate conidia are significantly smaller than those of *S. dennisii*: 9–16 × 4.5 µm versus 14.5–24 × 4–7 µm, respectively.

Stagonosporopsis rudbeckiae (Fairm.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515667.
Basionym: *Phoma rudbeckiae* Fairm., Proc. Rochester Acad. Sci. 1: 51. 1890.

Specimen examined: **The Netherlands**, from *Rudbeckia bicolor*, 1979, CBS 109180 = PD 79/175.

Stagonosporopsis trachelii (Allesch.) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515668.
Basionym: *Phoma trachelii* Allesch., Fungi Bavaria exs. 4: 360. 1897.
= *Ascochyta bohemica* Kabát & Bubák apud Bubák & Kabát, Hedwigia 44: 361. 1905.
≡ *Stagonosporopsis bohemica* (Kabát & Bubák) Boerema, Gruyter & Noordel., Persoonia 16(3): 361. 1997.

Specimens examined: **Sweden**, Svalöv, from *Campanula isophylla*, 1968, W. Södergren, CBS H-8972, ex-holotype culture 384.68. **The Netherlands**, from a leaf of *Campanula isophylla*, 1977, CBS 379.91 = PD 77/675.

Notes: Although this species has been described in *Stagonosporopsis* before (as *S. bohemica*, Boerema *et al.* 1997), this was based on a later homonym, and thus a recombination based on the oldest epithet is proposed here.

Stagonosporopsis valerianellae (Gindrat, Semecnik & Bolay) Aveskamp, Gruyter & Verkley, **comb. nov.** MycoBank MB515669.
Basionym: *Phoma valerianellae* Gindrat, Semecnik & Bolay, Revue Hort. Suisse Romande 40: 350. 1967.

Specimens examined: **The Netherlands**, Wageningen, from *Valerianella locusta* var. *oleracea*, 1966, G.H. Boerema, **holotype** L 965.300.24, **isotype** CBS H-7631, ex-isotype culture CBS 329.67 = PD 66/302; from *Valerianella locusta*, 1982, CBS 273.92 = PD 76/1019.

Residual species in the Didymellaceae:
The following *Phoma* species are embedded in the *Didymellaceae*, but could not be confidently assigned to one of the groups or new genera in this study due to lack of support for their respective clades. Several of the species listed here belong to this family based on LSU and/or ITS sequence data, but due to missing sequencing data on one of the loci used, these species could not be assigned. These species are provisionally retained under their current holomorph name until further analyses are conducted to place them in the new phylogenetic system.

Didymella macropodii Petr., *Hedwigia* **68**: 219. 1928.
Anamorph: *Phoma nigrificans* (P. Karst.) Boerema, Loer. & Wittern, J. Phytopathol. 115(3): 270. 1986.
Basionym: *Sphaeronaema nigrificans* P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 16: 17. 1888. (as "*Sphaeronema*").

Specimens examined: **Germany**, from *Brassica napus*, 1982, G.H. Boerema, CBS 100190 = PD 82/736. **Poland**, near Gryfice, from *Thlaspi arvense*, 1990, J. Marcinkowska, CBS 100191. **The Netherlands**, from an unidentified crucifer, 1984, G.H. Boerema, PD 84/512.

Didymella rabiei (Kovatsch.) Arx, in Müller & Arx, Beitr. Kryptogamenfl. Schweiz 11(2): 364. (1962).
Basionym: *Mycosphaerella rabiei* Kovatsch., The blight of chick pea: 70. 1936.
Anamorph: *Phoma rabiei* (Pass.) Khune ex Gruyter, Persoonia 18(1): 89. 2002.
Basionym: *Zythia rabiei* Pass., Comment. Soc. Crittog. Ital. 2(3): 437. 1867.

Specimens examined: **India**, from the seeds of *Cicer arietinum*, 1965, S. Sinha, CBS 534.65. **Syria**, from *Cicer arietinum*, 1981, W. Barz, CBS 581.83A.

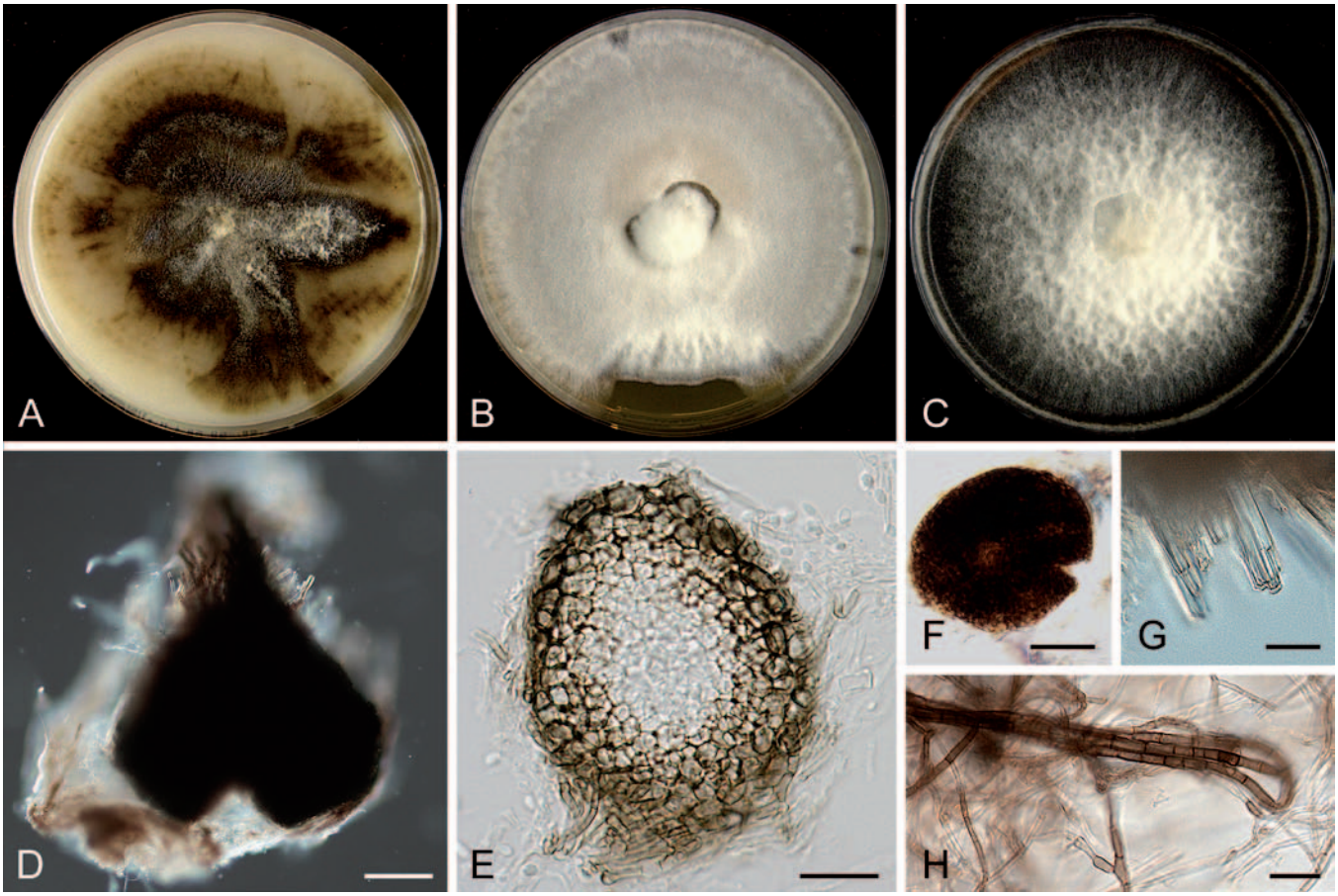


Fig. 13. *Phoma bulgarica* (CBS 357.84). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D. Pycnidia *in vivo*, isolated from manually infected sterilised stems of *Urtica dioica*. E. Pycnidial section. F. Pycnidium. G. Crystals. H. Hyphal strand. Scale bars: D, F = 100 µm; E, H = 50 µm; G = 10 µm.

Notes: The placement of this teleomorph in either the *Didymella* or *Mycosphaerella* has been debated regularly in the past (Müller and Arx 1962, Von Arx 1987, Trapero-Casas & Kaiser 1992, Wilson & Kaiser 1995, De Gruyter 2002, Barve *et al.* 2003). The most recent emendment was by De Gruyter (2002) who judged in favour of *Mycosphaerella rabiei* Kovatsch. ex Gruyter. However, as the genus *Mycosphaerella* is phylogenetically not linked with the *Pleosporales* (Schoch *et al.* 2006, 2009b, Crous *et al*. 2009c), the placement in *Didymella* appears to be more correct.

Didymella adianticola Aa & Boerema, Verslagen Meded. Plziektenk. Dienst Wageningen 159 (Jaarboek 1982): 25. 1983.
Anamorph: *Phoma adianticola* (E. Young) Boerema, *V*erslagen Meded. Plziektenk. Dienst Wageningen 159 (Jaarboek 1982): 25. 1983
Basionym: *Phyllosticta adianticola* E. Young, Mycologia 7: 144. 1915.

Specimens examined: **Costa Rica**, from a leaf of *Polystichum adiantiforme*, 1989, J. de Gruyter, CBS 258.92 = PD 89/1887. **U.S.A.**, Florida, from a leaf of *Polystichum adiantiforme*, 1982, G.H. Boerema, CBS H-16142, culture CBS 187.83 = PD 82/128.

Phoma aliena (Fr.) Aa & Boerema, apud Gruyter, Noordeloos & Boerema, Persoonia 16(4): 486. 1998.
Basionym: *Sphaeria aliena* Fr., Syst. Mycol. 2(2): 502. 1823.

Specimens examined: **The Netherlands**, from a twig of *Berberis* sp., 1982, J. de Gruyter, CBS 379.93 = PD 82/945; near Boskoop, from a twig of *Buxus sempervirens*, 1994, J. de Gruyter, CBS 877.97 = PD 94/1401.

Phoma aubrietiae (Moesz) Boerema, Gewasbescherming 1(4): 66. 1970.
Basionym: *Sclerophomella aubrietiae* Moesz, Balkán-Kutat Tud. Eredm. 3: 144. 1926.

Specimens examined: **The Netherlands**, Bodegraven, from seed of *Aubrietia hybrida* cv. Superbissima, 1965, G.H. Boerema, CBS H-16154, culture CBS 383.67 = PD 65/223; from a stem of *Aubrietia* sp., 1970, G.H. Boerema, CBS 627.97 = PD 70/714.

Phoma bulgarica Aveskamp, Gruyter & Verkley, **sp. nov.** MycoBank MB515671. Fig. 13.

Pycnidia solitaria, subglobosa, elongata vel obpyriformia, glabra, epapillata, brunnea, superficialia vel in agaro immersa, (140–)170–250(–295) µm. Pycnidia fertilia non vidi.

Etymology: Epithet refers to the country of origin, Bulgaria.

Conidiomata pycnidial solitary, subglobose to elongated or obpyriform, glabrous, non-papillate, brown, on the surface and immersed in the agar, measuring (140–)170–250(–295) µm. Pycnidia proved to be sterile. In older cultures pycnidial primordia are formed, which are surrounded by clusters of needle-shaped crystals.

Culture characteristics: Colonies on OA, 45–65 mm diam after 7 d, margin regular. Immersed mycelium hyaline, largely covered by mat of felty to compact whitish grey to lavender grey aerial mycelium; reverse iron-grey, but vinaceous-black where the aerial mycelium is present. Colonies on MEA 40–50 mm diam after 7 d,

margin regular. Immersed mycelium mainly hyaline, incidentally black when clustering into thicker hyphal strands. Aerial mycelium sparse, flat, olivaceous green to white near the colonies margin; reverse greenish olivaceous to olivaceous black. Colonies on CHA 70–85 mm diam after 7 d, or even covering the total agar surface, margin regular. Immersed mycelium as on MEA. Aerial mycelium occurring around the colony centre, white, compact to floccose; reverse leaden black. Application of NaOH did not have any effect.

Specimens examined: **Bulgaria**, Silkossia, Strandga Mountain, from leafs of *Trachystemon orientale*, 20 June 1980, S. Vanev, **holotype designated here** CBS H-20242, ex-holotype culture CBS 357.84; from *Trachystemon orientale*, 1982, CBS 124515 = PD 82/1058.

Notes: Strain PD 82/1058 differed from CBS 357.84 (which is described above) by a significantly different colony pattern on MEA. This strain was characterised by a growth of *ca*. 20 mm diam. after 7 d, with a strongly lobate margin. White to buff aerial mycelium was present in a few irregular zones, and had a compact to floccose structure. Pycnidial primordial are only produced in culture on MEA after addition of an autoclaved piece of *Urtica dioica* (stinging nettle).

Phoma calidophila Aveskamp, Gruyter & Verkley, Mycologia 101: 368. 2009.

Specimens examined: **Egypt**, from desert soil, Feb. 1980, M.I.A. Abdel-Kader, **neotype** CBS H-20168, ex-neotype culture CBS 448.83. Unknown European origin, from *Cucumis sativus*, 1984, G.H. Boerema, PD 84/109.

Phoma chenopodiicola Gruyter, Noordel. & Boerema, Persoonia 15(3): 395. 1993.

Specimens examined: **Peru**, from a stem of *Chenopodium quinoa* cv. Sajana, 1979, CBS 128.93= PD 79/140; from a stem of *Chenopodium quinoa* cv. Sajana, 1979, CBS 129.93 = PD 89/803.

Phoma complanata (Tode) Desm., *Michelia* **2** (7): 337. 1881. *Basionym*: *Sphaeria complanata* Tode, Fungi Mecklenburg. Sel. (Lüneburg) 2: 22. 1791.

Specimens examined: **The Netherlands**, Tilburg, from a stem of *Heracleum sphondylium*, Nov. 1997, H.A. van der Aa, CBS H-16194, culture CBS 100311; from a stem of *Angelica sylvestris*, 1974, G.H. Boerema, CBS 268.92 = PD 75/3.

Phoma crystallifera Gruyter, Noordel. & Boerema, Persoonia 15(3): 393. 1993.

Specimen examined: **Austria**, Kärnten, Wallenberg near Völkermarkt, from *Chamaespartium sagittale*, Apr. 1982, H.A. van der Aa, **holotype** L 992.177-456, ex-holotype culture CBS 193.82.

Phoma dactylidis Aveskamp, Gruyter & Verkley, **sp. nov.** MycoBank MB515671. Fig. 14.

Conidia dimorpha, intra idem pycnidium formata. Conidia typus 1 ellipsoidea vel ovoidea, interdum leniter allantoidea, glabra, hyalina, continua, 4.5–9(–9) × (2–)2.5–3.5 µm, (2–)3–6(–8) guttulis praedita. Conidia typus 2 cylindrica vel ellipsoidea, glabra, hyalina, saepe uniseptata, (9–)9.5–13.5(–14.5) × (2.5–)3.5–4.5 µm, interdum septata et guttulis (2–)4–8(–15) in quoque cellula. Matrix conidiorum salmonea.

Etymology: Named after the associated plant host genus, *Dactylis* sp.

Conidiomata pycnidial, solitary or confluous, produced on the agar surface, (sub-)globose, with some hyphal outgrows, (115–)135–230(–250) × (75–)95–195(–105) µm. *Ostioles* 1–4(–5), papillate. *Pycnidial wall* pseudoparenchymatous, composed of isodiametric cells, 4–8 cell layers, outer 2–4 cell layers pigmented, 10–27 µm thick. *Conidiogenous cells* phialidic, hyaline, simple, smooth, flask-shaped, *ca.* 4.5–6.5 × 3–5 µm. *Conidia* dimorphic, both originating from the same pycnidia. Conidia of type 1: ellipsoidal to ovoid, sometimes somewhat allantoid, thin-walled, smooth, hyaline, aseptate 4.5–9(–9) × (2–)2.5–3.5 µm, with (2–)3–6(–8) guttules. Regularly also large conidia occur: cylindrical to ellipsoidal, thin-walled, smooth, hyaline, often uniseptate (9–)9.5–13.5(–14.5) × (2.5–)3.5–4.5 µm, but sometimes septate and septate somewhat constricted at the septum, with (2–)4–8(–15) guttules per cell. Conidial matrix salmon.

Culture characteristics: Colonies on OA, 40–45 mm diam after 7 d, margin regular. Immersed mycelium hyaline, but some greenish black zones may occur, with tufts of with aerial mycelium. Abundant greenish black pycnidia are scattered over the medium, which are salmon coloured near the colony margin; reverse concolourous. Colonies on MEA 45–50 mm diam after 7 d, margin regular. Immersed mycelium completely covered by a felty greyish white aerial mycelium; reverse grey-olivaceous, becoming brown-olivaceous near the colony margin. Colonies on CHA similar as on MEA, but somewhat faster growing, 55–60 mm diam. after 7 d; reverse completely black. Application of NaOH results in a slight greenish discolouration of the agar, best to be observed on OA medium.

Specimen examined: **U.S.A.**, Oregon, on *Dactylis glomerata*, 1973, **holotype designated here** CBS H-20237, ex-holotype culture CBS 124513 = PD 73/1414.

Notes: *Phoma dactylidis* has thus far only been isolated once from the leaves of *Dactylis glomerata* in Oregon, U.S.A.. Other *Phoma* pathogens of *Dactylis* include *Ph. paspali* and *Ph. pratorum,* which both occur in New Zealand, but are relatively distantly related to *Ph. dactylidis*. Additionally, two related taxa have been found on this host, viz. the novel variety *Boeremia exigua* var. *gilvescens* and *Epicoccum nigrum* (Punithalingam *et al.* 1972). The clustering of this species suggests ecological or morphological similarities with *Ph. rhei* (BPP = 1.00; RBS = 100 %).

Phoma destructiva var. ***destructiva*** Plowr., Gard. Chron. II 16: 621. 1881.

Specimens examined: **Guadeloupe**, from fruit of *Lycopersicon esculentum*, 1987, CBS 133.93 = PD 88/961 = IMI 173142. **Tonga**, Friendly Islands, from decaying fruit of *Lycopersicon esculentum*, 1967, G.F. Laundon, CBS H-16200, culture CBS 378.73 = CECT 2877.

Phoma destructiva var. ***diversispora*** Gruyter & Boerema, apud De Gruyter, Boerema & Van der Aa, Persoonia 18(1): 28. 2002.

Specimen examined: **The Netherlands**, Berkel en Rodenrijs, from a leaf of *Lycopersicon esculentum*, Oct. 1977, G.H. Boerema, **holotype** CBS H-16199, ex-holotype culture CBS 162.78 = PD 77/725.

Phoma eupyrena Sacc., Michelia 1(5): 525. 1879.

Specimens examined: **Germany**, Kiel-Kitzeberg, from wheat field soil, 1966, W. Gams, CBS 527.66 = ATCC 22238; **The Netherlands**, from the tuber of *Solanum tuberosum*, 1991, J. de Gruyter, CBS 374.91 = PD 78/391.

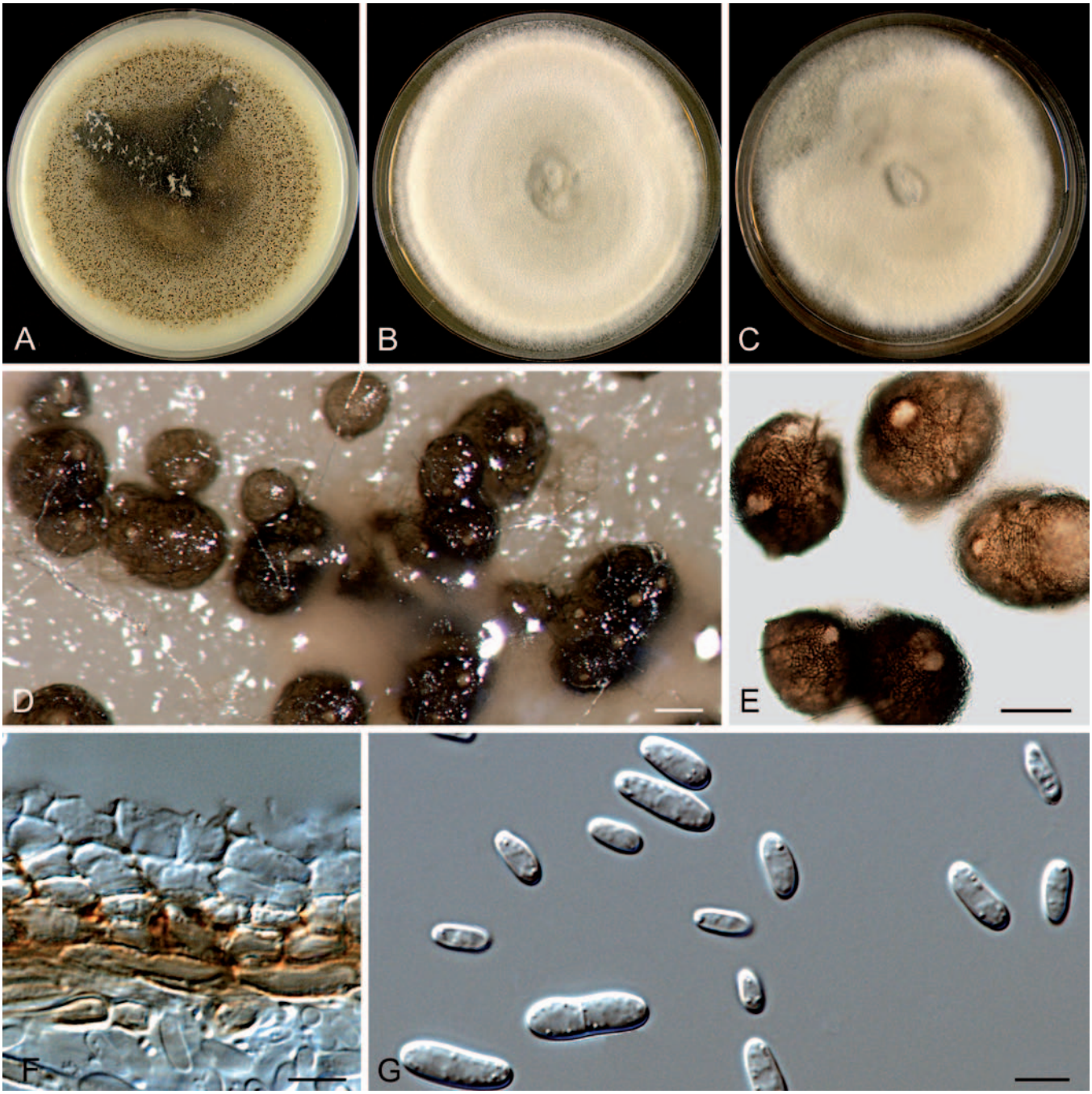


Fig. 14. *Phoma dactylidis* (CBS 124513). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D-E. Pycnidia. F. Section of the pycnidial wall. G. Conidia. Scale bars: D–E = 100 µm; F–G = 5 µm.

Phoma herbarum Westend., Bull. Acad. Roy. Sci. Belgique, Cl. Sci. 19(3): 118. 1852.

Specimens examined: **Belgium**, Herb. Crypt. Belge. Fasc. 20, No. 965, **lectotype**, on stems of *Onobrychis viciifolia*, 1854. Sweden, Sofieheim, from wood pulp, Apr. 1937, E. Rennerfelt, CBS 276.37 = MUCL 9920. **The Netherlands**, Emmeloord, from the stem of *Rosa multiflora* cv. Cathayensis, Apr. 1965, G.H. Boerema, CBS 615.75 = PD 73/665 = IMI 199779; Naaldwijk, from a stem base of *Nerium* sp., 1986, J. de Gruyter, CBS 502.91 = PD 82/276; Oirschot, from a twig of *Thuja* sp., 1987, J. de Gruyter, CBS 503. 91 = PD 87/499. **U.K.**, from paint, Aug. 1936, K.S.G. Cartwright, CBS 109.36. **U.S.A.**, Maryland, Washington area, from the fruit of *Malus sylvestris*, July 1963, M.A. Smith, CBS 567.63 = ATCC 15053 = MUCL 9889.

Phoma herbicola Wehm., Mycologia 38: 319. 1946.

Specimen examined: **U.S.A.**, Montana, Missoula, head of Seeley Lake, from water, CBS H-16581, culture CBS 629.97 = PD 76/1017.

Phoma huancayensis Turkenst., Fitopatologia 13: 68. 1978.

Specimens examined: **Peru**, Dep. Junin, Huancayo, near Vallis Mantaro, from a stem of *Solanum* sp., Feb. 1974, L.J. Turkensteen, **isotype** CBS H-7609, ex-isotype culture CBS 105.80 = PD 75/908; from *Chenopodium quinoa*, 1977, CBS 390.93 = PD 77/1173.

Phoma longicolla Aveskamp, Gruyter & Verkley, **sp. nov.** MycoBank MB515672. Fig. 15.

Conidia late ellipsoidea vel ovoidea, glabra, hyalina, continua, 6–8.5(–10) × (3.5–)4–5(–5.5) µm, (2–)3–9(–12) guttulis polaris praedita. Matrix conidiorum cremeo-alba.

Etymology: Refers to the elongated necks of the ostioles.

Conidiomata pycnidial, initially solitary, globose, glabrous, slightly papillate and olivaceous buff, produced on the agar surface, measuring (45–)50–115(–130) µm diam. Later developing to black

Fig. 15. *Phoma longicolla* (CBS 124514). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D–F. Pycnidia. G. Section of the pycnidial wall. H. Conidia. Scale bars: E–G = 100 µm; H = 50 µm; I–J = 10 µm.

broadly globose to irregular conidiomata with many white hyphal outgrows and with a clear elongated neck around the ostioles, giving it a irregular shape, measuring (170–)200–270(–285) × (115–)125–205(–220) µm. *Ostioles* 1–3(–4), on a long elongated neck (up to 200 µm long). Often these pycnidia merge to an irregular mass of confluent conidiomata. *Pycnidial wall* pseudoparenchymatous, composed of isodiametric cells, 5–7 layers, 17–22 µm thick. *Conidiogenous cells* phialidic, hyaline, simple, smooth, flask-shaped, *ca*. 4–5 × 3–5 µm. *Conidia* broadly ellipsoidal to ovoid, thin-walled, smooth, hyaline, aseptate 6–8.5(–10) × (3.5–)4–5(–5.5) µm, with (2–)3–9(–12) polar guttules. Conidial matrix crème-white.

Culture characteristics: Colonies on OA 50–55 mm diam. after 7 d, margin regular. Immersed mycelium hyaline with abundant pycnidia, in some sectors covered by a low mat of felty to floccose mouse grey aerial mycelium, with tufts of white mycelium near the colonies margin. In the sectors with aerial mycelium, pycnidia are only sparsely present; reverse hyaline, but leaden black and olivaceous grey where the aerial mycelium is present. Colony on MEA 50–55 mm diam. after 7 d, margin regular. Immersed mycelium completely covered by a floccose crème mat of white aerial mycelium; reverse greenish olivaceous to olivaceous-black. Colony on CHA 55–60 mm diam. after 7 d, margin regular. Immersed mycelium brown vinaceous to black. Aerial mycelium is occurring in sectors, felty, pale grey to white; reverse black with incidentally a pale purplish grey zone. Application of NaOH did not have any effect.

Specimens examined: **Spain**, Canary Isles, from *Opuntia* sp., 1980, J. de Gruyter, **holotype designated here** CBS H-20238, ex-holotype culture CBS 124514 = PD 80/1189; Canary Isles, Gran Canaria, from *Opuntia* sp., June 1982, H.A. van der Aa, CBS 347.82.

Notes: This species was isolated twice from *Opuntia* on the Canary Isles. Around the time of the second isolation (CBS 347.82), also *Ph. dimorpha* sp. nov. was isolated from the same location and host substrate. This species is described above. A third species that is found in association with *Opuntia* is *Ph. opuntiae*, which is, however, rather distinct in morphology and phylogeny.

Phoma medicaginis var. ***macrospora*** Boerema, R. Pieters & Hamers, Netherlands J. Pl. Pathol. 99(Suppl. 1): 19. 1993.

Specimens examined: **Canada**, Saskatchewan, Saskatoon, from seed of *Medicago sativa*, 1965, H.W. Mead, CBS 404.65 = IMI 116999. **U.S.A.**, Minnesota, from *Medicago sativa*, Sep. 1953, M.F. Kernkamp, **holotype** CBS H-16487, ex-holotype culture CBS 112.53.

Phoma medicaginis var. ***medicaginis*** Malbr. & Roum. apud Roumeguère, Fungi Selecti Galliaei Exs. 37: 3675. 1886.

Specimens examined: **Czech Republic**, from *Medicago sativa*, CBS 316.90 = CCM F-187. **Italy**, Perugia, from a leaf of *Medicago sativa*, 1963, M. Ribaldi, CBS H-16483, culture CBS 479.63. **The Netherlands**, from a leaf of *Medicago sativa*, 1966, M.M.J. Dorenbosch, CBS 533.66 = ATCC 16929 = PD 66/370. **Turkey**, Ankara, from *Medicago sativa*, 1942, S. Kuntay, CBS 107.42. **U.S.A.**, Minnesota, from *Medicago sativa*, Sep. 1953, M.F. Kernkamp, CBS 110.53; Minnesota, from *Medicago sativa*, Sep. 1953, M.F. Kernkamp, CBS 111.53.

Phoma microchlamydospora Aveskamp & Verkley, Mycologia 101: 374. 2009.

Specimens examined: **U.K.**, from an unknown vegetable plant, 1990, D. Hyall, CBS 491.90; from leaves of *Eucalyptus* sp., 1994, A.M. Ainsworth, **holotype** CBS H-20147, ex-holotype culture CBS 105.95.

Phoma nebulosa (Pers.) Berk., *Outl. Brit. Fung. (London)*: 314. 1860.
Basionym: *Sphaeria nebulosa* Pers., Observ. Mycol. 2: 69. 1799.

Specimens examined: **Austria**, Kaprun, from a stem of *Urtica dioica*, Jan. 1975, G.H. Boerema, CBS H-16510, culture CBS 503.75= ATCC 32163 = DSM 63391 = IMI 194766 = PD 75/4. **The Netherlands**, from a stem of *Mercurialis perennis*, 1983, CBS 117.93 = PD 83/90.

Phoma negriana Thüm., Die Pilze des Weinstockes, Vienna: 185. 1878. Originally described as "*Ph. negrianum*".

Specimens examined: **Germany**, Oberdollendorf am Rhein, from *Vitis vinifera*, July 1969, L. Kiewnik, CBS H-16511, culture CBS 358.71. **The Netherlands**, from *Vitis vinifera*, 1979, PD 79/74; from *Vitis vinifera*, 1979, PD 79/75; from *Vitis vinifera*, 1979, PD 79/76.

Phoma nigripycnidia Boerema, Gruyter & Noordel., Persoonia 16(3): 356. 1997.

Specimen examined: **Russia**, from a leaf of *Vicia cracca*, 1969, M. Ondrej, **holotype** L 992.163.150, ex-holotype culture CBS 116.96 = CCMF 243 = PD 95/7930.

Phoma omnivirens Aveskamp, Verkley & Gruyter, Mycologia 101: 375. 2009.

Specimens examined: **Belgium**, Gembloux, from *Phaseolus vulgaris*, 1968, L. Obando, **holotype** CBS H-20151, ex-holotype culture CBS 341.86. **India**, Japalbur, from an unknown substrate, 1977, D.P. Tiwari, CBS 654.77. **Papua New Guinea**, Varirata National Park, from soil, Aug. 1995, A. Aptroot, CBS 991.95. Varirata National Park. From soil, Aug. 1995, A. Aptroot, CBS 992.95. **Tanzania**, from *Statice* sp., 1990, J. de Gruyter, CBS 123397 = PD 90/1555. **The Netherlands**, from *Chrysanthemum indicum*, 1981, J. de Gruyter, CBS 123396 = PD 81/122.

Phoma putaminum Speg., Atti Soc. Crittog. Ital. 3: 66. 1881.

Specimens examined: **The Netherlands**, from a branch of *Ulmus* sp., 1975, G.H. Boerema, CBS 372.91 = PD 75/960. **Denmark**, from the rhizosphere of *Malus sylvestris*, Mar. 1968, E. Sønderhousen, CBS 130.69 = CECT 20054 = IMI 331916.

Phoma rhei (Ellis & Everh.) Aa & Boerema apud De Gruyter, Boerema & Van der Aa, Persoonia 18 (1): 42. 2002.
Basionym: *Ascochyta rhei* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 1893: 160. 1893.

Specimen examined: **New Zealand**, from a leaf of *Rheum rhaponticum*, CBS 109177 = LEV 15165 = PD 2000/9941.

Phoma selaginellicola Gruyter, Noordel., Aa & Boerema, Persoonia 15(3): 399. 1993.

Specimen examined: **The Netherlands**, from a leaf of *Selaginella* sp., 1977, G.H. Boerema, CBS 122.93 = PD 77/1049.

Phoma versabilis Boerema, Loer. & Hamers, Persoonia 16(2): 154. 1996.

Specimens examined: **Germany**, Westfalen, Oberdresselendorf, from stems of *Cardamine impatiens*, Oct. 1925, A. Ludwig, **holotype** L 995.229.369. **The Netherlands**, Wageningen, from a stem of *Silene* sp., 1982, G.H. Boerema, CBS 876. 97 = PD 82/1008; from *Stellaria media*, 2000, J. de Gruyter, PD 2000/1379.

DISCUSSION

What is *Phoma*?

According to the generic concept which is applied today, species of *Phoma* are relatively simple coelomycetes that are characterised by the *in vitro* production of mainly unicellular, hyaline conidia from monophialidic, doliiform to flask-shaped conidiogenous cells in pycnidial conidiomata (Boerema & Bollen 1975).

Many species that currently are accommodated in sections *Paraphoma*, *Pilosa* and *Plenodomus* are phylogenetically basal to the *Didymellaceae*, in which most other *Phoma* taxa, including the type species are accommodated. These results support the work of Reddy *et al.* (1998), who advocated that the genus *Plenodomus* should be reinstalled as a separate genus. Torres *et al.* (2005b) subsequently made a novel description in this genus, *Pl. morganjonesii*. A paper by De Gruyter *et al.* is in preparation, in which all species of *Phoma* section *Plenodomus* recognised by Boerema *et al.* (1994, 1996) and Boerema & De Gruyter (1999), will be taxonomically revised.

However, in the present study, it has become clear that the phylogenetic boundaries between *Phoma* and several closely related genera that are defined on their conidial characters are ambiguous. Species that produce consistently two-celled hyaline conidia classified therefore traditionally in the genus *Ascochyta* appear to have evolved independently multiple times during evolution together with typical *Phoma* taxa, in several lineages of the pleosporalean tree (Fig. 1). Also other conidial characters, such as the pigmentation of spores, as formed by *Phoma clematidis-rectae* (formerly in *Coniothyrium*) and *Microsphaeropsis olivacea*, appear not to be reliable for the delimitation of the genus *Phoma*. Thus, based on the trees presented in this study, it can be concluded that *Phoma*, as defined by Saccardo (1880, 1884) and emended by Boerema & Bollen (1975) is highly polyphyletic.

The close relation of *Phoma* with *Ascochyta* has often been observed before, as strains of both genera are often highly similar

in morphology (Wollenweber & Hochapfel 1937, Brewer & Boerema 1965, Boerema & Bollen 1975, Boerema 1997), physiology (Noordeloos *et al.* 1993, Faris-Mokaiesh *et al.* 1995), pathogenicity (Mendes-Perreira *et al.* 1999, Davidson *et al.* 2009) and nucleotide sequences (Faris-Mokaiesh *et al.* 1995, Fatehi *et al.* 2003, Schoch *et al.* 2006, Peever *et al.* 2007, Chilvers *et al.* 2009, De Gruyter *et al.* 2009). In the Saccardoan system, both genera were only distinguished by the presence or absence of conidial septa, and by the type of substrate: *Ascochyta* species were considered to be specific leaf-pathogens, whereas *Phoma* was solely associated with stem lesions (Boerema & Bollen 1975).

Brewer & Boerema (1965) contrasted the septation process of the conidia in *Ascochyta pisi* to this process in *Phoma exigua*. These authors suggested that in *Phoma* species euseptation occurs only after secession, whereas in *Ascochyta* the septation of the spores was considered to be an elemental part of conidiogenesis. Later, this was determined to be a genus-specific character (Boerema 1970). Additionally, Boerema and Bollen (1975) stated that both genera are distinct in conidiogenesis. According to these authors, the *Ascochyta* species produce conidia from either an accumulation of annelations, which give the conidigenous cell an annelidic appearance, or from a gradually thickening collar of periclinal annelations. In contrast, *Phoma* species produce true phialides with a collarette. This micromorphological difference of the conidiogenesis can only be observed using electron microscopy, as the appearance of a *Phoma* collarette is highly similar to the periclinal thickening of *Ascochyta* species. This observation is however not consistent with the conidial ontogeny of *Ph. fumosa*, which was observed to be annellidic by Sutton & Sandhu (1969).

The application of these characters for the purpose of generic delimitation was heavily questioned (Punithalingam 1979a), and nowadays these characters are hardly applied in the taxonomy of both genera, simply because the use of electron microscopy is expensive and sectioning of pycnidia is too time consuming. Due to this unclear classification system, and to the fact that not all species produce exclusively septate or aseptate conidia, species had synonyms in both genera (Boerema 1972, Boerema & Dorenbosch 1973, Van der Aa *et al.* 2000, Mel'nik 2000). Even nowadays the status of many species is unclear as *Phoma* and *Ascochyta* synonyms are often used simultaneously. Examples are *Ph. rabiei* and its synonym *A. rabiei* (Singh & Reddy 1993, Singh *et al.* 1997, Barve *et al.* 2003, Chongo *et al.* 2004, Pande *et al.* 2005, Hernandez-Bello *et al.* 2006, Peever *et al.* 2007), and *Ph. gossypiicola* and its synonym, *A. gossypii* (*e.g.* Shen *et al.* 2005). The concept of *Ph. clematidina* has appeared to comprise several taxa belonging in multiple genera, amongst which a *Didymella* with an unnamed *Ascochyta* anamorph (Woudenberg *et al.* 2009).

The results presented in this study further suggest a close relation between *Microsphaeropsis* and *Phoma*. Morphological studies of members of both genera (Jones 1976) reveal that conidiogenesis is similar, although the conidia of *Microsphaeropsis* differ from those of *Phoma* by the dark pigmentation and the presence of a double-layered cell wall. The pigmentation occurs only after conidial secession. Therefore, young pycnidia with colourless pycnidia may be easily confused with a *Phoma* species (Boerema *et al.* 2004).

In general, it can be concluded that *Phoma* should only be regarded as a general concept, as members sharing this morphology are found throughout the *Pleosporales*, although most members are found in the *Didymellaceae*. The type species of *Phoma* is only distantly related to the other members of this genus, but relatively close to *Ascochyta pisi*, the type species of the older name *Ascochyta*. However, based on the results observed in the present study, this genus is poorly elucidated. Therefore, we opt to retain the taxonomy of *Phoma* as is, with the exception of the groups that can be resolved further, such as *Boeremia*, *Epicoccum*, *Peyronellaea* and *Stagonosporopsis*.

Taxonomic revisions

The observations presented in the present paper suggest that LSU and SSU data, which contain approximately 270 informative sites in the alignment, are sufficient to distinguish various major groups in the *Pleosporales*. However, other, more variable loci should also be analysed to determine the phylogenetical basis for the species that are congeneric with the ex-type strain of *Phoma*. These species were found throughout the pleosporalean phylogeny that was reconstructed in the present paper. Molecular studies on the species that are currently accommodated in the section *Plenodomus* and *Pilosa* are in progress (De Gruyter *et al.* in prep.).

The type species of the genus *Phoma*, *Ph. herbarum,* resides in the *Didymellaceae* clade, a result that is in congruence with the observations of De Gruyter *et al.* (2009). However, based on the data generated in the present study, also the type species of *Ascochyta* (*A. pisi*), *Chaetasbolisia* (*C. erysiphoides*), and *Microsphaeropis* (*M. olivaceae*) are located in the same group (Fig. 2). Of those species, *Phoma* carries the oldest name, which was deposited by Fries in 1821, but as *Phoma sensu* Saccardo (1880) was conserved against *Phoma* Fries (McNeill *et al.* 2006), the genus *Ascochyta*, which was erected in 1830, would be the preferred name for the species in this genus. Nevertheless, because of the impact that recombination of *Phoma* in *Ascochyta* would have in phytopathology, we suggest to keep both generic names in use for the unresolved species in the *Didymellaceae*, disregarding the fact that both names are polyphyletic. Both genera can be regarded as polyphyletic concepts, until a proper study of the teleomorph genera related to the *Didymellaceae* has been conducted. Also the younger genera *Chaetasbolisia* and *Microsphaeropsis* should be retained as separate taxonomic entities, until at least all taxa are restudied both morphologically and phylogenetically. However, the clades that are resolved, and that are characterised by shared morphological or physiological characters, or have a shared ecological role, are elevated to generic level here. Consequences of this approach are the reinstatement of the genus *Peyronellaea* Goid., expansion of the formerly monotypic genus *Epicoccum* Link, emendment of the concept of *Stagonosporopsis* Died. and the erection of the novel genus *Boeremia*.

Teleomorph relations

In *Phoma* several teleomorphs have been recognised, but for the majority of *Phoma* species the sexual structures have yet to be discovered, as the induction of these structures requires special conditions; or simply because the species has lost its ability to propagate sexually. Boerema *et al.* (2004) only recognised *ca.* 40 species that produce teleomorphs.

The finding of multiple teleomorphs with phenotypically indistinguishable associated anamorphs is not uncommon in mycology, yet unwanted, and should be resolved in due course as more data become available. For example, such a situation also applies to major genera such as *Aspergillus* (Pitt & Samson 2007), *Botryosphaeria* (Crous *et al.* 2006), *Geotrichum* (De Hoog & Smith 2004), *Mycosphaerella* (Crous *et al.* 2009a, b) and *Penicillium* (Pitt 1979).

Boerema *et al.* (2004) linked *Phoma* to four teleomorph genera: *Didymella*, *Leptosphaeria*, *Mycosphaerella* and *Pleospora*. In recent studies it was shown that the association of *Phoma* with *Mycosphaerella* was untenable, because the involved teleomorphs were apparently morphologically similar but in fact *Didymella*. The genus *Mycosphaerella* is phylogenetically distinct and not even associated with the *Pleosporales* (Schoch *et al.* 2006, 2009a, b, Crous *et al*. 2009a, b), whereas their associated *Phoma* anamorphs proved to be genetically similar to *Didymella* (De Gruyter *et al.* 2009). As a consequence, the pawpaw (*Carica papaya*) pathogen *M. caricae* has been recombined into *D. caricae* in the present study.

Also the *Didymellaceae* clade is not yet completely resolved. Next to *Didymella*, also *Leptosphaerulina* and *Macroventuria* are accommodated in the *Didymellaceae*. *Macroventuria* resembles *Venturia* (Van der Aa *et al.* 1971); the ascospore morphology being highly comparable to that of *Didymella*. In contrast, *Leptosphaerulina* is distinct in morphology, producing ascospores with longitudinal and transverse septa, more resembling the ascospores of *Pleospora* and *Cucurbitaria* (Von Arx 1981). *Didymella* is a poorly studied genus that is in need of a comprehensive revision, as it plays such a crucial role in the delimitation of phytopathologically important genera. When studied more intensively, this genus may very well be split up into multiple genera that have a proper morphological basis.

Sexual states have thus far only been reported for a limited number of *Phoma* species. It seems unlikely that the ability to produce sexual reproductive structures is lost in so many species, whilst other, closely related species, or even species that emerge from these “asexual” species, do have a teleomorph state. It may be assumed that the sexual state of these species is cryptic, and can only be induced under the right conditions. These teleomorph structures, that probably much resemble the sexual structures formed by the genus *Didymella*, are probably the missing links that are required for further taxonomical delineation of the species in the *Didymellaceae*.

Can the sections be maintained?

The present study was initiated chiefly to clarify the status of *Phoma* and to judge the validity of the sections introduced by Boerema (1997). Aveskamp *et al.* (2008) already illustrated the ambiguity of some sections, as multiple characters that are regarded to be section-specific may be present in a single species. For example, *Ph. zeae-maydis* was regarded as the type species of the section *Macrospora*, due to the presence of its relatively large aseptate spores (De Gruyter 2002). However, this species also produces multicellular chlamydospores, resembling the chlamydospores formed in species that are accommodated in the section *Peyronellaea*. The recombination of this species into *Pey. zeae-maydis* in the present study, which is based on DNA phylogeny, indicates that the spore size is not an informative character at above-species level.

Another example of the ambiguity of the Boeremaean section is *Ph. destructiva*. Infraspecific taxa of this species are accommodated in two sections: *Ph. destructiva* var. *diversispora* was accommodated in section *Phyllostictoides*, wheras the type variety was linked to section *Phoma* due to the absence of septate conidia. Boerema *et al.* (2004) acknowledged this ambiguity problem and were forced to key out several species in multiple sectional dichotomous keys. In the previous study of De Gruyter *et al*. (2009) this ambiguity could not be illustrated as only sectional representatives were included. Here it is illustrated that, although some sections can be partially maintained, most of the sections are not supported from an evolutionary perspective.

Section *Heterospora*

The majority of the species that were ascribed to *Phoma* section *Heterospora* is recovered in Group R, from which the species are all recombined into the genus *Stagonosporopsis* in the present paper. The type species of section *Heterospora* however, *Ph. heteromorphospora*, is recovered basal to the *Didymellaceae* together with *Ph. dimorphospora*. Also *Ph. samarorum* is not retrieved in the main *Phoma* clade, but is associated with the *Phaeosphaeriaceae*.

Also within the *Didymellaceae*, the *Heterospora* section appears to be polyphyletic as *Ph. aquilegiicola*, *Ph. glaucii* and *Ph. clematidina* are distantly related to most other *Heterospora* species and form a distinct clade together with another *Clematidina* pathogen, *Ph. clematidis-rectae*, a species that has been regularly confused with the *Phoma clematidina* complex (Woudenberg *et al.* 2009). The species in this clade can be distinguished from the main body of the *Heterospora* species as they lack the production of large *Stagonospora*-type conidia in culture, although smaller, septate conidia may occur.

Section *Macrospora*

The five large-spored species of the section *Macrospora* included in this study are found scattered throughout the *Didymellaceae*, indicating that spore size is not a good taxonomic criterion for delimiting taxa above species level. *Phoma zeae-maydis* is genetically similar to most *Peyronellaea* species. This association is supported by the finding of dictyochlamydospores in most species in this clade (Aveskamp *et al.* 2009a).

Section *Paraphoma*

Also *Phoma* section *Paraphoma* (Van der Aa *et al.* 1990) appears to be polyphyletic. The section comprises 12 taxa that produce pycnidial conidiomata with setae (De Gruyter & Boerema 2002). Members of this section are found in clades 5, 6, and 8 of Fig. 1. *Phoma gardenia* is the only setae-producing species known in the *Didymellaceae*. Because of its ability to produce dictyochlamydospores, and based on the DNA phylogeny presented in Fig. 2, it is recombined into the genus *Peyronellaea* here.

The type species for the former section *Paraphoma* is *Ph. radicina*, which is accommodated in the *Phaeosphaeriaceae* group (clade 6). Remarkably, no other species that were ascribed to the section *Paraphoma* are found in the same family. Instead, *Ph. chrysanthemicola* (formerly ascribed to the section *Peyronellaea*) is found in close association with *Ph. radicina*. Both species are recognised as soil fungi and have a wide distribution with records from Europe, North-America and Asia (Boerema *et al.* 2004). The close association between *Ph. samarorum*, *Ph. chrysanthemicola* and *Ph. radicina* has been recorded before in a phylogenetical reconstruction of the section *Peyronellaea* in a study of Aveskamp *et al.* 2009a. The resolution of the clade in that study was, however, higher as the complete ITS regions 1 and 2 were applied in genetic analyses (Aveskamp *et al.* 2009a). Further linkage of the morphological and ecological characters to the phylogeny will be one of the main challenges for taxonomists working on the species in this group.

A third *Paraphoma* species, *Ph. terricola*, is recovered in clade 5 of Fig. 1, which resembles the *Cucurbitaceae*. This family

also hosts the setae-lacking species *Ph. pratorum*, which was classified in section *Phoma*. Several other coelomycete fungi are accommodated here as well, including *Phialophorophoma litoralis*, *Pleurophoma cava*, a sterile strain that once has been identified as *Coniothyrium* sp. and various *Pyrenochaeta* species. The close morphological relation between the genera *Pyrenochaeta*, *Pleurophoma* and *Phoma* section *Paraphoma* was already noted by Boerema *et al.* (1996) and Grondona *et al.* (1997). Like *Phialophorophoma litoralis* and *Pleurophoma cava*, *Pyrenochaeta* is characterised by the formation of elongated, filiform, multiseptate conidiophores, a character that is however not found in the various *Phoma* species embedded in this clade (De Gruyter *et al.* 2009). A further delineation of the species associated with the genera *Pyrenochaeta* and *Pleurophoma* and the *Phoma* section *Paraphoma* will be provided in a follow-up paper by De Gruyter *et al.* (2010).

Section *Peyronellaea*

The chlamydospore-producing species have been treated before by Aveskamp *et al.* (2009a), who revealed that also *Phoma* section *Peyronellaea* is artificial from an evolutionary point of view. Most species, including the type *Ph. glomerata*, cluster in group K of Fig. 2, along with many other (uni- and multicellular) chlamydospore producing species. To be in accordance with the phylogenetic results, this cluster is elevated to generic level, which is named after the section *Peyronellaea.* A second group of species belonging to this section is recovered in clade L, which groups species that produce botryoid or epicoccoid dictyochlamydospores, including *Epicoccum nigrum*. Two species, *Ph. pimprina* and *Ph. sorghina* are recombined into *Epicoccum* here. Species that produce pseudoscleroid chlamydospores, such as *Ph. violicicola* and *Ph. chrysanthemicola* were found to cluster outside the *Didymellaceae*.

Section *Phoma*

Species ascribed to *Phoma* section *Phoma* are retrieved in practically all clades of the trees produced in the present study. This supports the general idea that this section has been used as a “waste-bin” for phomoid taxa that could not be placed in other sections or genera due to the lack or presence of typical sectional characters.

The type species of this section, and also of the genus as a whole, is *Ph. herbarum* (Boerema 1964). The reference strains of this species are accommodated amongst the basal polytomous species of the *Didymellaceae*. This suggests that it has branched off from most other members of this family in an early phase of the development of the *Didymellaceae* and probably evolved further without recombining with other taxa.

Although the description of *Ph. crinicola* is highly similar to that of other species in the *B. exigua* clade presented in Fig. 2, it has never been recognised as such due to the absence of septate conidia. Nevertheless, the remaining characters do not contradict with the description given for *Ph. exigua* (Van der Aa *et al.* 2000). The pycnidia of *Ph. crinicola* usually carry a single ostiole, but pycnidia are regularly observed lacking an apparent ostiole. This may correspond with the ostiolar openings of many species found within the *exigua* clade, which are often lined or filled with papillate, hyaline cells.

Similar findings are *Ph. aurea* and *Ph. nigricans* in clade K, which is mainly filled with chlamydospore-forming species that were previously associated with the section *Peyronellaea*. Both species were originally described from New Zealand (Johnston & Boerema 1981, De Gruyter *et al.* 1993), but may be commonly present on the whole Australasian continent (De Gruyter *et al.* 1993, 1998). Two other species, belonging to section *Phoma*, but found in this clade are *Ph. anserina* and *Ph. eucalyptica*. Both species produce swollen cells in older cultures (De Gruyter & Noordeloos 1992), which may be an initial phase of chlamydospore formation.

Fifteen species are phylogenetically only distantly related to the *Didymellaceae*, and should therefore be excluded from the genus. These species include the current *Ph. apiicola*, *Ph. capitulum*, *Ph. fallens*, *Ph. fimeti*, *Ph. flavescens*, *Ph. flavigena*, *Ph. glaucispora*, *Ph. haematocycla*, *Ph. lini*, *Ph. minutispora*, *Ph. multipora*, *Ph. opuntiae*, *Ph. pratorum*, *Ph. valerianae*, and *Ph. vasinfecta*. The problem in recombining these species is, however, the absence of characters that could link these taxa to a specific genus. No teleomorphs are known in this group.

Section *Phyllostictoides*

All taxa belonging to *Phoma* section *Phyllostictoides* are retrieved in the *Didymellaceae* clade of Fig. 1 (Clade 8). This is remarkable as this large section has been regarded, just like section *Phoma*, to be a repository for all species that could not be accommodated elsewhere. Nevertheless, within the *Didymellaceae* this section falls apart as species occur in many distinct clades.

The major body of the *Phyllostictoides* species is retrieved in group N, in which all *Ph. exigua*-related species and varieties are found (Aveskamp *et al.* 2009b), as well as *Ph. crinicola* and *Ph. hedericola*, which were associated with *Phoma* section *Phoma*. A second group in which many *Phyllostictoides* taxa cluster is clade R. This clade comprises many species of the former section *Heterospora,* and several species that were excluded from this section and transferred to *Phyllostictoides* by Boerema *et al.* (1997), such as *Ph. cucurbitacearum* and *Ph. ligulicola*.

Section *Pilosa*

Only one of both members of the section Pilosa was included in the present study. The type of this section, *Ph. betae*, produces a teleomorph in *Pleospora*, a genus that is typified by *Pl. herbarum*. Both species are related and are found in the *Pleosporaceae* and *Leptosphaeriaceae* clade, although the genetic distance between these species is significant. This finding illustrates the difficulties that are experienced when delineating the *Pleosporaceae* (Dong *et al.* 1998).

Section *Plenodomus*

Thus far the only section created by Boerema that still may be monophyletic is the section *Plenodomus*, of which all the members are found in the *Leptosphaeriaceae*. However, some species associated with other sections, such as *Ph. apiicola*, *Ph. valerianae*, *Ph. vasinfecta* (section *Phoma)* and *Ph. violicola* (section *Peyronellaea*) are also linked to this clade and are found to be closely related to the *Plenodomus* species. The section *Plenodomus* is associated with a *Leptosphaeria* teleomorph, but for the aberrant *Phoma* states found in this clade, no teleomorphs are known. Boerema *et al.* (2004) mentioned five *Leptosphaeria* species that produce *Phoma* anamorphs, but that do not fit within the *Plenodomus* concept. These species, including *L. sacchari*, *L. haematitis*, *L. libanotis*, *L. purpurea* and *L. weimeri* were however not to our disposal, and were therefore not studied. Apparently the genus *Leptosphaeria* produces multiple anamorphs.

Most taxonomic studies on the *Leptosphaeriaceae* reveal a monophyletic group, although in these studies, only a limited

number of species, belonging to either *Leptosphaeria* or *Phoma* section *Plenodomus*, have been included (Morales *et al.* 1995, Reddy *et al.* 1998, Torres *et al.* 2005b). Other studies indicate that this genus is paraphyletic (Dong *et al.* 1998, Câmara *et al.* 2002). Due to the inclusion of only two *Leptosphaeria* species in the present study, it cannot be unambiguously stated whether this section is mono- or paraphyletic.

Both species included, *L. maculans* and *L. biglobosa*, are assumed to represent a heterogeneous assemblage of cryptic taxa (Howlett *et al*. 2001, Mendes-Pereira *et al*. 2003, Barrins *et al*. 2004, Voigt *et al*. 2005). Although many recombinations have been made in the past, this has obscured a proper understanding of *Phoma* section *Plenodomus* and *Leptosphaeria* (Boerema *et al.* 1996). Due to the complexity of this group, we will attempt to resolve its phylogeny in a separate paper (De Gruyter *et al.* prep.).

Section *Sclerophomella*

The thickened, sclerotisised pycnidial wall, and the formation of poroid pycnidial openings instead of an ostiole, are the main characters of *Phoma* section *Sclerophomella*. These characters appear not to reflect the evolutionary history of the genus. Only in group O, a cluster of species is retrieved that is known for their ostiole absence, although not in all species the thickened pycnidial wall is observed. Most other species belonging to section *Sclerophomella* appear to be unrelated as they have emerged from non-*Sclerophomella* multiple times during evolution. Therefore these species are found scattered throughout the phylogeny of the Pleosporales. The type species of this section is *Ph. complanata*, which is found in the basal polytomy of the *Didymellaceae*.

Many of the morphological characters that were used by Boerema *et al.* (1997) to create an infrageneric subdivision of *Phoma*, appear not to be evolutionary informative when compared to sequence data. The main characters that were applied to distinguish sections, like the thickness of the pycnidial walls, chlamydospore structure and presence of *Stagonosporopsis* synanamorphs are only of limited value. Several characters, such as percentage of septated spores may be genetically driven, but are certainly also highly influenced by the growth media and culturing conditions (Rai 2000). This has led to much confusion surrounding the taxonomic placement of many species in either *Ascochyta* or *Phoma*, such as *A. rabiei* (*e.g.* Barve *et al.* 2003, Pande *et al.* 2005, Peever *et al.* 2007) vs. *Ph. rabiei* (*e.g.* Singh & Reddy 1993, Singh *et al.* 1997, De Gruyter 2002).

In short, the Boeremaean sectional subdivision is hardly of any evolutionary relevance, suggesting that future classification of taxonomic novelties into these sections should be avoided. Nevertheless, the morphological identification system that was developed based on this subdivision (Boerema *et al.* 2004) is still applicable, as this system can be still aid in morphological species recognition.

DNA Barcoding

A further aim of this study was the development of species-specific DNA barcodes for species of *Phoma*. The preferred DNA barcode region for *Fungi* is ITS (Druzhininia *et al.* 2005, Summerbell *et al*. 2005, Seifert 2008, 2009). Cytochrome Oxidase I (COI) was for a long time considered to be a good candidate gene for barcoding fungi (Seifert *et al.* 2007, Nguyen & Seifert 2008), although some recent studies indicate the variation between copies within a single strain (Geiser *et al.* 2007, Gilmore *et al.* 2009). Also Aveskamp *et al.* (2009b) found that the COI locus was not robust, and thus far, COI barcodes have only been applied in an oligonucleotide array identification system for *Penicillium* spp. (Chen *et al.* 2009). The value of ITS as primary barcode region is, however, not sufficient to delineate all taxa. Especially amongst the species clustered in clade N, which represents the species that are associated to the *Ph. exigua* species complex, ITS is not sufficient to distinguish the various species. This finding is in congruence with results obtained in previous studies, in which the ITS region has been applied in an attempt to distinguish the species within the *Ph. exigua* complex but without success (MacDonald *et al.* 2000, Abeln *et al.* 2002, Cullen *et al.* 2006). Nevertheless, the other taxa included in this study have been found on long-branched clades, which are mainly due to the variation in TUB and ITS sequences. Another locus that is considered to be helpful for developing DNA barcodes, and which can distinguish many more taxa in the *Ph. exigua* complex is the Actin gene (Aveskamp *et al.* 2009b), which is sequenced with a primer combination developed by Carbone & Kohn (1999). This locus has, however, not been included in the present study, as infraspecific genetic variation, even within the *Didymellaceae*, was too high to align the obtained sequences. Also Calmodulin and Translation Elongation Factor 1-α loci have been tested, but none of the primers combinations used (Carbone & Kohn 1999) could guarantee successful amplification of all strains.

Observations and results presented here represent only a preliminary step towards resolving questions related to the taxonomy of the genus *Phoma*. With the numerous species awaiting to be discovered, the taxonomic system of this complex will probably be changed again as more clades are added. Nevertheless, it is hoped that the present study on *Phoma* systematics, together with the "*Phoma Identification Manual*", will provide a solid foundation on which the *Didymellaceae* in general, and the *Phoma* species in particular, can be further delineated.

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