

Redisposition of phoma-like anamorphs in *Pleosporales*

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Abstract: The anamorphic genus *Phoma* was subdivided into nine sections based on morphological characters, and included teleomorphs in *Didymella*, *Leptosphaeria*, *Pleospora* and *Mycosphaerella*, suggesting the polyphyly of the genus. Recent molecular, phylogenetic studies led to the conclusion that *Phoma* should be restricted to *Didymellaceae*. The present study focuses on the taxonomy of excluded *Phoma* species, currently classified in *Phoma* sections *Plenodomus*, *Heterospora* and *Pilosa*. Species of *Leptosphaeria* and *Phoma* section *Plenodomus* are reclassified in *Plenodomus*, *Subplenodomus* gen. nov., *Leptosphaeria* and *Paraleptosphaeria* gen. nov., based on the phylogeny determined by analysis of sequence data of the large subunit 28S nrDNA (LSU) and Internal Transcribed Spacer regions 1 & 2 and 5.8S nrDNA (ITS). *Phoma heteromorphospora*, type species of *Phoma* section *Heterospora*, and its allied species *Phoma dimorphospora*, are transferred to the genus *Heterospora* stat. nov. The *Phoma acuta* complex (teleomorph *Leptosphaeria doliolum*), is revised based on a multilocus sequence analysis of the LSU, ITS, small subunit 18S nrDNA (SSU), β -tubulin (TUB), and chitin synthase 1 (CHS-1) regions. Species of *Phoma* section *Pilosa* and allied *Ascochyta* species were determined to belong to *Pleosporaceae* based on analysis of actin (ACT) sequence data. Anamorphs that are similar morphologically to *Phoma* and described in *Ascochyta*, *Asteromella*, *Coniothyrium*, *Plectophomella*, *Pleurophoma* and *Pyrenochaeta* are included in this study. *Phoma*-like species, which grouped outside the *Pleosporineae* based on a LSU sequence analysis, are transferred to the genera *Aposphaeria*, *Paraconiothyrium* and *Westerdykella*. The genera *Medicopsis* gen. nov. and *Nigrograna* gen. nov. are introduced to accommodate the medically important species formerly known as *Pyrenochaeta romeroi* and *Pyrenochaeta mackinnonii*, respectively.

Key words: coelomycetes, *Coniothyriaceae*, *Cucurbitariaceae*, *Leptosphaeriaceae*, *Melanommataceae*, molecular phylogeny, *Montagnulaceae*, *Phaeosphaeriaceae*, *Pleosporaceae*, *Sporormiaceae*, taxonomy, *Trematosphaeriaceae*.

Taxonomic novelties: New genera: *Medicopsis* Gruyter, Verkley & Crous, *Nigrograna* Gruyter, Verkley & Crous, *Paraleptosphaeria* Gruyter, Verkley & Crous, *Subplenodomus* Gruyter, Verkley & Crous. **New species:** *Aposphaeria corallinolutea* Gruyter, Aveskamp & Verkley, *Paraconiothyrium maculiculis* Verkley & Gruyter. **New combinations:** *Coniothyrium carteri* (Gruyter & Boerema) Verkley & Gruyter, *C. dolichi* (Mohanty) Verkley & Gruyter, *C. glycinis* (R.B. Stewart) Verkley & Gruyter, *C. multiporum* (V.H. Pawar, P.N. Mathur & Thirum.) Verkley & Gruyter, *C. telephii* (Allesch.) Verkley & Gruyter, *Heterospora* (Boerema, Gruyter & Noordel.) Gruyter, Verkley & Crous, *H. chenopodii* (Westend.) Gruyter, Aveskamp & Verkley, *H. dimorphospora* (Speg.) Gruyter, Aveskamp & Verkley, *Leptosphaeria errabunda* (Desm.) Gruyter, Aveskamp & Verkley, *L. etheridgei* (L.J. Hutchison & Y. Hirats.) Gruyter, Aveskamp & Verkley, *L. macrocapsa* (Trail) Gruyter, Aveskamp & Verkley, *L. pedicularis* (Fuckel) Gruyter, Aveskamp & Verkley, *L. rubefaciens* (Togliani) Gruyter, Aveskamp & Verkley, *L. sclerotioides* (Sacc.) Gruyter, Aveskamp & Verkley, *L. sydowii* (Boerema, Kesteren & Loer.) Gruyter, Aveskamp & Verkley, *L. veronicae* (Hollós) Gruyter, Aveskamp & Verkley, *Medicopsis romeroi* (Borelli) Gruyter, Verkley & Crous, *Nigrograna mackinnonii* (Borelli) Gruyter, Verkley & Crous, *Paraconiothyrium flavescens* (Gruyter, Noordel. & Boerema) Verkley & Gruyter, *Paracon. fuckelii* (Sacc.) Verkley & Gruyter, *Paracon. fusco-maculans* (Sacc.) Verkley & Gruyter, *Paracon. lini* (Pass.) Verkley & Gruyter, *Paracon. tiliae* (F. Rudolphi) Verkley & Gruyter, *Paraleptosphaeria dryadis* (Johanson) Gruyter, Aveskamp & Verkley, *Paralept. macrospora* (Thüm.) Gruyter, Aveskamp & Verkley, *Paralept. nitschkei* (Rehm ex G. Winter) Gruyter, Aveskamp & Verkley, *Paralept. orobanches* (Schweinitz : Fr.) Gruyter, Aveskamp & Verkley, *Paralept. praetermissa* (P. Karst.) Gruyter, Aveskamp & Verkley, *Plenodomus agnitus* (Desm.) Gruyter, Aveskamp & Verkley, *Plen. biglobosus* (Shoemaker & H. Brun) Gruyter, Aveskamp & Verkley, *Plen. chrysanthemi* (Zachos, Constantinou & Panag.) Gruyter, Aveskamp & Verkley, *Plen. collinsoniae* (Dearn. & House) Gruyter, Aveskamp & Verkley, *Plen. confertus* (Niessl ex Sacc.) Gruyter, Aveskamp & Verkley, *Plen. congestus* (M.T. Lucas) Gruyter, Aveskamp & Verkley, *Plen. enteroleucus* (Sacc.) Gruyter, Aveskamp & Verkley, *Plen. fallaciosus* (Berl.) Gruyter, Aveskamp & Verkley, *Plen. hendersoniae* (Fuckel) Gruyter, Aveskamp & Verkley, *Plen. inflouescens* (Boerema & Loer.) Gruyter, Aveskamp & Verkley, *Plen. libanotidis* (Fuckel) Gruyter, Aveskamp & Verkley, *Plen. lindquistii* (Frezzi) Gruyter, Aveskamp & Verkley, *Plen. lupini* (Ellis & Everh.) Gruyter, Aveskamp & Verkley, *Plen. pimpinellae* (Lowen & Sivan.) Gruyter, Aveskamp & Verkley, *Plen. tracheiphilus* (Petri) Gruyter, Aveskamp & Verkley, *Plen. visci* (Moesz) Gruyter, Aveskamp & Verkley, *Pleospora fallens* (Sacc.) Gruyter & Verkley, *Pleo. flavigena* (Constantinou & Aa) Gruyter & Verkley, *Pleo. incompta* (Sacc. & Martelli) Gruyter & Verkley, *Pyrenochaetopsis pratorum* (P.R. Johnst. & Boerema) Gruyter, Aveskamp & Verkley, *Subplenodomus apiicola* (Kleb.) Gruyter, Aveskamp & Verkley, *Subplen. drobnjakensis* (Bubák) Gruyter, Aveskamp & Verkley, *Subplen. valerianae* (Henn.) Gruyter, Aveskamp & Verkley, *Subplen. violicola* (P. Syd.) Gruyter, Aveskamp & Verkley, *Westerdykella capitulum* (V.H. Pawar, P.N. Mathur & Thirum.) de Gruyter, Aveskamp & Verkley, *W. minutispora* (P.N. Mathur ex Gruyter & Noordel.) Gruyter, Aveskamp & Verkley. **New names:** *Pleospora angustis* Gruyter & Verkley, *Pleospora halimiones* Gruyter & Verkley.

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INTRODUCTION

The anamorphic genus *Phoma* includes many important plant pathogens. The taxonomy of *Phoma* has been studied intensively in the Netherlands for more than 40 years resulting in the development of a generic concept as an outline for identification of *Phoma* species (Boerema 1997). In this concept species of the genus *Phoma* are classified based on their morphological

characters into nine sections: *Phoma*, *Heterospora*, *Macrospora*, *Paraphoma*, *Peyronellaea*, *Phyllostictoides*, *Pilosa*, *Plenodomus* and *Sclerophomella* (Boerema 1997). The species placed in each of the sections were systematically described culminating in the publication of the “*Phoma* Identification Manual” (Boerema *et al.* 2004), which contained the descriptions of 223 specific and infra-specific taxa of *Phoma*, and more than 1000 synonyms in other coelomycetous genera. The classification of the *Phoma* species in

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sections based on morphology is artificial (Boerema *et al.* 2004), and several species can be classified in more than one section as they reveal multiple “section-specific” characters.

A large, well-studied *Phoma* culture collection that includes more than 1100 strains of *Phoma* resulted from the extensive morphological studies conducted on *Phoma* in The Netherlands. That culture collection is the basis of an intensive molecular phylogenetic study of the genus *Phoma*, which commenced in 2006. Molecular studies of species of *Phoma* prior to the onset of this project concentrated on the development of molecular detection methods for specific, important plant pathogenic *Phoma* species, such as *Ph. macdonaldii*, *Ph. tracheiphila*, *Stagonosporopsis cucurbitacearum* (as *Ph. cucurbitacearum*) and *Boeremia foveata* (as *Ph. foveata*) (Aveskamp *et al.* 2008). The phylogeny of the type species of the nine *Phoma* sections and morphologically similar coelomycetes was determined utilising the sequence data of the large subunit 28S nrDNA (LSU) and the small subunit 18S nrDNA (SSU) regions (de Gruyter *et al.* 2009). Results of that study demonstrated that the type species of the nine *Phoma* sections all grouped in *Pleosporales*. The type species of five *Phoma* sections, *Phoma*, *Phyllostictoides*, *Sclerophomella*, *Macrospora* and *Peyronellaea* and similar genera, grouped in a distinct clade in *Didymellaceae*. The type species of the remaining four *Phoma* sections, *Heterospora*, *Paraphoma*, *Pilosa* and *Plenodomus*, clustered in several clades outside *Didymellaceae* based on the LSU and SSU sequence analysis leading to the conclusion that these species should be excluded from *Phoma* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010).

The molecular phylogeny of the *Phoma* species in *Didymellaceae* was determined in a subsequent study (Aveskamp *et al.* 2010) and, as the phylogenetic placement of the sectional type species already suggested, included species mainly from sections *Phoma*, *Phyllostictoides*, *Sclerophomella*, *Macrospora* and *Peyronellaea*. The molecular phylogeny of 11 *Phoma* species classified in *Phoma* section *Paraphoma* based on their setose pycnidia was investigated using LSU and SSU sequences (de Gruyter *et al.* 2010) and this section was highly polyphyletic, with species clustering mainly in *Phaeosphaeriaceae* and *Cucurbitariaceae*.

The purpose of the present study was to clarify the molecular phylogeny of the *Phoma* species currently classified in sections *Plenodomus* and *Pilosa*, along with *Phoma* species which were determined to be distantly related to the generic type species *Ph. herbarum* in previous molecular studies. Additionally, phoma-like isolates of coelomycetes currently classified in *Ascochyta* and *Coniothyrium* and clustering outside the *Didymellaceae* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010) are included in this study along with a number of phoma-like species that do not belong to *Pleosporineae*.

In the present study, the initial focus was to determine the molecular phylogeny of *Phoma betae* (teleom. *Pleospora betae*) and *Ph. lingam* (teleom. *Leptosphaeria maculans*), type species of the *Phoma* sections *Pilosa* and *Plenodomus*, respectively, at the generic rank based on the sequence data of the LSU and the SSU regions. In a subsequent study, the sequence data of both the LSU and the ITS regions were used for a revised classification of the *Phoma* species currently classified in *Phoma* section *Plenodomus*. Only a limited number of the species currently classified in this section have a confirmed *Leptosphaeria* teleomorph.

The *Phoma acuta* species complex was subject of a more detailed study. The teleomorph of *Ph. acuta* is *Leptosphaeria doliolum*, type species of the genus *Leptosphaeria*. A multilocus analysis of sequence data of the SSU, LSU, ITS, β -tubulin (TUB),

and chitin synthase 1 (CHS-1) regions was performed. The phylogeny of *Phoma* species of section *Pilosa*, with a *Pleospora* teleomorph (*Pleosporaceae*) was studied utilising actin (ACT) sequence data.

Phoma-like species currently attributed to the genera *Aposphaeria*, *Asteromella*, *Coniothyrium*, *Phoma*, *Plenodomus*, *Pleurophoma* and *Pyrenochaeta*, which could not be classified in the *Pleosporineae* based on their molecular phylogeny, were included in a LSU sequence analysis. All *Phoma* taxa that are unrelated to *Didymellaceae* and treated in this paper are redispersed to other genera.

A further aim of this study was to establish a single nomenclature for well-resolved anamorph–teleomorph relationships as discussed by Hawksworth *et al.* (2011). In cases where one anamorph–teleomorph generic relation is involved in a monophyletic lineage, one generic name was chosen based on priority and the other named teleomorph or anamorph state is treated as a synonym. Similar approaches towards single nomenclature have been employed in *Botryosphaeriales* (Crous *et al.* 2006, 2009a, b, Phillips *et al.* 2008), *Pleosporales* (Aveskamp *et al.* 2010), and *Hypocreales* (Lombard *et al.* 2010a–c, Chaverri *et al.* 2011, Gräfenhan *et al.* 2011, Schroers *et al.* 2011).

MATERIALS AND METHODS

Isolate selection, culture studies and DNA extraction

The generic abbreviations used in this study are: *Ascochyta* (A.), *Coniothyrium* (C.), *Heterospora* (H.), *Leptosphaeria* (L.), *Paraconiothyrium* (*Paracon.*), *Paraleptosphaeria* (*Paralep.*), *Phoma* (Ph.), *Plenodomus* (*Plen.*), *Pleospora* (*Pleo.*), *Pyrenochaeta* (Py.), *Subplenodomus* (*Subplen.*) and *Westerdykella* (W.). The isolates included in this study were obtained from the culture collections of the Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands (CBS-KNAW) and the Dutch National Plant Protection Organization, Wageningen, The Netherlands (PD) (Table 1). The freeze-dried isolates were revived overnight in 2 mL malt/peptone (50 % / 50 %) liquid medium and subsequently transferred and maintained on oatmeal agar (OA) (Crous *et al.* 2009c). The isolates, which were stored at -196 °C, were directly transferred to OA. Cultures growing on OA and malt extract agar (MEA) (Crous *et al.* 2009c) were studied morphologically as described in detail by Boerema *et al.* (2004). The genomic DNA isolation was performed using the Ultraclean Microbial DNA isolation kit (Mo Bio Laboratories, Carlsbad, California) according to the instructions of the manufacturer. All DNA extracts were diluted 10 × in milliQ water and stored at 4 °C before use.

PCR and sequencing

For nucleotide sequence comparisons, partial regions of SSU, LSU and ITS, as well as part of the ACT, TUB and CHS-1 genes were amplified. The SSU region was amplified with the primers NS1 and NS4 (White *et al.* 1990) and the LSU region was amplified with the primers LR0R (Rehner & Samuels 1994) and LR7 (Vilgalys & Hester 1990). The ITS and TUB regions were amplified as described by Aveskamp *et al.* (2009) using the primer pair V9G (de Hoog & Gerrits van den Ende 1998) and ITS4 (White *et al.* 1990) for the ITS and the BT2Fw and BT4Rd primer pair (Woudenberg *et al.* 2009) for the TUB locus. The ACT and CHS-1 regions

were amplified using the primer pairs ACT-512F / ACT-783R and CHS-354R / CHS-79F (Carbone & Kohn 1999). The amplification reactions were performed and analysed as described by de Gruyter *et al.* (2009).

Sequencing of the PCR amplicons was conducted using the same primer combinations, although the primer LR5 (Vilgalys & Hester 1990) was used as an additional internal sequencing primer for LSU. The sequence products were purified using Sephadex columns (Sephadex G-50 Superfine, Amersham Biosciences, Roosendaal, Netherlands) and analysed with an ABI Prism 3730XL Sequencer (Applied Biosystems) according to the manufacturer's instructions. Consensus sequences were computed from both forward and reverse sequences using the Bionumerics v. 4.61 software package (Applied Maths, Sint-Martens-Latem, Belgium) and were lodged with GenBank. All sequences of reference isolates included in this study were obtained from GenBank (Table 1).

Phylogenetic analyses

To determine the phylogeny of *Phoma betae* and *Ph. lingam* at rank, the SSU and LSU sequence data of two isolates were aligned with the sequences of 46 reference isolates in the *Pleosporales* that were obtained from GenBank (Table 1), 14 of which were classified in the *Pleosporaceae* or *Leptosphaeriaceae*. The phylogeny of *Phoma* section *Plenodomus* was determined with the combined data set of LSU and ITS sequences of 87 isolates, including 53 isolates currently classified in *Leptosphaeria* and *Phoma* section *Plenodomus*. *Phoma apiicola*, *Ph. dimorphospora*, *Ph. heteromorphospora*, *Ph. lupini*, *Ph. valerianae*, *Ph. vasinfecta* and *Ph. violicola* classified in *Phoma* sections *Phoma* or *Heterospora* (Boerema *et al.* 2004) grouped in previous molecular phylogenetic studies outside *Didymellaceae* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010), and are therefore treated here.

In the study of the *Leptosphaeria doliolum* complex, that includes the subspecies of *Ph. acuta*, viz. subsp. *acuta*, *errabunda* and also *Ph. acuta* subsp. *acuta* f. sp. *phlogis*, a phylogenetic analysis was performed utilising the ITS, ACT, TUB, CHS-1 sequences of 18 isolates. *Phoma macrocapsa*, *Ph. sydowii* and *Ph. veronicicola* being closely related to this species complex were included.

The species concept of phoma-like anamorphs in *Pleosporaceae* was determined by alignments of the ACT sequences of 15 isolates and five reference isolates. *Phoma fallens*, *Ph. glaucispora* and *Ph. flavigena* were also included. These species were originally classified in *Phoma* sect. *Phoma* (de Gruyter & Noordeloos 1992, de Gruyter *et al.* 1998). However, a molecular phylogenetic study demonstrated that these species grouped in a clade representing *Leptosphaeriaceae* and *Pleosporaceae* (Aveskamp *et al.* 2010). Sequence data were compared with those of isolates currently classified in the genera *Phoma*, *Ascochyta* and *Coniothyrium*, as well as isolates of *Leptosphaeria clavata* and the generic type species *Pleospora herbarum*. *Phoma incompta* is the only species classified in *Phoma* section *Sclerophomella*, which proved to be unrelated to *Didymellaceae* (Aveskamp *et al.* 2010).

The phoma-like species that could not be attributed to *Pleosporineae* (Zhang *et al.* 2009) were studied with the LSU sequences of 40 isolates, including 20 reference isolates representing the anamorph genera *Beverwykella*, *Neottiosporina*, *Paraconiothyrium*, as well as the teleomorph genera *Byssothecium*, *Falciformispora*, *Herpotrichia*, *Melanomma*, *Paraphaeosphaeria*, *Pleomassaria*, *Preussia*, *Roussoella*, *Splanchnonema*, *Sporormiella*, *Thyridaria*, *Trematosphaeria* and *Westerdykella*.

Four *Phoma* species were included which are currently described in *Phoma* section *Phoma*, viz. *Ph. capitulum*, *Ph. flavescens*, *Ph. lini*, and *Ph. minutispora* (de Gruyter & Noordeloos 1992, de Gruyter *et al.* 1993). In addition, the human pathogens *Pyrenochaeta romeroi* and *Py. mackinnonii*, which could not be classified in a recent study dealing with phoma-like species with setose pycnidia (de Gruyter *et al.* 2010), were included.

The multiple alignments were automatically calculated by the BioNumerics software package, but manual adjustments for improvement were made by eye where necessary. For multilocus alignments, the phylogenetic analyses were done for each dataset individually, and where similar tree topologies were obtained, an analysis was performed on the combined alignment of all the gene regions in the multilocus alignment. Neighbour-Joining (NJ) distance analyses were conducted using PAUP (Phylogenetic Analysis Using Parsimony) v. 4.0b10 (Swofford 2003) with the uncorrected "p", Jukes-Cantor and Kimura 2-parameter substitution models. The robustness of the trees obtained was evaluated by 1000 bootstrap replications. A Bayesian analysis was conducted with MrBayes v. 3.1.2 (Huelsenbeck & Ronqvist 2001) in two parallel runs, using the default settings but with the following adjustments: the GTR model (trees 1–3, 5) with gamma-distributed rate and the HKY+ γ -model (tree 4) were selected for the partitions using the Findmodel freeware (<http://hcv.lanl.gov/content/hcv-db/findmodel/findmodel.html>), and a MCMC heated chain was set with a "temperature" value of 0.05. The number of generations and sample frequencies were set at 5 million and 10 (trees 3–5) or 100 (trees 1, 2) respectively and the run was automatically stopped as soon as the average standard deviation of split frequencies reached below 0.01. The resulting trees were printed with TreeView v. 1.6.6 (Page 1996) and alignments and trees were deposited into TreeBASE (www.treebase.org).

RESULTS

The data for the aligned sequence matrices for the trees obtained in the different studies are provided below. In the case that alignments of multiple loci are involved, the topologies of the obtained trees for each locus were compared by eye to confirm that the overall tree topology of the individual datasets were similar to each other and to that of the tree obtained from the combined alignment. The NJ analyses with the three substitution models showed similar tree topologies and were congruent to those obtained in the Bayesian analyses. The results of the molecular phylogenetic analyses are supplied below; the summarised additional ecology and distribution data of the taxa involved were adopted from Boerema *et al.* (2004), where the references to original literature are provided.

Phylogeny of *Phoma lingam* and *Ph. betae*, the type species of *Phoma* sections *Plenodomus* and *Pilosa* (*Pleosporineae*)

The aligned sequence matrix obtained for the SSU and LSU regions had a total length of 2 671 nucleotide characters, 1 367 and 1 304 respectively. In the alignment, an insertion in the SSU at the positions 478–832 was observed for the cultures CBS 216.75, CBS 165.78, CBS 138.96, CBS 331.37 and CBS 674.75. This insertion was excluded from further phylogenetic analyses. The combined dataset used in the analyses included 48 taxa and contained 2 316 characters with 101 and 213 unique site patterns for SSU and LSU,

Table 1. Isolates used in this study and their GenBank accession numbers. Name changes and newly generated sequences are indicated in bold.

Species name, final identification	Former identification	CBS no.	Other no.	ITS	SSU	LSU	ACT	TUB	CHS-1	Host, substrate	Country
<i>Aposphaeria corallinolutea</i> sp. nov.	<i>Pleurophoma</i> sp.	CBS 131286	PD 83367			JF740329				<i>Kerria japonica</i> (Rosaceae)	Netherlands
	<i>Pleurophoma</i> sp.	CBS 131287	PD 83831			JF740330				<i>Fraxinus excelsior</i> (Oleaceae)	Netherlands
<i>Aposphaeria populina</i>		CBS 543.70				EU754130				<i>Populus canadensis</i> (Salicaceae)	Netherlands
	<i>Pyrenochaeta</i> sp.	CBS 350.82				JF740265				<i>Picea abies</i> (Pinaceae)	Germany
	<i>Pleurophoma</i> sp.	CBS 130330	PD 84/221			JF740328				<i>Cornus mas</i> (Cornaceae)	Netherlands
<i>Beverwykella pulmonaria</i>		CBS 283.53	ATCC 32983, IFO 6800			GU301804				<i>Fagus sylvatica</i> (Fagaceae)	Netherlands
<i>Byssothecium circinans</i>		CBS 675.92	ATCC 52767, ATCC 52678, IMI 266220			AY016357				<i>Medicago sativa</i> (Fabaceae)	USA
<i>Chaetodiplodia</i> sp.	<i>Chaetodiplodia</i> sp.	CBS 453.68					JF740115			<i>Helminthone portulacoides</i> (Chenopodiaceae)	Netherlands
<i>Chaetosphaeronema hispidulum</i>		CBS 216.75			EU754045	EU754144				<i>Anthyllus vulneraria</i> (Fabaceae)	Germany
<i>Cochliobolus sativus</i>			DAOM 226212		DQ677995	DQ678045				(Poaceae)	Unknown
<i>Coniothyrium carteri</i> comb. nov.	<i>Phoma carteri</i>	CBS 101633	PD 84/74	JF740180		GQ387593				<i>Quercus</i> sp. Fagaceae)	Netherlands
	<i>Phoma carteri</i>	CBS 105.91		JF740181	GQ387533	GQ387594				<i>Quercus robur</i> (Fagaceae)	Germany
<i>Coniothyrium dolichi</i> comb. nov.	<i>Pyrenochaeta dolichi</i>	CBS 124143	IMI 217261	JF740182		GQ387610				<i>Dolichos biflorus</i> (Fabaceae)	India
	<i>Pyrenochaeta dolichi</i>	CBS 124140	IMI 217262	JF740183	GQ387550	GQ387611				<i>Dolichos biflorus</i> (Fabaceae)	India
<i>Coniothyrium glycines</i> comb. nov.	<i>Phoma glycinicola</i>	CBS 124455	IMI 294986	JF740184	GQ387536	GQ387597				<i>Glycine max</i> (Fabaceae)	Zambia
	<i>Phoma glycinicola</i>	CBS 124141	PG-1	JF740185		GQ387598				<i>Glycine max</i> (Fabaceae)	Zimbabwe
<i>Coniothyrium multiporum</i> comb. nov.	<i>Phoma multipora</i>	CBS 501.91	PD 83/888	JF740186		GU238109				Unknown	Egypt
	<i>Phoma multipora</i>	CBS 353.65	IMI 113689, ATCC 16207, HACC 164	JF740187		JF740268				Saline soil	India
<i>Coniothyrium palmarum</i>		CBS 400.71		AY720708	EU754054	EU754153				<i>Chamaerops humilis</i> (Arecaceae)	Italy
<i>Coniothyrium telephii</i> comb. nov.	<i>Phoma septicalis</i>	CBS 188.71		JF740188	GQ387538	GQ387599				Air	Finland
	<i>Phoma septicalis</i>	CBS 856.97		JF740189	GQ387539	GQ387600				Mineral wool	Finland
	<i>Phoma septicalis</i>	CBS 101636	PD 86/1186	JF740190	GQ387540	GQ387601				<i>Glycine max</i> (Fabaceae)	Zimbabwe
<i>Cucurbitaria berberidis</i> , anam.		CBS 363.93		JF740191	GQ387545	GQ387606				<i>Berberis vulgaris</i> (Berberidaceae)	Netherlands
<i>Pyrenochaeta berberidis</i>											
<i>Didymella exigua</i>		CBS 183.55			EU754056	EU754155				<i>Rumex arifolius</i> (Polygonaceae)	France

Table 1. (Continued).

Species name, final identification	Former identification	CBS no.	Other no.	ITS	SSU	LSU	ACT	TUB	CHS-1	Host, substrate	Country
<i>Didymella lycopersici</i> , anam. <i>Boeremia lycopersici</i>		CBS 378.67		JF740097	GU237950					<i>Lycopersicon esculentum</i> (Solanaceae)	Netherlands
<i>Falcisormispora lignatilis</i>			BCC 21118			GU371827				<i>Elaeis guineensis</i> (Arecaceae)	Thailand
<i>Herpotrichia juniperi</i>		CBS 200.31				DQ678080				<i>Juniperus nana</i> (Cupressaceae)	Switzerland
<i>Heterospora chenopodii</i> comb. nov.	<i>Phoma heteromorphospora</i>	CBS 448.68		FJ427023	EU754088	EU754187				<i>Chenopodium album</i> (Chenopodiaceae)	Netherlands
	<i>Phoma heteromorphospora</i>	CBS 115.96	PD 94/1576	JF740227		EU754188				<i>Chenopodium album</i> (Chenopodiaceae)	Netherlands
<i>Heterospora dimorphospora</i> comb. nov.	<i>Phoma dimorphospora</i>	CBS 345.78	PD 76/1015	JF740203		GU238069				<i>Chenopodium quinoa</i> (Chenopodiaceae)	Peru
	<i>Phoma dimorphospora</i>	CBS 165.78	PD 77/884	JF740204	JF740098	JF740281				<i>Chenopodium quinoa</i> (Chenopodiaceae)	Peru
<i>Leptosphaeria conoidea</i>	<i>Leptosphaeria conoidea</i> , anam. <i>Phoma dolium</i>	CBS 616.75	ATCC 32813, IMI 199777, PD 74/56	JF740201	JF740099	JF740279				<i>Lunaria annua</i> (Brassicaceae)	Netherlands
	<i>Leptosphaeria conoidea</i> , anam. <i>Phoma dolium</i>	CBS 125977	PD 82/888	JF740202		JF740280				<i>Senecio</i> sp. (Asteraceae)	Netherlands
<i>Leptosphaeria dolium</i>	<i>Leptosphaeria dolium</i> subsp. <i>dolium</i> var. <i>dolium</i> , anam. <i>Phoma acuta</i> subsp. <i>acuta</i>	CBS 505.75	PD 75/141	JF740205	GQ387515	GQ387576	JF740126	JF740144	JF740162	<i>Urtica dioica</i> (Urticaceae)	Netherlands
	<i>Leptosphaeria dolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	CBS 541.66	PD 66/221	JF740206			JF740127	JF740145	JF740163	<i>Rudbeckia</i> sp. (Asteraceae)	Netherlands
	<i>Phoma acuta</i> subsp. <i>acuta</i> f.sp. <i>phloxis</i>	CBS 155.94	PD 77/80	JF740207		JF740282	JF740128	JF740146	JF740164	<i>Phlox paniculata</i> (Polemoniaceae)	Netherlands
	<i>Phoma acuta</i> subsp. <i>acuta</i> f.sp. <i>phloxis</i>	CBS 125979	PD 78/37	JF740208		JF740283	JF740129	JF740147	JF740165	<i>Phlox paniculata</i> (Polemoniaceae)	Netherlands
	<i>Leptosphaeria dolium</i> subsp. <i>dolium</i> var. <i>dolium</i> , anam. <i>Phoma acuta</i> subsp. <i>acuta</i>	CBS 504.75	PD 74/55	JF740209			JF740130	JF740148	JF740166	<i>Urtica dioica</i> (Urticaceae)	Netherlands
	<i>Leptosphaeria dolium</i> subsp. <i>dolium</i> var. <i>dolium</i> , anam. <i>Phoma acuta</i> subsp. <i>acuta</i>	CBS 130000	PD 82/701	JF740210			JF740131	JF740149	JF740167	<i>Urtica dioica</i> (Urticaceae)	Netherlands
<i>Leptosphaeria errabunda</i> comb. nov.	<i>Leptosphaeria dolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	CBS 617.75	ATCC 32814, IMI 199775, PD 74/201	JF740216		JF740289	JF740132	JF740150	JF740168	<i>Solidago</i> sp. (hybrid) (Asteraceae)	Netherlands

Table 1. (Continued).

Species name, final identification	Former identification	CBS no.	Other no.	ITS	SSU	LSU	ACT	TUB	CHS-1	Host, substrate	Country
<i>Leptosphaeria doliolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	<i>Leptosphaeria doliolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	CBS 125978	PD 74/61	JF740217		JF740290	JF740133	JF740151	JF740169	<i>Delphinium</i> sp. (<i>Ranunculaceae</i>)	Netherlands
<i>Leptosphaeria doliolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	<i>Leptosphaeria doliolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	CBS 129999	PD 78/569	JF740218			JF740134	JF740152	JF740170	<i>Aconitum</i> sp. (<i>Ranunculaceae</i>)	Netherlands
<i>Leptosphaeria doliolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	<i>Leptosphaeria doliolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	CBS 129998	PD 84/462	JF740219			JF740135	JF740153	JF740171	<i>Gaillardia</i> (<i>Asteraceae</i>)	Netherlands
<i>Leptosphaeria doliolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	<i>Leptosphaeria doliolium</i> subsp. <i>errabunda</i> , anam. <i>Phoma acuta</i> subsp. <i>errabunda</i>	CBS 129997	PD 78/631	JF740220			JF740136	JF740154	JF740172	<i>Achillea millefolium</i> (<i>Apiaceae</i>)	Netherlands
<i>Phoma etheridgei</i> comb. nov.	<i>Phoma etheridgei</i>	CBS 125980	DAOM 216539, PD 95/1483	JF740221		JF740291				<i>Populus tremuloides</i> (<i>Salicaceae</i>)	Canada
<i>Leptosphaeria macrocapsa</i> comb. nov.	<i>Phoma macrocapsa</i>	CBS 640.93	PD 78/139	JF740237		JF740304	JF740138	JF740156	JF740174	<i>Mercurialis perennis</i> (<i>Euphorbiaceae</i>)	Netherlands
<i>Leptosphaeria pedicularis</i> comb. nov.	<i>Phoma pedicularis</i>	CBS 126582	PD 77/710	JF740223		JF740293				<i>Gentiana punctata</i> (<i>Gentianaceae</i>)	Switzerland
	<i>Phoma pedicularis</i>	CBS 390.80	PD 77/711	JF740224		JF740294	JF740137	JF740155	JF740173	<i>Pedicularis</i> sp. (<i>Scrophulariaceae</i>)	Switzerland
<i>Leptosphaeria rubefaciens</i> comb. nov.	<i>Phoma rubefaciens</i>	CBS 387.80	IMI 248432, ATCC 42533, PD 78/809	JF740242		JF740311				<i>Tilia</i> (x) <i>europaea</i> (<i>Malvaceae</i>)	Netherlands
<i>Leptosphaeria sclerotioidea</i> comb. nov.	<i>Phoma rubefaciens</i> <i>Phoma sclerotioidea</i>	CBS 223.77 CBS 144.84	CECT 20025, PD 82/1061	JF740243 JF740192		JF740312 JF740269				<i>Quercus</i> sp. (<i>Fagaceae</i>) <i>Medicago sativa</i> (<i>Fabaceae</i>)	Switzerland Canada
	<i>Phoma sclerotioidea</i>	CBS 148.84	PD 80/1242	JF740193		JF740270				<i>Medicago sativa</i> (<i>Fabaceae</i>)	Canada
<i>Leptosphaeria slovacica</i>	<i>Leptosphaeria slovacica</i> , anam. <i>Phoma leonuri</i>	CBS 389.80	PD 79/171	JF740247	JF740101	JF740315				<i>Balota nigra</i> (<i>Lamiaceae</i>)	Netherlands
	<i>Leptosphaeria slovacica</i> , anam. <i>Phoma leonuri</i>	CBS 125975	PD 77/1161	JF740248		JF740316				<i>Balota nigra</i> (<i>Lamiaceae</i>)	Netherlands
<i>Leptosphaeria sydowii</i> comb. nov.	<i>Phoma sydowii</i>	CBS 385.80	PD 74/477	JF740244		JF740313	JF740139	JF740157	JF740175	<i>Senecio jacobaea</i> (<i>Asteraceae</i>)	UK
	<i>Phoma sydowii</i>	CBS 125976	PD 84/472	JF740245		JF740314	JF740140	JF740158	JF740176	<i>Senecio jacobaea</i> (<i>Asteraceae</i>)	Netherlands

Table 1. (Continued).

Species name, final identification	Former identification	CBS no.	Other no.	ITS	SSU	LSU	ACT	TUB	CHS-1	Host, substrate	Country
	<i>Phoma sydowii</i>	CBS 297.51		JF740246			JF740141	JF740159	JF740177	<i>Papaver rhoeas</i> (<i>Papaveraceae</i>)	Switzerland
<i>Leptosphaeria veronicae</i> comb. nov.	<i>Phoma veronicicola</i>	CBS 145.84	CECT 20059, PD 78/273	JF740254		JF740320	JF740142	JF740160	JF740178	<i>Veronica chamaedryoides</i> (<i>Scrophulariaceae</i>)	Netherlands
	<i>Phoma veronicicola</i>	CBS 126583	PD 74/227	JF740255		JF740321	JF740143	JF740161	JF740179	<i>Veronica 'Shirley Blue'</i> (<i>Scrophulariaceae</i>)	Netherlands
<i>Massarina eburnea</i>			H 3953, HHUF 26621, JCM 14422		AB521718	AB521735				<i>Fagus sylvatica</i> (<i>Fagaceae</i>)	UK
<i>Massarina eburnea</i>		CBS 473.64	ETH 2945		GU296170	GU301840				<i>Fagus sylvatica</i> (<i>Fagaceae</i>)	Switzerland
<i>Medicopsis romeroi</i> comb. nov.	<i>Pyrenochaeta romeroi</i>	CBS 252.60	ATCC 13735, FMC 151, UAMH 10841		EU754108	EU754207				Human, maduromycosis	Venezuela
	<i>Pyrenochaeta romeroi</i>	CBS 122784	PD 84/1022			EU754208				<i>Hordeum vulgare</i> (<i>Gramineae</i>)	Unknown
<i>Melanomma pulvis-pyrius</i>		CBS 371.75				GU301845				Wood	France
		CBS 400.97			DQ678020	DQ678072				<i>Fagus</i> sp. (<i>Fagaceae</i>)	Belgium
<i>Neophaeosphaeria filamentosa</i>		CBS 102202	BPI 802755	JF740259	GQ387516	GQ387577				<i>Yucca rostrata</i> (<i>Agavaceae</i>)	Mexico
<i>Neosetophoma samarorum</i>		CBS 138.96	PD 82/653		GQ387517	GQ387578				<i>Phlox paniculata</i> (<i>Polemoniaceae</i>)	Netherlands
<i>Neotiosporina paspali</i>		CBS 331.37			EU754073	EU754172				<i>Paspalum notatum</i> (<i>Poaceae</i>)	USA
<i>Nigrogana mackinnonii</i> comb. nov.	<i>Pyrenochaeta mackinnonii</i>	CBS 674.75	FMC 270			GQ387613				Human, black grain mycetoma	Venezuela
	<i>Pyrenochaeta mackinnonii</i>	CBS 110022			GQ387552					Human, mycetoma	Mexico
<i>Paraconiothyrium flavescens</i> comb. nov.	<i>Phoma flavescens</i>	CBS 178.93	PD 82/1062			GU238075				Soil	Netherlands
<i>Paraconiothyrium fuckelii</i> comb. nov.	<i>Coniothyrium fuckelii</i>	CBS 797.95			GU238204	GU237960				<i>Rubus</i> sp. (<i>Rosaceae</i>)	Denmark
<i>Paraconiothyrium fusco-maculans</i> comb. nov.	<i>Plenodomus fusco-maculans</i>	CBS 116.16				EU754197				<i>Malus</i> sp. (<i>Rosaceae</i>)	USA
<i>Paraconiothyrium lini</i> comb. nov.	<i>Phoma lini</i>	CBS 253.92	PD 70/998			EU238093				Wisconsin tank	Netherlands
<i>Paraconiothyrium maculiculis</i> sp. nov.	<i>Pleurophoma pleurospora</i>	CBS 101461	IMI 320754, UTHSC 87-144			EU754200				Human, cutaneous lesions	USA
<i>Paraconiothyrium minutans</i>		CBS 122788	PD 07/03486739		EU754074	EU754173				Unknown	UK
		CBS 122786	PD 99/1064-1			EU754174				<i>Clematis</i> sp. (<i>Ranunculaceae</i>)	Netherlands
<i>Paraconiothyrium tiliae</i> comb. nov.	<i>Asteromella tiliae</i>	CBS 265.94				EU754139				<i>Tilia platyphyllos</i> (<i>Tiliaceae</i>)	Austria
<i>Paraleptosphaeria dryadis</i> comb. nov.	<i>Leptosphaeria dryadis</i>	CBS 643.86		JF740213		GU301828				<i>Dryas octopetala</i> (<i>Rosaceae</i>)	Switzerland

Table 1. (Continued).

Species name, final identification	Former identification	CBS no.	Other no.	ITS	SSU	LSU	ACT	TUB	CHS-1	Host, substrate	Country
<i>Paraleptosphaeria macrospora</i> comb. nov.	<i>Phoma macrospora</i>	CBS 114198	UPSC 2686	JF740238		JF740305				<i>Rumex domesticus</i> (Chenopodiaceae)	Norway
<i>Paraleptosphaeria nitschkei</i> comb. nov.	<i>Leptosphaeria nitschkei</i>	CBS 306.51		JF740239		JF740308				<i>Cirsium spinosissimum</i> (Asteraceae)	Switzerland
<i>Paraleptosphaeria orobanches</i> comb. nov.	<i>Phoma korffii</i>	CBS 101638	PD 97/12070	JF400230		JF740299				<i>Epifagus virginiana</i> (Orobanchaceae)	USA
<i>Paraleptosphaeria praetermissa</i> comb. nov.	<i>Leptosphaeria praetermissa</i>	CBS 114591		JF740241		JF740310				<i>Rubus idaeus</i> (Rosaceae)	Sweden
<i>Paraphaeosphaeria michoti</i>		CBS 652.86	ETH 9483		GQ387520	GQ387581				<i>Typha latifolia</i> (Typhaceae)	Switzerland
<i>Paraphoma radicina</i>		CBS 111.79	IMI 386094, PD 76/437		EU754092	EU754191				<i>Malus sylvestris</i> (Rosaceae)	Netherlands
<i>Phaeosphaeria nodorum</i>		CBS 110109			EU754076	EU754175				<i>Lolium perenne</i> (Gramineae)	Denmark
<i>Phoma herbarum</i>		CBS 615.75		FJ427022	EU754087	EU754186				<i>Rosa multiflora</i> (Rosaceae)	Netherlands
<i>Phoma paspali</i>		CBS 560.81	PD 92/1569		GU238227	G238124				<i>Paspalum dilatatum</i> (Poaceae)	New Zealand
<i>Plenodomus agnitus</i> comb. nov.	<i>Leptosphaeria agnita</i> , anam. <i>Phoma agnita</i>	CBS 121.89	PD 82/903	JF740194		JF740271				<i>Eupatorium cannabinum</i> (Asteraceae)	Netherlands
<i>Plenodomus biglobosus</i> comb. nov.	<i>Leptosphaeria agnita</i> , anam. <i>Phoma agnita</i>	CBS 126584	PD 82/561	JF740195		JF740272				<i>Eupatorium cannabinum</i> (Asteraceae)	Netherlands
<i>Plenodomus chrysanthemii</i> comb. nov.	<i>Leptosphaeria biglobosa</i>	CBS 119951		JF740198	JF740102	JF740274				<i>Brassica rapa</i> (Brassicaceae)	Netherlands
<i>Plenodomus collinsoniae</i> comb. nov.	<i>Phoma vasinflecta</i> , synanam. <i>Phielophora chrysanthemii</i>	CBS 127249	DAOM 229269	JF740199		JF740275				<i>Brassica juncea</i> (Brassicaceae)	France
<i>Plenodomus collinsoniae</i> comb. nov.	<i>Leptosphaeria collinsoniae</i>	CBS 539.63		JF740253	GU238230	GU238151				<i>Chrysanthemum</i> sp. (Asteraceae)	Greece
<i>Plenodomus confertus</i> comb. nov.	<i>Leptosphaeria conferta</i> , anam. <i>Phoma conferta</i>	CBS 120227	JCM 13073, MAFF 239583	JF740200		JF740276				<i>Vitis coignetiae</i> (Vitaceae)	Japan
<i>Plenodomus congestus</i> comb. nov.	<i>Leptosphaeria congesta</i> , anam. <i>Phoma congesta</i>	CBS 375.64		AF439459		JF740277				<i>Anacyclus radiatus</i> (Asteraceae)	Spain
<i>Plenodomus enteroleucus</i> comb. nov.	<i>Phoma enteroleuca</i> var. <i>enteroleuca</i>	CBS 244.64		AF439460		JF740278				<i>Erigeron canadensis</i> (Asteraceae)	Spain
<i>Plenodomus enteroleucus</i> comb. nov.	<i>Phoma enteroleuca</i> var. <i>enteroleuca</i>	CBS 142.84	PD 81/654, CECT20063	JF740214		JF740287				<i>Catalpa bignonioides</i> (Bignoniaceae)	Netherlands
<i>Plenodomus fallaciosus</i> comb. nov.	<i>Phoma enteroleuca</i> var. <i>enteroleuca</i>	CBS 831.84		JF740215		JF740288				<i>Triticum aestivum</i> (Poaceae)	Germany
<i>Plenodomus fallaciosus</i> comb. nov.	<i>Leptosphaeria fallaciosa</i>	CBS 414.62	ETH 2961	JF740222		JF740292				<i>Satureia montana</i> (Lamiaceae)	France

Table 1. (Continued).

Species name, final identification	Former identification	CBS no.	Other no.	ITS	SSU	LSU	ACT	TUB	CHS-1	Host, substrate	Country
<i>Plenodomus hendersoniae</i> comb. nov.	<i>Phoma intricans</i>	CBS 113702	UPSC 1843	JF740225		JF740295				<i>Salix cinerea</i> (Salicaceae)	Sweden
	<i>Phoma intricans</i>	CBS 139.78		JF740226		JF740296				<i>Pyrus malus</i> (Rosaceae)	Netherlands
<i>Plenodomus influorescens</i> comb. nov.	<i>Phoma enteroleuca</i> var. <i>inflourescens</i>	CBS 143.84	PD 78883, CECT 20064	JF400228		JF740297				<i>Fraxinus excelsior</i> (Oleaceae)	Netherlands
	<i>Phoma enteroleuca</i> var. <i>inflourescens</i>		PD 73/1382	JF400229		JF740298				<i>Lilium</i> sp. (Liliaceae)	Netherlands
<i>Plenodomus libanotidis</i> comb. nov.	<i>Leptosphaeria libanotis</i>	CBS 113795	UPSC 2219	JF400231		JF740300				<i>Seseli libanotis</i> (Apiaceae)	Sweden
<i>Plenodomus lindquistii</i> comb. nov.	<i>Leptosphaeria lindquistii</i> anam. <i>Phoma macdonaldii</i>	CBS 386.80	PD 77/336	JF400232		JF740301				<i>Helianthus annuus</i> (Asteraceae)	former Yugoslavia
	<i>Leptosphaeria lindquistii</i> anam. <i>Phoma macdonaldii</i>	CBS 381.67		JF400233		JF740302				<i>Helianthus annuus</i> (Asteraceae)	Canada
<i>Plenodomus lingam</i>	<i>Leptosphaeria maculans</i> , anam. <i>Phoma lingam</i>	CBS 275.63	MUCL 9901, UPSC 1025	JF400234	JF740103	JF740306				<i>Brassica</i> sp. (Brassicaceae)	UK
	<i>Leptosphaeria maculans</i> , anam. <i>Phoma lingam</i>	CBS 260.94	PD 78989	JF400235		JF740307	JF740116			<i>Brassica oleracea</i> (Brassicaceae)	Netherlands
<i>Plenodomus lupini</i> comb. nov.	<i>Leptosphaeria maculans</i> , anam. <i>Phoma lingam</i>	CBS 147.24					JF740117			Unknown	Unknown
	<i>Phoma lupini</i>	CBS 248.92	PD 79/141	JF740236		JF740303				<i>Lupinus mutabilis</i> (Fabaceae)	Peru
<i>Plenodomus pimpinellae</i> comb. nov.	<i>Leptosphaeria pimpinellae</i> , anam. <i>Phoma pimpinellae</i>	CBS 101637	PD 92/41	JF740240		JF740309				<i>Pimpinella anisum</i> (Apiaceae)	Israel
<i>Plenodomus tracheiphila</i> comb. nov.	<i>Phoma tracheiphila</i>	CBS 551.93	PD 81/782	JF740249	JF740104	JF740317				<i>Citrus limonium</i> (Rutaceae)	Israel
	<i>Phoma tracheiphila</i>	CBS 127250	PD 09/04597/141	JF740250		JF740318				<i>Citrus</i> sp. (Rutaceae)	Italy
<i>Plenodomus visci</i> comb. nov.	<i>Plectophomella visci</i>	CBS 122783	PD 74/1021	JF740256	EU754096	EU754195				<i>Viscum album</i> (Viscaceae)	France
<i>Plenodomus wasabiae</i>	<i>Phoma wasabiae</i>	CBS 120119	FAU 559	JF740257		JF740323				<i>Wasabia japonica</i> (Brassicaceae)	Taiwan
	<i>Phoma wasabiae</i>	CBS 120120	FAU 561	JF740258		JF740324				<i>Wasabia japonica</i> (Brassicaceae)	Taiwan
<i>Pleomassaria siparia</i>		CBS 279.74				AY004341				<i>Betula verrucosa</i> (Betulaceae)	Netherlands
<i>Pleospora angustis</i> nom. nov.	<i>Leptosphaeria clavata</i>	CBS 296.51					JF740122			Unknown	Switzerland
<i>Pleospora betae</i>	<i>Pleospora betae</i> , anam. <i>Phoma betae</i>	CBS 523.66	PD 66/270, IHEM 3915		EU754080	EU754179	JF740118			<i>Beta vulgaris</i> (Chenopodiaceae)	Netherlands
	<i>Pleospora betae</i> , anam. <i>Phoma betae</i>	CBS 109410	PD 77/113			EU754178	JF740119			<i>Beta vulgaris</i> (Chenopodiaceae)	Netherlands
<i>Pleospora calvescens</i>	<i>Pleospora calvescens</i> , anam. <i>Ascochyta caulina</i>	CBS 246.79	PD 77/655		EU754032	EU754131	JF740120			<i>Atriplex hastata</i> (Chenopodiaceae)	Germany

Table 1. (Continued).

Species name, final identification	Former identification	CBS no.	Other no.	ITS	SSU	LSU	ACT	TUB	CHS-1	Host, substrate	Country
	<i>Pleospora calvescens</i> , anam. <i>Ascochyta caulina</i>	CBS 343.78					JF740121			<i>Atriplex hastata</i> (Chenopodiaceae)	Netherlands
<i>Pleospora chenopodii</i>	<i>Ascochyta hyalospora</i>	CBS 206.80	PD 74/1022		JF740095	JF740266	JF740109			<i>Chenopodium quinoa</i> (Chenopodiaceae)	Bolivia
	<i>Pleospora calvescens</i> , anam. <i>Ascochyta caulina</i>	CBS 344.78	PD 68/682				JF740110			<i>Atriplex hastata</i> (Chenopodiaceae)	Netherlands
<i>Pleospora fallens</i> comb. nov.	<i>Phoma fallens</i>	CBS 161.78	LEV 1131				JF740106			<i>Olea europaea</i> (Oleaceae)	New Zealand
	<i>Phoma glaucispora</i>	CBS 284.70	PD 97/2400				JF740107			<i>Nerium oleander</i> (Apocynaceae)	Italy
<i>Pleospora flavigena</i> comb. nov.	<i>Phoma flavigena</i>	CBS 314.80	PD 91/1613				JF740108			Water	Romania
<i>Pleospora halimiones</i> nom. nov.	<i>Ascochyta obiones</i>	CBS 432.77	IMI 282137		JF740096	JF740267	JF740113			<i>Helimione portulacoides</i> (Chenopodiaceae)	Netherlands
	<i>Ascochyta obiones</i>	CBS 786.68					JF740114			<i>Helimione portulacoides</i> (Chenopodiaceae)	Netherlands
<i>Pleospora herbarum</i>		CBS 191.86	IMI 276975		GU238232	GU238160	JF740123			<i>Medicago sativa</i> (Fabaceae)	India
<i>Pleospora incompta</i> comb. nov.	<i>Phoma incompta</i>	CBS 467.76					JF740111			<i>Olea europaea</i> (Oleaceae)	Greece
	<i>Phoma incompta</i>	CBS 526.82					JF740112			<i>Olea europaea</i> (Oleaceae)	Italy
<i>Pleospora typhicola</i>	<i>Pleospora typhicola</i> , anam. <i>Phoma typhanum</i>	CBS 132.69			JF740105	JF740325	JF740124			<i>Typha angustifolia</i> (Typhaceae)	Netherlands
	<i>Pleospora typhicola</i> , anam. <i>Phoma typhanum</i>	CBS 602.72					JF740125			<i>Typha</i> sp. (Typhaceae)	Netherlands
<i>Pleurophoma pleurospora</i>	<i>Pleurophoma</i> sp.	CBS 116668			JF740326					<i>Cytisus scoparius</i> (Fabaceae)	Netherlands
	<i>Pleurophoma</i> sp.	CBS 130329	PD 82/371			JF740327				<i>Lonicera</i> sp. (Caprifoliaceae)	Netherlands
<i>Preussia funiculata</i>		CBS 659.74			GU296187	GU301864				Soil	Senegal
<i>Pseudorobillardia phragmitis</i>		CBS 398.61	IMI 070678			EU754203				<i>Phragmites australis</i> (Poaceae)	UK
<i>Pyrenochaeta cava</i>		CBS 257.68	IMI 331911	JF740260	EU754100	EU754199				Wheat field soil	Germany
<i>Pyrenochaeta lycopersici</i>		CBS 267.59		JF740261	GU387551	GU387612				<i>Lycopersicon esculentum</i> (Solanaceae)	Netherlands
<i>Pyrenochaeta nobilis</i>		CBS 407.76		EU930011	EU754107/ DQ898287	EU754206				<i>Laurus nobilis</i> (Lauraceae)	Italy
<i>Pyrenochaetopsis leptospora</i>		CBS 101635	PD 71/1027	JF740262	GU387566	GU387627				Secale cereale (Poaceae)	Europe

Table 1. (Continued).

Species name, final identification	Former identification	CBS no.	Other no.	ITS	SSU	LSU	ACT	TUB	CHS-1	Host, substrate	Country
<i>Pyrenochaetopsis pratorum</i> comb. nov.	<i>Phoma pratorum</i>	CBS 445.81	PDDCC 7049, PD 80/1254	JF740263		GU238136				<i>Lolium perenne</i> , leaf (Poaceae)	New Zealand
<i>Pyrenophora tritici-repentis</i>		CBS 286.93	PD 80/1252	JF740264		JF740331				<i>Dactylis glomerata</i> (Poaceae)	New Zealand
<i>Rousssoella hysterooides</i>		CBS 125434	HH 26988		AY544716	AY544672				(Poaceae)	Italy
<i>Setomelanomma holmii</i>		CBS 110217			GQ387572	GQ387633				<i>Picea pungens</i> (Pinaceae)	USA
<i>Setophoma terrestris</i>		CBS 335.29			GQ387526	GQ387587				<i>Allium sativum</i> (Alliaceae)	USA
<i>Splanchnonema platani</i>		CBS 221.37			DQ678013	DQ678065				<i>Platanus occidentalis</i> (Platanaceae)	USA
<i>Sporormiella minima</i>		CBS 524.50			DQ678003	DQ678056				Dung of goat	Panama
<i>Stagonosporopsis cucurbitacearum</i>		CBS 133.96			GU238234	GU238181				<i>Cucurbita</i> sp. (Cucurbitaceae)	New Zealand
<i>Subplenodomus apicola</i> comb. nov.	<i>Phoma apicola</i>	CBS 285.72		JF740196		GU238040				<i>Apium graveolens</i> var. rapaceum (Umbelliferae)	Germany
	<i>Phoma apicola</i>	CBS 504.91	PD 78/1073	JF740197		JF740273				<i>Apium graveolens</i> (Umbelliferae)	Netherlands
<i>Subplenodomus drobnjensis</i> comb. nov.	<i>Phoma drobnjensis</i>	CBS 269.92	PD 88/896	JF740211	JF740100	JF740285				<i>Eustoma exaltatum</i> (Gentianaceae)	Netherlands
	<i>Phoma drobnjensis</i>	CBS 270.92	PD 83/650	JF740212		JF740286				<i>Gentiana makinoi</i> Royal Blue (Gentianaceae)	Netherlands
<i>Subplenodomus valerianae</i> comb. nov.	<i>Phoma valerianae</i>	CBS 630.68	PD 68/141	JF740251		GU238150				<i>Valeriana phu</i> (Valerianaceae)	Netherlands
	<i>Phoma valerianae</i>	CBS 499.91	PD 73/672	JF740252		JF740319				<i>Valeriana officinalis</i> (Valerianaceae)	Netherlands
<i>Subplenodomus violicola</i> comb. nov.	<i>Phoma violicola</i>	CBS 306.68		FJ427054	GU238231	GU238156				<i>Viola tricolor</i> (Violaceae)	Netherlands
	<i>Phoma violicola</i>	CBS 100272		FJ427055		JF740322				<i>Viola tricolor</i> (Violaceae)	New Zealand
<i>Thyridaria rubronotata</i>		CBS 419.85				GU301875				<i>Acer pseudoplatanus</i> (Aceraceae)	Netherlands
<i>Trematosphaeria pertusa</i>		CBS 122368				FJ201990				<i>Fraxinus excelsior</i> (Oleaceae)	France
<i>Westerdykella capitulum</i> comb. nov.	<i>Phoma capitulum</i>	CBS 337.65	PD 91/1614, ATCC 16195, HACC 167, IMI 113693			GU238054				Saline soil	India
<i>Westerdykella minutispora</i> comb. nov.	<i>Phoma minutispora</i>	CBS 509.91	PD 77/920			GU238108				Saline soil	India
<i>Westerdykella ornata</i>		CBS 379.55				GU301880				Mangrove mud	Mozambique

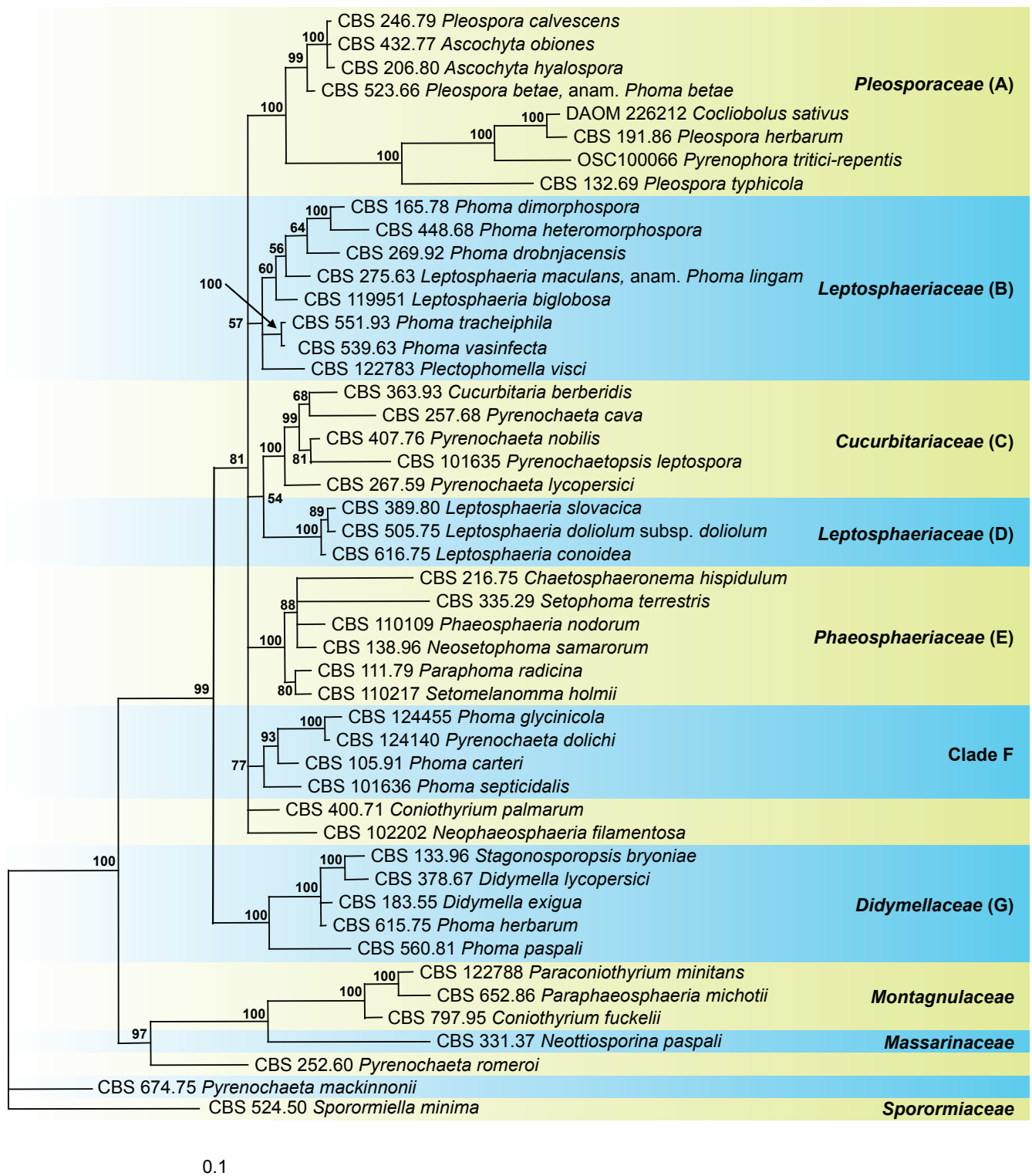


Fig. 1. The phylogeny of *Phoma lingam* and *Phoma betae*, the type species of *Phoma* sections *Plenodomus* and *Pilosa*, based on the strict consensus tree from a Bayesian analysis of 48 LSU/SSU sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Sporormiella minima* (CBS 524.50).

respectively. The tree (Fig. 1) was rooted to *Sporormiella minima* (CBS 524.50). The Bayesian analysis resulted in 6 5442 trees after 3 272 000 generations, from which the burn-in was discarded and the consensus tree and posterior probabilities were calculated based on 56 028 trees (Fig. 1).

The families that belong to *Pleosporineae*, represented by the species grouping in clades A–G, clustered in a strongly supported clade (99 % posterior probability). Clade A, representing those species classified in *Pleosporaceae*, was strongly supported (100 %) and included two subclades. *Pleospora betae* (anam. *Ph.*

betae), clustered with *Pleospora calvescens* (anam. *Ascochyta caulina*), *A. obiones* and *A. hyalospora*; all recorded as pathogens on *Chenopodiaceae*. The generic type species *Pleospora herbarum*, a plurivorous species, grouped with *Cochliobolus sativus*, *Pyrenophora tritici-repentis* and *Pleospora typhicola* (anam. *Ph. typhina*), all recorded from *Poaceae*. Clade B includes *Leptosphaeria maculans* (anam. *Ph. lingam*) and clustered with *Leptosphaeria biglobosa*. In clade B also other important plant pathogens of *Phoma* section *Plenodomus* can be found, such as *Ph. tracheiphila*, *Ph. vasinfecta*, *Ph. drobnjacensis*, and *Plectophomella*

visci. *Phoma heteromorphospora*, type species of *Phoma* section *Heterospora* (Boerema *et al.* 1997) and *Ph. dimorphospora* also grouped in this *Leptosphaeria* clade, in congruence with previous findings (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010).

Leptosphaeria doliolum (anam. *Ph. acuta*), type species of the genus *Leptosphaeria*, is found in Clade D, clustering with *L. conoidea* and *L. slovacica*. *Leptosphaeria doliolum* and its relatives comprise a sister clade C with species classified in *Cucurbitariaceae*, including *Cucurbitaria berberidis*, the three *Pyrenochaeta* species, *Py. cava*, *Py. lycopersici* and *Py. nobilis*, and *Pyrenochaetopsis leptospora*.

Phaeosphaeria nodorum and its relatives *Neosetophoma samarorum*, *Setophoma terrestris*, *Chaetosphaeronema hispidulum*, *Paraphoma radicina* and *Setomelanomma holmii*, represent *Phaeosphaeriaceae* in clade E as has previously been found (de Gruyter *et al.* 2009, 2010).

A distinct clade F includes *Ph. glycinicola*, *Ph. carteri*, *Ph. septicialis*, and the taxonomic confusing species *Pyrenochaeta dolichi* (Grondona *et al.* 1997). The position of *Coniothyrium palmarum* and *Neophaeosphaeria filamentosa* could not be clarified, but both species are also treated below in a phylogeny including close relatives based on ITS and LSU regions (Fig. 2). *Didymella exigua*, type species of the genus *Didymella*, and *Ph. herbarum* represent *Didymellaceae*, and clustered in a well-supported clade (G) in congruence with previous studies (de Gruyter *et al.* 2009, 2010, Aveskamp *et al.* 2010). The molecular phylogeny of species which group in this analysis outside of *Pleosporineae* in *Montagnulaceae*, *Massarinaceae* and *Sporormiaceae* were further analysed utilising LSU sequence data of a broader range of taxa (Fig. 5).

***Phoma* section *Plenodomus* and close allies**

The aligned sequence matrix obtained for the LSU and ITS regions had a total length of 1 921 nucleotide characters, 1 332 and 589 respectively. The combined dataset used in the analyses included 87 taxa and contained 1921 characters with 298 and 118 unique site patterns for LSU and ITS respectively. The tree (Fig. 2) was rooted to *Ph. herbarum* (CBS 615.75), the representative isolate of the type species of *Phoma* (Boerema *et al.* 2004). The Bayesian analysis resulted in 100 002 trees after 5 000 000 generations, from which the burn-in was discarded and the consensus tree and posterior probabilities were calculated based on 90 930 trees (Fig. 2).

The species currently classified in *Leptosphaeria* and *Phoma* section *Plenodomus* grouped in clades A and B representing *Leptosphaeriaceae*, including the type species *Ph. lingam* and *Leptosphaeria doliolum*, respectively. Isolates of the taxa that represent *Cucurbitariaceae*, *Cucurbitaria berberidis* and its related species *Pyrenochaeta cava*, *Py. nobilis*, *Py. lycopersici* and *Pyrenochaetopsis leptospora*, clustered in a distinct clade D only distantly related to *Leptosphaeriaceae*. This finding agrees with a recent study (de Gruyter *et al.* 2010). *Phoma pratorum* clustered with *Pyrenochaetopsis leptospora*.

Leptosphaeria biglobosa grouped in a subclade A1 with *Ph. wasabiae*, the cause of black rot disease on *Wasabia japonica* (*Brassicaceae*) and *Ph. pimpinellae*, a necrotroph on *Pimpinella anisum* (*Apiaceae*). *Leptosphaeria maculans*, considered as closely related to the *L. biglobosa* complex, proved to be more distantly related in clade A1. In this subclade, other important pathogens can be found, such as *Ph. tracheiphila*, a quarantine organism on *Citrus* spp. (*Rutaceae*), *Ph. vasinfecta*, a pathogen

on *Chrysanthemum* spp. (*Asteraceae*), *L. lindquistii* (anam. *Ph. macdonaldii*), a worldwide pathogen on *Helianthus annuus* (*Asteraceae*) and *Ph. lupini*, a seed borne pathogen known from *Lupinus* spp. (*Fabaceae*). Subclade A1 also comprises both varieties of *Ph. enteroleuca*, opportunistic pathogens on deciduous trees and shrubs, and the necrotrophic species *L. agnita* (anam. *Ph. agnita*), *Ph. congesta* (both recorded on *Asteraceae*), *Ph. conferta* (mainly on *Brassicaceae*), *L. hendersoniae* (on *Salicaceae*), *L. fallaciosa*, *L. collinsoniae* (mainly on *Lamiaceae*) and *L. libanotis* (on *Apiaceae*). *Plectophomella visci*, recorded from leaves of *Viscum album* (*Viscaceae*), also clustered in the *Leptosphaeriaceae*. The genus *Plenodomus* is re-introduced here to accommodate the species in subclade A1, which are allied to *Ph. lingam*.

Subclade A2 comprises pathogenic species often causing leaf spots such as *Ph. apiicola* on *Apium graveolens* (*Apiaceae*), *Ph. drobnjacensis* (on *Gentianaceae*), *Ph. violicola* (on *Violaceae*) as well as the necrotrophic species *Ph. valerianae*, on *Valeriana* spp. (*Valerianaceae*). *Phoma apiicola* and *Ph. valerianae* were classified in *Phoma* section *Phoma*, and *Ph. violicola* was classified in *Phoma* sect. *Peyronellaea*; however, the relationship of these species in *Leptosphaeriaceae* is clearly demonstrated (Fig. 2), and therefore the species are transferred to the new genus *Subplenodomus*. These results are in congruence with a recent study where *Ph. violicola*, *Ph. apiicola* and *Ph. valerianae* clustered in a clade representing both *Leptosphaeriaceae* and *Pleosporaceae* (Aveskamp *et al.* 2010).

Four *Leptosphaeria* species, *L. macrospora* (soil) and the necrotrophic species *L. nitschkei* (on *Asteraceae*), *L. praetermissa*, on *Rubus idaeus* (*Rosaceae*) and *L. dryadis*, on *Dryas* spp. (*Rosaceae*) grouped in a subclade A3 and are transferred here to a new genus *Paraleptosphaeria*. *Phoma korfii* also clustered in this subclade. The European species *Ph. heteromorphospora*, type species of *Phoma* section *Heterospora*, and the American counterpart *Ph. dimorphospora*, both pathogens on *Chenopodiaceae*, grouped in a distinct subclade A4. *Phoma* sect. *Heterospora* is raised to generic rank to accommodate both species in *Leptosphaeriaceae*.

Clade B comprises necrotrophic species related to the type species *L. doliolum* (anam. *Ph. acuta*). The phylogeny of this species complex, and the closely related species *Ph. veronicicola*, *Ph. macrocapsa* and *Ph. sydowii*, is treated below. The necrotrophic species *Ph. sclerotoides*, *L. conoidea* (anam. *Ph. doliolum*), *L. slovacica* (anam. *Ph. leonuri*) and *Ph. pedicularis* also proved to be related. The species *Ph. rubefaciens* and *Ph. etheridgei* also belong to clade B, but these species, both recorded on trees, are more distantly related.

The *Phoma* species in clades A and B are in majority currently described as anamorphs of the genus *Leptosphaeria*, or belong to *Phoma* section *Plenodomus*. These *Phoma* anamorphs are only distantly related to the type species *Ph. herbarum* and its relatives in *Didymellaceae*, and therefore these species described in section *Plenodomus* are excluded from the genus *Phoma*. Clade C is more distantly related to *Leptosphaeriaceae* and comprises species that are related to *Coniothyrium palmarum* in *Coniothyriaceae*. Two subclades are recognised in clade C: *Ph. glycinicola*, *Py. dolichi* and *Ph. carteri* group with the generic type species *C. palmarum*, whereas two isolates of *Ph. septicialis* group with *Ph. multipora*. The teleomorph *Neophaeosphaeria filamentosa* clustered basal to this clade. Clade D includes the genera *Cucurbitaria*, *Pyrenochaetopsis* and *Pyrenochaeta*, which represent *Cucurbitariaceae*. This finding is in congruence with previous studies (de Gruyter *et al.* 2010).

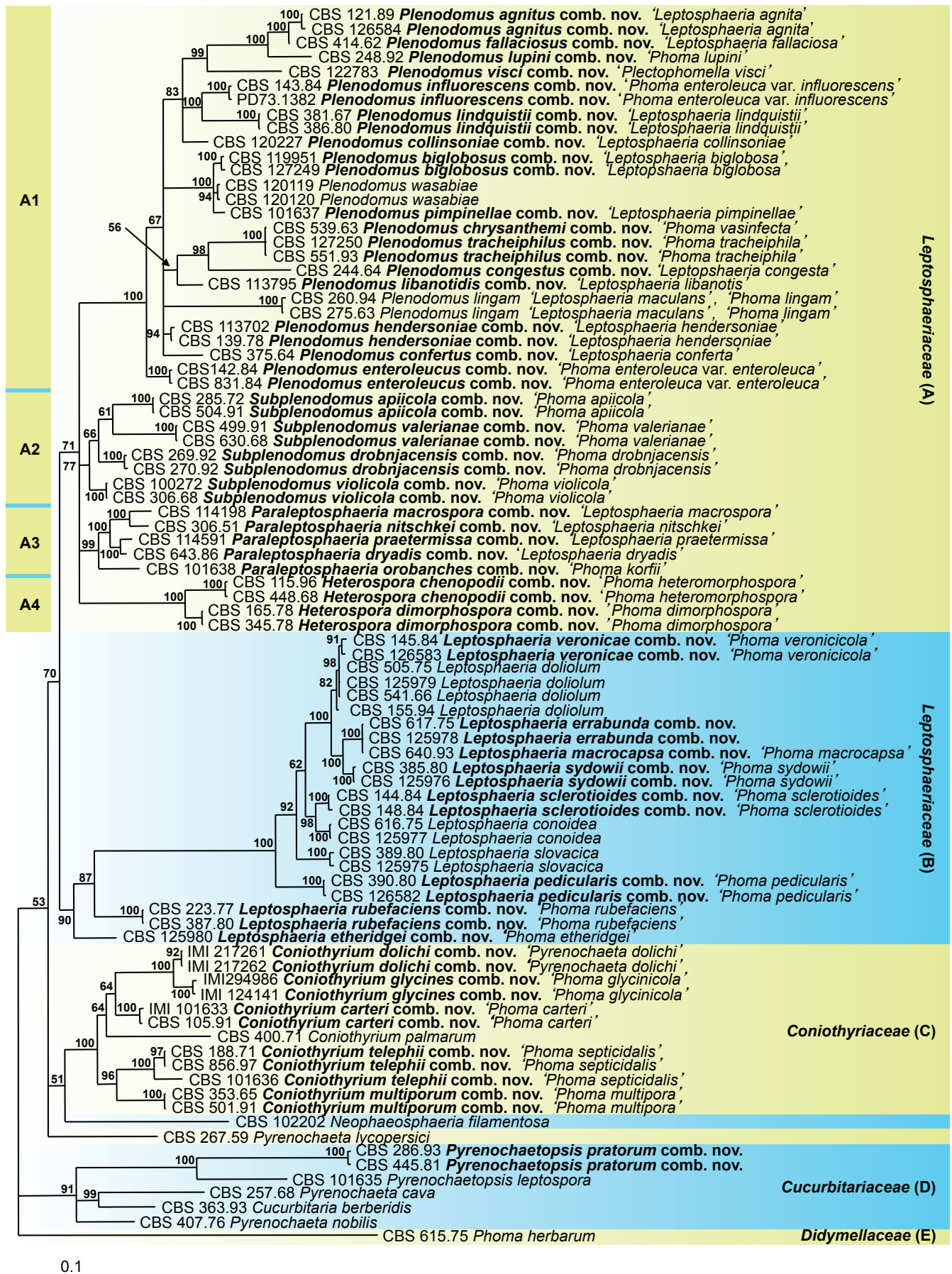


Fig. 2. The phylogeny of *Phoma* section *Plenodomus* and *Leptosphaeria*, based on the strict consensus tree from a Bayesian analysis of 87 LSU/ITS sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Phoma herbarum* (CBS 615.75).

Phylogeny of the *Leptosphaeria doliolum* complex

The aligned sequence matrix obtained for the ITS, ACT, TUB and CHS-1 regions had a total length of 1 345 nucleotide characters; ITS 522, ACT 240, TUB 332 and CHS-1 251, respectively. The combined dataset used in the analyses included 18 taxa and contained 1 345 characters with 98 unique site patterns. The tree (Fig. 3) was rooted to "*Ph. pedicularis*" (CBS 390.80). The Bayesian analysis resulted in 6 002 trees after 30 000 generations, from which the burn-in was discarded and the consensus tree and posterior probabilities were calculated based on 3 341 trees.

The phylogenetic tree revealed two clades with high posterior probabilities, 98 and 99 % respectively, clade A with *Ph. acuta* subsp. *errabunda* and *Ph. macrocapsa*, and clade B with *Ph. acuta* subsp. *acuta* (anamorph of *Leptosphaeria doliolum*) and *Ph. acuta* subsp. *acuta* f. sp. *phlogis*. *Phoma sydowii*, a necrotroph on *Asteraceae*, *Senecio* spp. in particular, proved to be closely related to *Ph. acuta* subsp. *errabunda*. The isolate CBS 297.51 preserved as *Ph. acuta* is similar to *Ph. sydowii*, a synonym of *L. sydowii*, see below. *Phoma veronicicola*, as a necrotroph specifically occurring on *Veronica* spp. (*Scrophulariaceae*), also proved to be related to *Leptosphaeria doliolum*.

Phylogeny of *Phoma* section *Pilosa*

The aligned sequence matrix obtained for the ACT region had a total length of 252 nucleotide characters (20 taxa), and contained 165 unique sites. The tree was rooted to *Ph. lingam* (CBS 147.24 and CBS 260.94). The Bayesian analysis resulted in 34 802 trees after 174 000 generations, from which the burn-in was discarded, and the consensus tree and posterior probabilities were calculated based on 11 728 trees (Fig. 4).

The phylogenetic tree representing the *Pleosporaceae* includes *Ph. betae*, type species of *Phoma* section *Pilosa*. This section is characterised by producing pycnidia that are covered by mycelial hairs. *Phoma betae* clearly groups with other pycnidial fungi pathogenic on *Chenopodiaceae*, including *Ascochyta obiones*, *A. hyalospora* and *A. caulina* and *Chaetodiplodia* sp. All species produce similar hairy pycnidia, but are classified in *Ascochyta* or *Coniothyrium* due to conidial septation, or brown pigmentation of conidia, respectively.

A subclade comprises the cosmopolitan *Pleospora herbarum* and related species. The species involved are associated with various hosts or substrates. The most closely related *Ph. incompta* is a specific pathogen on *Olea europea* (*Oleaceae*). *Phoma incompta* was classified in *Phoma* section *Sclerophomella* because of its thick-walled pycnidia (de Gruyter & Noordeloos 1992, Boerema & de Gruyter 1998). The pycnidial characters of *Ph. incompta*, pycnidia covered with mycelial hairs and with an indistinct ostiole visible as a pallid spot (de Gruyter & Noordeloos 1992) however, agrees with those of *Ph. betae* and *Ph. typhina*.

Phoma fallens proved to be closely related to *Ph. glaucispora* in keeping with the similar *in vitro* characters, especially the low growth-rate and the size and shape of its conidia (Boerema *et al.* 2004). Both species originate from southern Europe, and have been associated with spots on fruits and leaves of *Olea europea*, or leaf spots on *Nerium oleander*, respectively. An isolate preserved as *Leptosphaeria clavata*, CBS 259.51, proved to be closely related. The origin of the isolate, deposited by E. Müller, is unknown; however, it is likely that the isolate was obtained from *Poaceae*, *Triticum vulgare* or *Dactylis glomerata* (Müller 1950). *Phoma flavigena*, once isolated from water

and also recorded from southern Europe, proved to be more distantly related in *Pleosporaceae*.

Phylogeny of phoma-like anamorphs excluded from the suborder *Pleosporineae*

The aligned sequence matrix obtained for the LSU regions had a total length of 808 nucleotide characters, with 208 unique site patterns. The phylogenetic tree (Fig. 5) was rooted to *Pseudorobillarda phragmitis* (CBS 398.61). The Bayesian analysis resulted in 48 402 trees after 242 000 generations, from which the burn-in was discarded and the consensus tree and posterior probabilities were calculated based on 24 876 trees.

Clade A includes the reference isolates of the teleomorph *Paraphaeosphaeria* and the anamorph *Paraconiothyrium* classified in *Montagnulaceae*. This teleomorph/anamorph relation agrees with previous molecular phylogenetic studies (Verkley *et al.* 2004, Damm *et al.* 2008, de Gruyter *et al.* 2009). Other phoma-like species in this clade are *Ph. lini*, *Plenodomus fusco-maculans*, *Pleurophoma pleurospora* (CBS 101461) and *Asteromella tilliae*. *Phoma lini*, a saprobe frequently recorded on dead stems of *Linum* spp., was described in *Phoma* section *Phoma* (de Gruyter *et al.* 1993). Re-examination of the conidia revealed that they are hyaline and thin-walled; however, also darker, greenish to yellowish coniothyrium-like conidia were observed. The conidiogenous cells are phoma-like, doliiform to ampulliform.

The isolate *Asteromella tilliae* (CBS 265.94) clearly represents a species of *Paraconiothyrium*, and therefore, the teleomorph name *Didymosphaeria petrakiana*, *Didymosphaeriaceae*, is probably incorrect. It was already mentioned by Butin & Kehr (1995) that "considering the taxonomical placement of the teleomorph, the authors were informed about forthcoming taxonomic changes".

The morphological characters of the isolate CBS 101461, considered as representing the generic type species *Pleurophoma pleurospora*, resembles *Paraconiothyrium* as was previously discussed (de Gruyter *et al.* 2009). The sterile ex-type strain of *Plenodomus fusco-maculans*, CBS 116.16, recorded from *Malus* sp., also grouped with the *Paraconiothyrium* isolates.

Coniothyrium fuckelii clustered in the *Paraphaeosphaerial* *Paraconiothyrium* clade, in agreement with previous studies (Damm *et al.* 2008, Aveskamp *et al.* 2010), and therefore, the species is transferred to the genus *Paraconiothyrium*. Two phoma-like species obtained from *Citrus scoparius* and *Lonicera* sp. respectively (CBS 116668 and CBS 130329), cluster near *Montagnulaceae* and *Massarinaceae*. The morphological characters of the species are typical for *Pleurophoma pleurospora*. The taxonomic position of both isolates at familial rank could not be determined. The morphology of *Phoma flavescens* proved to be most similar to that of *Paraconiothyrium*, it definitely does not belong to *Phoma*, and therefore the species is transferred to *Paraconiothyrium*. Sequence data of additional species clustering nearby are required to resolve the current classification of *Ph. flavescens*. None of the phoma-like anamorphs included in this study grouped in clade B, which represents *Massarinaceae*.

Clade C includes the recently assigned ex-epitype strain of *Trematosphaeria pertusa*, isolate CBS 122368 (Zhang *et al.* 2008) and *Falciformispora lignatilis*. Both *T. pertusa* and *F. lignatilis* represent *Trematosphaeriaceae* (Suetrong *et al.* 2009). A second isolate preserved as *Trematosphaeria pertusa*, CBS 400.97, proved to be only distantly related, and clustered in clade D with *Aposphaeria populina* and *Melanomma pulvis-pyrius* in

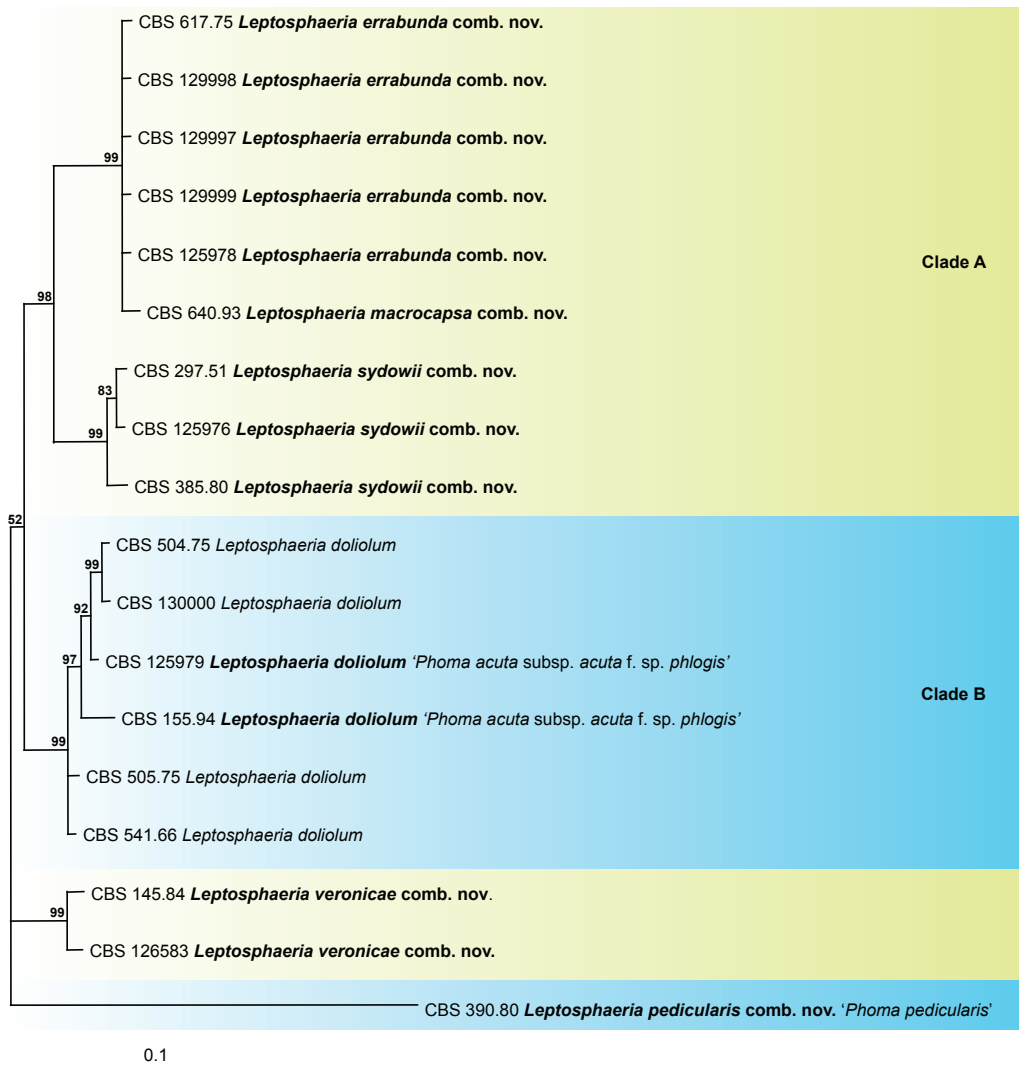


Fig. 3. The phylogeny of the *Leptosphaeria doliolum* complex, based on the strict consensus tree from a Bayesian analysis of 18 ITS/ACT/TUB/CHS-1 sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Leptosphaeria pedicularis* comb. nov. (CBS 390.80).

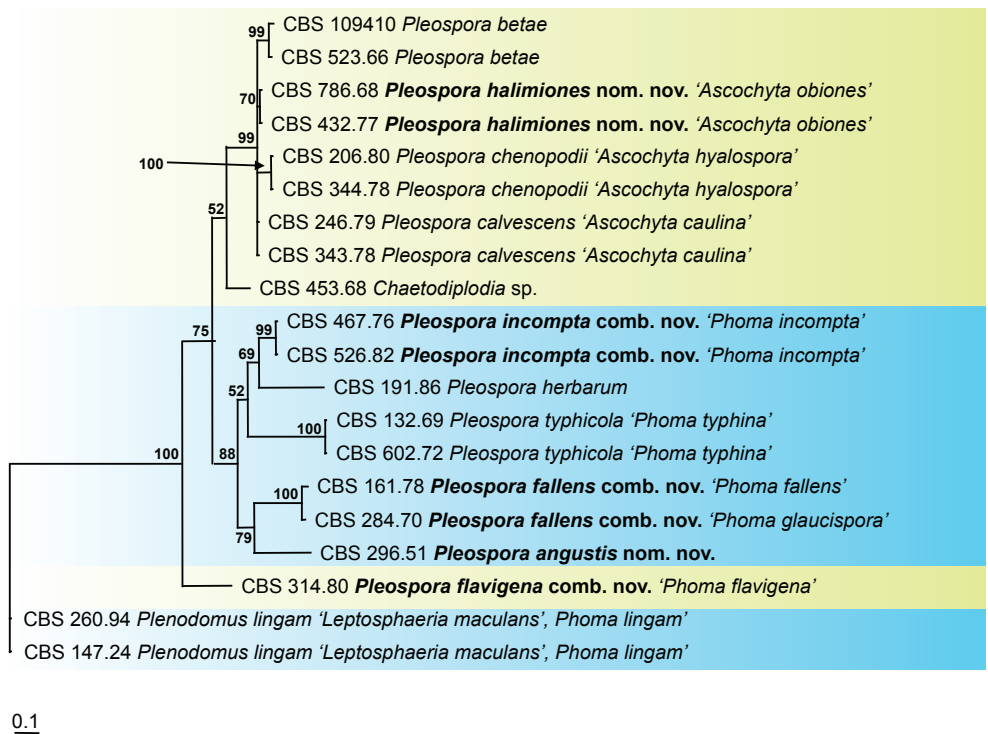


Fig. 4. The phylogeny of phoma-like anamorphs in the *Pleosporaceae* based on the strict consensus tree from a Bayesian analysis of 20 ACT sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Plenodomus lingam* (CBS 147.24, CBS 260.94).

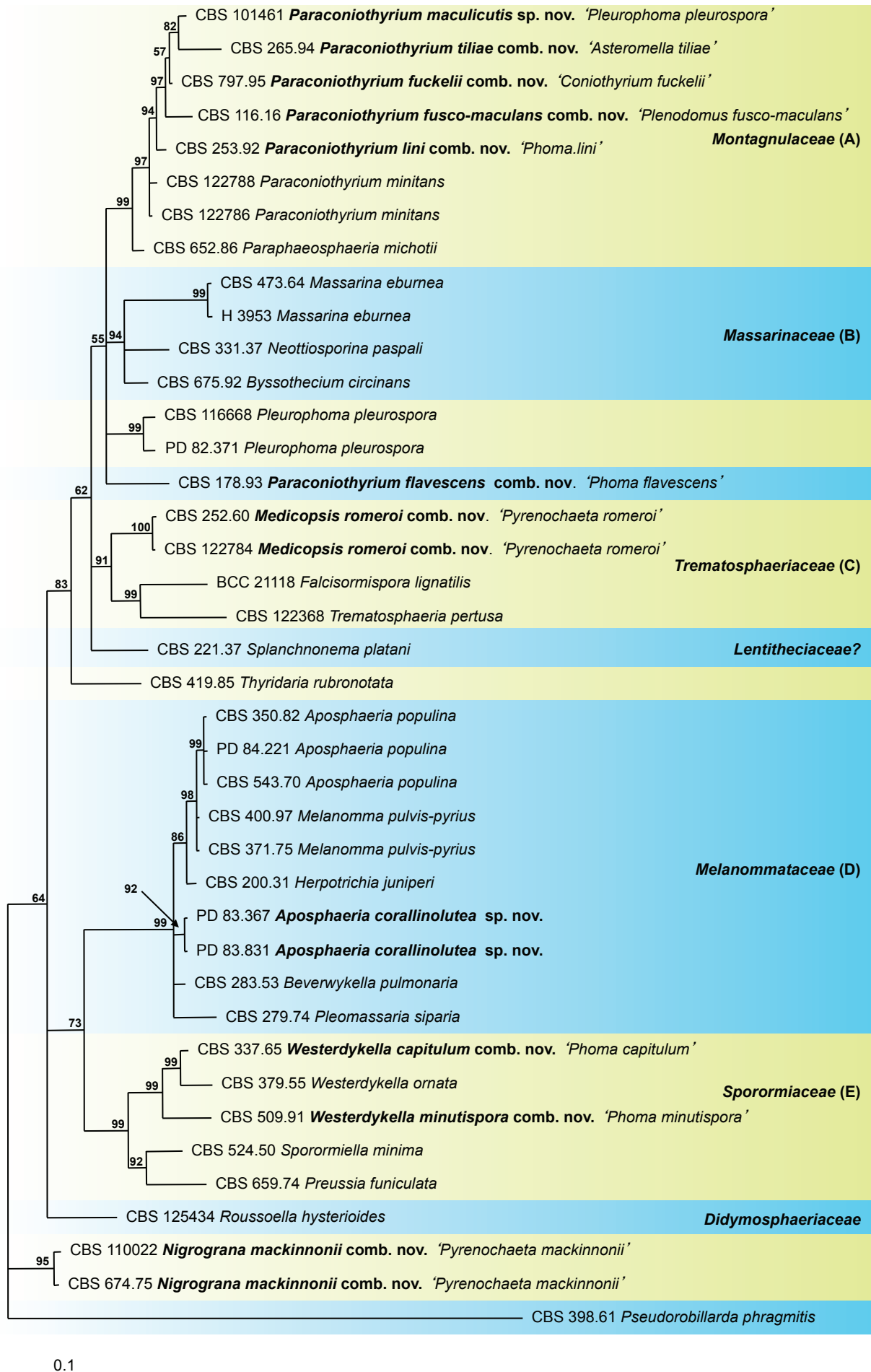


Fig. 5. LSU The phylogeny of phoma-like isolates excluded from the *Pleosporineae*, based on the strict consensus tree from a Bayesian analysis of 40 LSU sequences. The Bayesian posterior probabilities are given at the nodes. The tree was rooted to *Pseudorobillarda phragmitis* (CBS 398.61).

Melanommataceae. This isolate is considered as an incorrect identification (Mugambi & Huhndorf 2009), and we consider this sterile isolate as representative of *Melanomma pulvis-pyrius*. Clade C also comprises the human pathogen *Pyrenochaeta romeroi*. This species certainly does not belong to *Pyrenochaeta* (de Gruyter et al. 2010) and therefore, we describe the new genus *Medicopsis* in *Trematosphaeriaceae* to accommodate this species.

A well-supported clade D represents the *Melanommataceae* and includes *Melanomma pulvis-pyrius*, *Herpotrichia juniperi* and *Beverwijkella pulmonaria*, in congruence with Zhang et al. (2009). There were four phoma-like isolates present in the collections of CBS and PD, i.e. CBS 350.82, PD 83/367, PD 83/831 and PD 84/221, which could not be identified according to their morphological characters. The isolates were preserved as *Pleurophoma* spp. This study demonstrates that two strains represent *Aposphaeria populina*, whereas the other two strains represent the new species described here as *Aposphaeria corallinolutea*. Further studies in *Melanommataceae* are needed to clarify the phylogeny of *Aposphaeria* in *Melanommataceae*.

Sporormiaceae (clade E) is represented by *Sporormiella minima* and *Preussia funiculata*. *Phoma capitulum* and *Ph. minutispora*, well-defined soil-borne fungi from Asia, group in this clade. Both species are related with the anamorph *Westerdykella ornata*, and therefore the species are transferred to *Westerdykella* in *Sporormiaceae*.

Pyrenochaeta mackinnonii could not be assigned to familial rank. A blast search in GenBank with its LSU sequence suggested a relation with *Versicolorisporum triseptum*. However, the typical 3-septate conidia of this anamorph are different. Neither could *V. triseptum* be assigned at familial rank in *Pleosporales* (Tanaka et al. 2009). We therefore introduce the new genus *Nigrograna* to accommodate *Py. mackinnonii*.

TAXONOMY

Leptosphaeriaceae M.E. Barr, Mycotaxon 29: 503. 1987.

Heterospora (Boerema, Gruyter & Noordel.) Gruyter, Verkley & Crous, **stat. nov.** MycoBank MB564701.

Basionym: *Phoma* sect. *Heterospora* Boerema, Gruyter & Noordel., Persoonia 16: 336. 1997.

Type species: *Heterospora chenopodii* (Westend.) Gruyter, Aveskamp & Verkley, see below (= *Phoma heteromorphospora* Aa & Kesteren).

Heterospora chenopodii (Westend.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564702.

Basionym: *Phyllosticta chenopodii* Westend., Bull. Acad. Roy. Sci. Belgique Ser. 2, 2: 567. 1857; not *Phyllosticta chenopodii* Sacc., Syll. Fung. 3: 55. 1884 = *Phoma exigua* Desm. var. *exigua*; not *Plenodomus chenopodii* (P. Karst. & Har.) Arx, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 51: 72. 1957 = *Phoma chenopodii*col. Gruyter, Noordel. & Boerema, Persoonia 15: 395. 1993; not *Phoma chenopodii* Pavgi & U.P. Singh, Mycopathol. Mycol. Appl. 30: 265. 1966. nom. illeg. = *Phoma chenopodii* S. Ahmad, Sydowia 2: 79. 1948.

= *Septoria westendorpii* G. Winter, Hedwigia 26: 26. 1887. nom. nov.; not *Phoma westendorpii* Tosquinet, Westend., Bull. Acad. Roy. Sci. Belgique Ser. 2, 2: 564. 1857.

= *Phoma variospora* Aa & Kesteren, Persoonia 10: 268. 1979, nom. nov., nom. illeg. [not *Phoma variospora* Shreem., Indian J. Mycol. Pl. Pathol. 8: 221. 1979 ("1978")].

= *Phoma heteromorphospora* Aa & Kesteren, Persoonia 10: 542. 1980, nom. nov.

Specimens examined: **Belgium**, Beverloo, from leaves of *Chenopodium suecicum* (*album*) and *Chenopodium urbicum* (*Chenopodiaceae*), no date, G.D. Westendorp, Herb. Crypt. (Ed. Beyaert-Feys), No. 959. BR, **holotype** of *Phyllosticta chenopodii* Westend. ex herb. G.D. Westendorp. **Netherlands**, Baarn, from leaf spots in *Chenopodium album*, 3 Jul. 1968, H.A. van der Aa, **epitype designated here** CBS H-16386, culture ex-epitype CBS 448.68; Heelsum, from leaf spots in *Chenopodium album*, Sep. 1994, J. de Gruyter, CBS 115.96 = PD 94/1576.

Notes: Van der Aa & van Kesteren (1979) provided a nom. nov. since the epithet "*chenopodii*" was occupied in *Phoma*. For more details of the taxonomy of the species see van der Aa & van Kesteren (1979). Although *Leptosphaeria chenopodii-albi* was described from leaves of *Chenopodium album* (Crane & Shearer 1991) no cultures are available for comparison.

Heterospora dimorphospora (Speg.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564703.

Basionym: *Phyllosticta dimorphospora* Speg., Anales Mus. Nac. Buenos Aires 13: 334. 1910.

= *Phoma dimorphospora* (Speg.) Aa & Kesteren, Persoonia 10: 269. 1979.

= *Stagonospora chenopodii* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 40: 60. 1887 (sometimes erroneously listed as *Stag. chenopodii* "House").

Specimens examined: **Argentina**, La Plata, from leaves of *Chenopodium hircinum* (*Chenopodiaceae*), 13 Oct. 1906, C. Spegazzini, Colect. micol. Museo Inst. Spegazzini, No. 11.353, LPS, **holotype** of *Phyllosticta dimorphospora* Speg. **Lima**, from stem of *Chenopodium quinoa*, 1977, L.J. Turkensteen, CBS 165.78 = PD 77/884. **Peru**, from lesions in stems of *Chenopodium quinoa*, 1976, V. Otazu, **epitype designated here** CBS H-16203, culture ex-epitype CBS 345.78 = PD 76/1015.

Note: For more details of the taxonomy of the species see van der Aa & van Kesteren (1979).

Leptosphaeria Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 234. 1863.

= *Leptophoma* Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 124: 73. 1915.

Type species: *Leptosphaeria doliolum* (Pers. : Fr.) Ces. & De Not., see below.

Note: For full synonymy, including the species listed below, see Crane & Shearer (1991) and Boerema et al. (2004).

Leptosphaeria conoidea (De Not.) Sacc., Fungi Venet. Nov. Vel. Crit. Ser. 2: 314. 1875.

Basionym: *Leptosphaeria doliolum* var. *conoidea* De Not., Mycoto. Veneti, No. 76. 1873.

= *Leptosphaeria doliolum* subsp. *pinguicula* Sacc., Michelia 2: 598. 1882.

= *Phoma acuta* subsp. *amplior* Sacc. & Roum., Rev. Mycol. 6: 30. 1884.

= *Phoma hoehnellii* subsp. *amplior* (Sacc. & Roum.) Boerema & Kesteren, Trans. Brit. Mycol. Soc. 67: 299. 1976.

= *Phoma doliolum* P. Karst., Meddel. Soc. Fauna Fl. Fenn. 16: 9. 1888.

= *Plenodomus microsporus* Berl., Bull. Soc. Mycol. France 5: 55. 1889.

Specimens examined: **Netherlands**, Zaltbommel, from dead stem of *Lunaria annua* (*Brassicaceae*), Jan. 1974, G.H. Boerema, CBS 616.75 = ATCC 32813 = IMI 199777 = PD 74/56; Montfoort, *Senecio* sp. (*Asteraceae*), 1982, CBS 125977 = PD 82/888.

Leptosphaeria doliolum (Pers. : Fr.) Ces. & de Not., Comment. Soc. Crittog. Ital. 1: 234. 1863.

Basionym: *Sphaeria doliolum* Pers. : Fr., Icon. Desc. Fung. Min. Cognit. (Leipzig) 2: 39. 1800.

= *Sphaeria acuta* Hoffm. : Fr, Veg. cryptog. 1: 22. 1787. Syst. Mycol. 2: 507. 1823.

≡ *Phoma acuta* (Hoffm. : Fr.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 125. 1870 (as “*acutum*”).

≡ *Leptophoma acuta* (Hoffm. : Fr.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 124: 73. 1915.

≡ *Plenodomus acutus* (Hoffm. : Fr.) Bubák, Ann. Mycol. 13: 29. 1915 [as “(Fuckel)”].

= *Phoma phlogis* Roum., Rev. Mycol. 6: 160. 1884.

= *Phoma hoehnelii* var. *urticae* Boerema & Kesteren, Trans. Brit. Mycol. Soc. 67: 299. 1976.

Specimens examined: **Netherlands**, from stem of *Rudbeckia* sp. (Asteraceae), Sep. 1966, M.M.J. Dorenbosch, CBS 541.66 = PD 66/221; from stem of *Urtica dioica* (Urticaceae), 1974, G.H. Boerema, CBS 504.75 = PD 74/55; Rhenen, from *Urtica dioica*, Feb. 1975, G.H. Boerema, CBS 505.75 = PD 75/141; Wageningen, from stem of *Phlox paniculata* (Polemoniaceae), 1977, G.H. Boerema, CBS 155.94 = PD 77/80; from stem of *Phlox paniculata*, 1978, G.H. Boerema, CBS 125979 = PD 78/37; from stem of *Urtica dioica*, 1982, G.H. Boerema, CBS 130000 = PD 82/701.

Notes: Isolate CBS 541.66 was preserved as *Phoma acuta* subsp. *errabunda* (teleom. *Leptosphaeria errabunda*, see below); however, the isolate clustered with *L. doliolum*. Both isolates CBS 155.94 and CBS 125979 were considered as *forma specialis* “*phlogis*” (Boerema *et al.* 1994) of the anamorph *Ph. acuta* subsp. *acuta*. The subspecies *acuta* was created by the differentiation of *Phoma acuta* subsp. *amplior* Sacc. & Roum., but the latter is a synonym of *Ph. doliolum*, reclassified here as *L. conoidea*, see above. *Sphaeria acuta* Hoffm. was applied as basionym for different anamorphs an a teleomorph of various species of *Leptosphaeria* leading to a confusing nomenclature. The epitet has been unambiguously tied to *Ph. acuta* by Boerema & Gams (1995).

Leptosphaeria errabunda (Desm.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564704.

Basionym: *Phoma errabunda* Desm., Ann. Sci. Nat., Bot. Ser. 3, 11: 282. 1849.

≡ *Phoma acuta* subsp. *errabunda* (Desm.) Boerema, Gruyter & Kesteren, Persoonia 15: 465. 1994.

= *Leptophoma doliolum* Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 124: 75. 1915 [not *Phoma doliolum* P. Karst. = *Leptosphaeria conoidea* (De Not.) Sacc., see above].

≡ *Plenodomus doliolum* (Höhn.) Höhn., Ber. Deutsch. Bot. Ges. 36: 139. 1918.

≡ *Phoma hoehnelii* Kesteren, Netherlands J. Pl. Pathol. 78: 116. 1972, nom. nov.

= *Leptosphaeria doliolum* subsp. *errabunda* Boerema, Gruyter & Kesteren, Persoonia 15: 466. 1994.

Specimens examined: **Netherlands**, Leeuwarden, from stem of *Delphinium* sp. (Ranunculaceae), 1974, CBS 125978 = PD 74/61; Ferwerderadeel, from *Solidago* sp., hybrid (Asteraceae), Mar. 1974, G.H. Boerema, CBS 617.75 = ATCC 32814 = IMI 199775 = PD 74/201; from stem of *Aconitum* sp. (Ranunculaceae), CBS 129999 = PD 78/569; from stem of *Achillea millefolium* (Asteraceae), CBS 129997 = PD 78/631; from *Gaillardia* sp. (Asteraceae), 1984, G.H. Boerema, CBS 129998 = PD 84/462.

Notes: The isolate CBS 617.75 = ATCC 32814 was deposited as the anamorph *Ph. hoehnelii* var. *hoehnelii*, but interpreted as *L. doliolum* subsp. *conoidea* (Dong *et al.* 1998). The isolate clustered with *L. errabunda* in this study.

Leptosphaeria etheridgei (L.J. Hutchison & Y. Hirats.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564712.

Basionym: *Phoma etheridgei* L.J. Hutchison & Y. Hirats., Canad. J. Bot. 72: 1425. 1994.

Specimen examined: **Canada**, Alberta, from bark of gall, on trunk of *Populus tremuloides* (Salicaceae), Jul. 1989, P. Crane, **holotype** DAOM 216539, culture ex-holotype DAOM 216539 = CBS 125980 = PD 95/1483.

Leptosphaeria macrocapsa (Trail) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564713.

Basionym: *Phoma macrocapsa* Trail, Scott. Naturalist (Perth) 8: 327. 1886.

≡ *Plenodomus macrocapsa* (Trail) H. Ruppr., Sydowia 13: 20. 1959.

Specimen examined: **Netherlands**, from stem of *Mercurialis perennis* (Euphorbiaceae), 1978, G.H. Boerema, CBS 640.93 = PD 78/139.

Leptosphaeria pedicularis (Fuckel) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564714.

Basionym: *Phoma pedicularis* Fuckel, Reisen Nordpolarmeer 3: 318. 1874 (as “*pedicularidis*”); not *Phoma pedicularis* Wehm., Mycologia 38: 319. 1946 (= *Phoma herbicola* Wehm).

= *Sphaeronaema gentianae* Moesz, Bot Közlem. 14: 152. 1915 (as “*Sphaeronaema*”).

≡ *Plenodomus gentianae* (Moesz) Petr., Ann. Mycol. 23: 54. 1925.

Specimens examined: **Switzerland**, Kanton Graubünden, Albulapass, from dead stem of *Pedicularis* sp. (Scrophulariaceae), 1977, CBS 390.80 = PD 77/711 = ATCC 42535 = IMI 248430; Zürich, from *Gentiana punctata* (Gentianaceae), 1977, CBS 126582 = PD 77/710.

Leptosphaeria rubefaciens (Togliani) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564715.

Basionym: *Phoma rubefaciens* Togliani, Ann. Sper. Agr. II, 7: 1626. 1953.

Specimens examined: **Switzerland**, Zürich, Albis, from twig of *Quercus* sp. (Fagaceae), Aug. 1976, W. Gams, CBS 223.77. **Netherlands**, Oploo, from wood of *Tilia* (×) *europaea* (Tiliaceae), 1978, G.H. Boerema, CBS 387.80 = ATCC 42533 = IMI 248432 = PD 78/809.

Leptosphaeria sclerotioides (Sacc.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564716.

Basionym: *Phoma sclerotioides* Sacc., Fungi Herb. Bruxelles 21. 1892; Syll. Fung. 11: 492. 1895.

= *Plenodomus sclerotioides* Preuss, Klotzsch. Herb. Vivum Mycol. System Fungorum German., No. 1281. 1849, nom. nud. (no description).

= *Plenodomus meliloti* Mark.-Let., Bolezni Rast. 16: 195. 1927.

Specimens examined: **Canada**, British Columbia, from *Medicago sativa* (Fabaceae), 1980, J. Drew Smith, CBS 148.84 = PD 80/1242; Alberta, from root of *Medicago sativa*, Mar. 1984, G.H. Boerema, CBS 144.84 = CECT 20025 = PD 82/1061.

Note: Seven varieties of this species have been recognised (Wunsch *et al.* 2011) in a phylogenetic analysis using 10 loci.

Leptosphaeria slovacica Picb., Sborn. Vysoké Skoly. Zemed. v Brno 7: 7. 1927.

= *Phoma leonuri* Letendre, Revue Mycol. 6: 229. 1884.

≡ *Plenodomus leonuri* (Letendre) Moesz & Smarods in Moesz, Magyar Bot. Lapok 31: 38. 1932.

Specimens examined: **Netherlands**, from dead stem of *Ballota nigra* (Lamiaceae), 1977, CBS 125975 = PD 77/1161; Arnhem, from dead stem of *Ballota nigra*, 1979, G.H. Boerema, CBS 389.80 = PD 79/171.

Leptosphaeria sydowii (Boerema, Kesteren & Loer.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564717.

Basionym: *Phoma sydowii* Boerema, Kesteren & Loer., Trans. Brit. Mycol. Soc. 77: 71. 1981, nom. nov.

= *Sphaeronaema senecionis* Syd. & P. Syd., Ann. Mycol. 3: 185. 1905; not *Phoma senecionis* P. Syd., Beibl. Hedwigia 38: 136. 1899.

≡ *Plenodomus senecionis* (Syd. & P. Syd.) Bubák, Ann. Mycol. 13: 29. 1915.

≡ *Plenodomus senecionis* (Syd. & P. Syd.) Petr., Ann. Mycol. 19: 192. 1921, isonym.

= *Plenodomus rostratus* Petr., Ann. Mycol. 21: 199. 1923; not *Phoma rostrata* O'Gara, Mycologia 7: 41. 1915 (not *Leptosphaeria rostrata* M.L. Far & H.T. Horner, Nova Hedwigia 15: 250. 1968).

Specimens examined: **Switzerland**, Kt. Zürich, Zollikon, from *Papaver rhoeas* (*Papaveraceae*), Oct. 1949, E. Müller, CBS 297.51. **Netherlands**, from *Senecio jacobaea* (*Asteraceae*), G.H. Boerema, 1984, CBS 125976 = PD 84/472. **UK**, Scotland, Isle of Lewis, Hebrides, from dead stem of *Senecio jacobaea*, 1974, R.W.G. Dennis, CBS 385.80 = PD 74/477.

Notes: *Leptosphaeria senecionis* (Fuckel) G. Winter was suggested as the possible teleomorph (Boerema *et al.* 2004). Because the teleomorph connection has not been proven, however, we did not include it as a synonym that would have priority as the correct name. The isolate CBS 297.51 was originally identified as *L. doliolum* var. *doliolum*.

Leptosphaeria veronicae (Hollós) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564718.

Basionym: *Sphaeronaema veronicae* Hollós, Ann. Hist.-Nat. Mus. Natl. Hung. 4: 341. 1906.

≡ *Phoma veronicicola* Boerema & Loer., Trans. Brit. Mycol. Soc. 84: 297. 1985, nom. nov. (not *Phoma veronicae* Roum., Revue Mycol. 6: 160. 1884).

Specimens examined: **Netherlands**, from stem of *Veronica* "Shirley Blue" (*Scrophulariaceae*), 1974, CBS 126583 = PD 74/227; Huis ter Heide, from dead stem of *Veronica chamaedryoides*, Mar. 1978, H.A. van Kesteren, **neotype** CBS H-7632, culture ex-neotype CBS 145.84 = CECT 20059 = PD 78/273.

Paraleptosphaeria Gruyter, Verkley & Crous, **gen. nov.** MycoBank MB564720.

Pseudothecia immersed, subglobose, solitary or aggregated, thick-walled, pseudoparenchymatous to scleropectenchymatous, ostiolate, unilocular. *Asci* bitunicate, broadly ellipsoidal, 8-spored, interascal filaments pseudoparaphyses, *Ascospores* biserial, broadly fusiform, transversally 3–5-septate, hyaline to yellow-brownish. *Conidiomata* pycnidial, globose to subglobose, scleropectenchymatous, with papillate pore, unilocular. *Conidiogenous cells* phialidic, ampulliform to doliiform. *Conidia* hyaline, aseptate, oblong to ellipsoidal. Sclerotia sometimes produced.

Type species: *Paraleptosphaeria nitschkei* (Rehm ex G. Winter) Gruyter, Aveskamp & Verkley (see below).

Notes: Munk (1957) recognised *Leptosphaeria* section *Para-Leptosphaeria*, an invalid taxon, as a heterogenous group. The section was differentiated from *Eu-Leptosphaeria*, which included the generic type species *L. doliolum*. *Leptosphaeria nitschkei* was considered a typical representative of section *Eu-Leptosphaeria* (Müller & von Arx 1950). However, this molecular phylogeny demonstrates that *L. nitschkei* is only distantly related to *L. doliolum*.

We introduce *Paraleptosphaeria* to accommodate *L. nitschkei* and its relatives. These necrotrophic species are morphologically closely allied to *Leptosphaeria*. The former classification of *Leptosphaeria* in sections *Eu-Leptosphaeria* and *Para-Leptosphaeria* cannot be upheld from an evolutionary point of view, as two other species attributed to section *Eu-Leptosphaeria*, namely *L. agnita* and *L. maculans* (Munk 1957), were found to group in *Plenodomus*.

Paraleptosphaeria dryadis (Johanson) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564721.

Basionym: *Melanomma dryadis* Johanson, Hedwigia 29: 160. 1890.

≡ *Leptosphaeria dryadophila* Huhndorf, Bull. Illinois Nat. Hist. Surv. 34: 484 (1992), nom. illeg. via nom. superfl.

= *Leptosphaeria dryadis* Rostr., Bot. Tidsskr. 25: 305. 1903.

Specimen examined: **Switzerland**, Kt. Ticino, Leventina, Alpe Campolungo, from *Dryas octopetala* (*Rosaceae*), 24 July 1980, A. Leuchtman, CBS 643.86.

Note: An explanation of the nomenclature of *Leptosphaeria dryadis* has been provided by Chen *et al.* (2002).

Paraleptosphaeria macrospora (Thüm.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564722.

Basionym: *Leptosphaeria macrospora* Thüm. Mycotheca Univ. 1359. 1879, nom. nov.

≡ *Metasphaeria macrospora* (Fuckel) Sacc., Syll. Fung. 2: 158. 1883.

Replaced synonym: *Pleospora macrospora* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 138. 1870, nom. illeg., Art. 53.1. [not *Pleospora macrospora* (De Not.) Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 218. 1863].

Specimen examined: **Norway**, Troms, Tromsøya, from *Rumex domesticus* (*Polygonaceae*), 20 Aug. 1988, K. & L. Holm, CBS 114198 = UPSC 2686.

Paraleptosphaeria nitschkei (Rehm ex G. Winter) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564723.

Basionym: *Leptosphaeria nitschkei* Rehm ex G. Winter, Ascomyceten, Fascicle 1, No. 15. 1870, nom. nud. (Flora, Jena und Regensburg 55: 510. 1872).

Specimens examined: **Austria**, Öttscher in Niederösterreich, c. 4500', from *Cacalia* sp. (= *Adenostyles* sp., *Asteraceae*), June 1869, Lojka, **holotype** of *Leptosphaeria nitschkei* Rehm Ascomyceten 15b, S. **Switzerland**, Kt. Graubünden, Lü, from *Cirsium spinosissimum* (*Asteraceae*), 16 July 1948, E. Müller, **epitype designated here** CBS H-20822, culture ex-epitype CBS 306.51.

Note: The name *Leptosphaeria nitschkei* was considered a nom. nud. by Crane and Shearer (1991) who cited Art. 32.1 but gave no further explanation. In Flora, Jena und Regensburg 55: 510. 1872 Rehm refers to additional notes by G. Winter that include a Latin description. Therefore, we consider this name as valid, following Müller (1950) who provided a detailed description *in vivo*.

Paraleptosphaeria orobanches (Schweinitz : Fr.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564724.

Basionym: *Sclerotium orobanches* Schweinitz, Schriften Naturf. Ges. Leipzig 1: 57. 1822 : Fr., Syst. Mycol. 2: 257. 1822.

= *Phoma korffii* Boerema & Gruyter, Persoonia 17: 275. 1999.

Specimen examined: **USA**, Ringwood Swamp, Lloyd-Cornell, from stem of *Epifagus virginiana* (*Orobanchaceae*), 13 Sep. 1995, T. Uturriaga, R.P. Korf, P. Mullin, **holotype** of *Sclerotium orobanches* Schweinitz, CUP 63537, culture ex-holotype CBS 101638 = PD 97/12070.

Note: A *Phoma* synanamorph of *Sclerotium orobanches* was reported by Yáñez-Morales *et al.* (1998) and described as *Phoma korfii* (Boerema & Gruyter 1999).

Paraleptosphaeria praetermissa (P. Karst.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564725.

Basionym: *Sphaeria praetermissa* P. Karst., Bidrag Kannedom Finlands Natur Folk 23: 89. 1873.

= *Leptosphaeria praetermissa* (P. Karst.) Sacc., Syll. Fung. 2: 26. 1883.

Specimen examined: **Sweden**, Dalarna, Folkärna, from *Rubus idaeus* (*Rosaceae*), 21 Mar. 1993, K. & L. Holm, CBS 114591.

Plenodomus Preuss, *Linnaea* 24: 145. 1851.

= *Phoma* sect. *Plenodomus* (Preuss) Boerema, Kesteren & Loer., Trans. Brit. Mycol. Soc. 77: 61. 1981.

- = *Diploplenodomus* Diedicke, Ann. Mycol. 10: 140. 1912.
- = *Plectophomella* Moesz, Magyar Bot. Lapok 21: 13. 1922.
- = *Apocytospora* Höhn., Mitt. Bot. Lab. TH Wien 1: 43. 1924.
- = *Deuterophoma* Petri, Boll. R. Staz. Patalog. Veget. Roma 9: 396. 1929.

Type species: *Plenodomus rabenhorstii* Preuss, *Linnaea* 24: 145. 1851 (dubious synonym, see below) = *Plenodomus lingam* (Tode : Fr.) Höhn., see below.

Note: For full synonymy of the anamorph names of the species listed below, see Boerema *et al.* (1994). For additional synonyms of the teleomorph names of the species below that have been recorded on Asteraceous hosts, see Khashnobish *et al.* (1995).

Plenodomus agnitus (Desm.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564726.

Basionym: *Sphaeria agnita* Desm., Ann. Sci. Nat., Bot. Ser. 3, 16: 313. 1851.

- = *Leptosphaeria agnita* (Desm.) Ces. & De Not., Comm. Soc. Crittog. Ital. 1: 236. 1863.
- = *Plenodomus chondrillae* Died., Ann. Mycol. 9: 140. 1911; Krypt.-fl. Brandenburg 9: 236. 1912.
- = *Phoma agnita* Gonz. Frag., Mem. Real Acad. Ci. Barcelona 15: 6. 1920.

Specimens examined: **Netherlands**, from stem of *Eupatorium cannabinum* (*Asteraceae*), 1982, W.M. Loerakker, CBS 126584 = PD 82/561; from stem of *Eupatorium cannabinum*, 1982, W.M. Loerakker, CBS 121.89 = PD 82/903.

Plenodomus biglobosus (Shoemaker & H. Brun) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564727.

Basionym: *Leptosphaeria biglobosa* Shoemaker & H. Brun, Canad. J. Bot. 79: 413. 2001.

Specimens examined: **France**, Le Rheu, from stem of *Brassica juncea* (*Brassicaceae*), CBS 127249 = DAOM 229269. **Netherlands**, from *Brassica rapa* (*Brassicaceae*), 2006, R. Veenstra, CBS 119951.

Notes: *Leptosphaeria biglobosa* was originally described as a less virulent segregate of *L. maculans* (Shoemaker & Brun 2001). The species, also indicated as Tox⁰ isolates, has been described from cultivated *Brassica* species as the cause of upper stem lesions and considered as less damaging than *L. maculans* (West *et al.* 2002). However, in Poland *L. biglobosa* is the predominant cause of these symptoms (Jedryczka *et al.* 1999, Huang *et al.* 2005). The current species concept of *L. biglobosa* is broadly defined with six distinct subclades recognised by multilocus phylogenetic analyses of ITS, β -tubulin and actin sequences (Mendes-Pereira *et al.* 2003, Vincenot *et al.* 2008). These subclades are named after the host or geographic origin of the isolates involved. It has been suggested

that the clades represent distinct subspecies formed over time by reproductive isolation (Mendes-Pereira *et al.* 2003). Alignments of the ITS sequences of *Ph. wasbiae*, *Ph. pimpinellae* and *L. biglobosa* isolates were compared with those of the representative strains of the *L. biglobosa* subclades obtained from GenBank, and both *Ph. wasbiae* and *Ph. pimpinellae* grouped in this species complex (unpubl. data). Both species are maintained here, awaiting a redescription of the taxa representing all clades in the *L. biglobosa* complex.

Plenodomus chrysanthemi (Zachos, Constantinou & Panag.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564728.

Basionym: *Cephalosporium chrysanthemi* Zachos, Constantinou & Panag., Ann. Inst. Phytopath. Benaki, N.S. 55. 1960.

- = *Phialophora chrysanthemi* (Zachos, Constantinou & Panag.) W. Gams, Cephalosporium-artige Schimmelpilze (Stuttgart): 207. 1971.
- = *Phoma vasinfesta* Boerema, Gruyter & Kesteren, Persoonia 15: 484. 1994.

Specimen examined: **Greece**, from *Chrysanthemum* sp. (*Asteraceae*), Apr. 1963, D.G. Zachos, **holotype** CBS H-7576, culture ex-holotype CBS 539.63.

Note: The species was also described as *Phoma tracheiphila* f. sp. *chrysanthemi* (Baker *et al.* 1985).

Plenodomus collinsoniae (Dearn. & House) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564729.

Basionym: *Leptosphaeria collinsoniae* Dearn. & House, Bull. New York State Mus. Nat. Hist. 233–234: 36. 1921.

Specimen examined: **Japan**, Osawa river, Komukai, Miyagi, from *Vitis coignetiae* (*Vitaceae*), 27 Sep. 2003, Y. Takahashi, CBS 120227 = JCM 13073 = MAFF 239583.

Plenodomus confertus (Niessl ex Sacc.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564730.

Basionym: *Leptosphaeria conferta* Niessl ex Sacc., Syll. Fung. 2: 20. 1883.

- = *Phoma conferta* P. Syd. ex Died., Krypt.-fl. Brandenburg 9: 142. 1912.

Specimen examined: **Spain**, Cais do Tejo, from dead stem of *Anacyclus radiatus* (*Asteraceae*), Mar. 1961, M.T. Lucas, CBS 375.64.

Plenodomus congestus (M.T. Lucas) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564731.

Basionym: *Leptosphaeria congesta* M.T. Lucas, Trans. Brit. Mycol. Soc. 46: 362. 1963.

- = *Phoma congesta* Boerema, Gruyter & Kesteren, Persoonia 15: 461. 1994.

Specimen examined: **Spain**, Póvoa de Santa Iria, Estremadura, from stem of *Erigeron canadensis* (*Asteraceae*), Mar. 1961, M.T. Lucas, **holotype** of *Leptosphaeria congesta* M.T. Lucas, dried culture LISE 1638, culture ex-holotype CBS 244.64.

Plenodomus enteroleucus (Sacc.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564753.

Basionym: *Phoma enteroleuca* Sacc. var. *enteroleuca*, *Michelia* 1: 358. 1878.

Specimens examined: **France**, Alençon, from *Pyrus communis* (*Rosaceae*), 1878, C. C. Gillet, **holotype** of *Phoma enteroleuca* var. *enteroleuca*, Herb. Sacc. '19', PAD. **Germany**, Monheim, from leaf spots of *Triticum aestivum* (*Poaceae*), 15 Aug. 1984, M. Hossfeld, CBS H-3684, culture CBS 831.84. **Netherlands**, Bennekom, from discoloured wood of *Catalpa bignonioides* (*Bignoniaceae*), 1981, G.H. Boerema, **epitype designated here** CBS H-16209, culture ex-epitype CBS 142.84 = PD 81/654 = CECT 20063.

Plenodomus fallaciosus (Berl.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564732.

Basionym: *Leptosphaeria fallaciosa* Berl., Bull. Soc. Mycol. France. 5: 43. 1889.

Specimen examined: France, Var, Ste. Baume, from *Satureia montana* (Lamiaceae), July 1951, E. Müller, CBS 414.62 = ETH 2961.

Plenodomus hendersoniae (Fuckel) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564754.

Basionym: *Cucurbitaria hendersoniae* Fuckel, Symb. Myc. p. 172. 1870.

- ≡ *Melanomma hendersoniae* (Fuckel) Sacc., Syll. Fung. 2: 109. 1883.
- ≡ *Chiajaea hendersoniae* (Fuckel) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 129: 152. 1920.
- ≡ *Leptosphaeria hendersoniae* (Fuckel) L. Holm, Symb. Bot. Upsal. 14: 26. 1957.

= *Phoma intricans* M.B. Schwarz, Meded. Phytopath. Lab. Willie Commelin Scholten 8: 44. 1922.

Specimens examined: Sweden, Uppland, Jerusalem, from *Salix cinerea* (Salicaceae), 10 Apr. 1986, K. & L. Holm, CBS 113702 = UPSC 1843. Netherlands, Wilhelminadorp, from bark of *Pyrus malus* (Rosaceae), June 1977, H.A.Th. van der Scheer, CBS 139.78.

Plenodomus inflorescens (Boerema & Loer.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564755.

Basionym: *Phoma enteroleuca* var. *inflorescens* Boerema & Loer., Trans. Brit. Mycol. Soc. 84: 290. 1985.

Specimens examined: Netherlands, from *Lilium* sp. (Liliaceae), 1973, G.H. Boerema, PD 73/1382; Emmeloord, from *Fraxinus excelsior* (Oleaceae), 1978, J.D. Janse, **holotype** of *Phoma enteroleuca* var. *inflorescens*, CBS H-16208, culture ex holotype CBS 143.84 = PD 78/883 = CECT 20064.

Note: The isolate PD 73/1382 is no longer available for study.

Plenodomus libanotidis (Fuckel) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564756.

Basionym: *Pleospora libanotidis* Fuckel, Jahrb. Nassauischen Vereins Naturk. 27–28: 24. 1873 (as “*libanotis*”).

≡ *Leptosphaeria libanotidis* (Fuckel) Sacc., Syll. Fung. 2: 16. 1883 (as “*libanotis*”).

= *Phoma sanguinolenta* Rostr., Tidsskr. Landkon. 5(7): 384. 1888 (not *Phoma sanguinolenta* Grove, J. Bot. 23: 164. 1885).

≡ *Phoma rostrupii* Sacc., Syll. Fung. 11: 490. 1895, nom. nov.

Specimen examined: Sweden, Uppland, Gröna strand, from *Seseli libanotis* (Apiaceae), 19 May 1987, K. & L. Holm, CBS 113795 = UPSC 2219.

Plenodomus lindquistii (Frezzi) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564757.

Basionym: *Leptosphaeria lindquistii* Frezzi, Revista Invest. Agropec., Sér. 5, 5: 79. 1968.

= *Phoma macdonaldii* Boerema, Persoonia 6: 20. 1970.

Specimens examined: Canada, from *Helianthus annuus* (Asteraceae), 1967, W.C. McDonald, CBS 381.67. Former Yugoslavia, from stem of *Helianthus annuus*, 1977, A. Maric, CBS 386.80 = PD 77/336.

Note: Strain CBS 381.67 is ex-holotype of *Phoma macdonaldii* Boerema, pycnidial state of *Leptosphaeria lindquistii* Frezzi (Boerema 1970).

Plenodomus lingam (Tode : Fr.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 120: 463. 1911.

Basionym: *Sphaeria lingam* Tode : Fr., Fungi mecklenb. 2: 51. 1791. : Fr., Syst. Mycol. 2: 507. 1823.

≡ *Phoma lingam* (Tode : Fr.) Desm., Ann. Sci. Nat., Bot. Ser. 3, 11: 281. 1849.

= *Sphaeria maculans* Desm., Ann. Sci. Nat., Bot. Ser. 3, 6: 77. 1846, nom. illeg.

≡ *Leptosphaeria maculans* (Desm.) Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 235. 1863.

= *Plenodomus rabenhorstii* Preuss, Linnaea 24: 145. 1851, nom. dub.

Specimens examined: Netherlands, near Goes, from *Brassica oleracea* (Brassicaceae), 1978, M.M.J. Dorenbosch, CBS 260.94 = PD 78/989. Origin unknown, Mar. 1924, A. Weber, CBS 147.24. UK, from *Brassica* sp. (Brassicaceae), 1963, B.C. Sutton, CBS 275.63 = MUCL 9901 = UPSC 1025.

Notes: The combination *Plen. lingam* as published by van Höhnel (1911) was preferred over *Plen. rabenhorstii* Preuss (1851) by Boerema & van Kesteren (1964) because the type material of *Plen. rabenhorstii* had been lost during the Second World War. Therefore, *Plen. rabenhorstii* is indicated here as a *nomen dubium*. *Leptosphaeria maculans* causes a serious stem base canker (blackleg) on cultivated *Brassica* spp. (Brassicaceae) in Europe, Australia and North America (West *et al.* 2001, Fitt *et al.* 2006).

Plenodomus lupini (Ellis & Everh.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564758.

Basionym: *Phoma lupini* Ellis & Everh., Bull. Washburn Lab. Nat. Hist. 1: 6. 1884.

≡ *Asteromella lupini* (Ellis & Everh.) Petr., Sydowia 9: 495. 1955 (not *Phoma lupini* N.F. Buchw., Møller, Fungi Faeröes 2: 153. 1958, nom. illeg.).

Specimen examined: Peru, Andes region, from stem lesion of *Lupinus mutabilis* (Fabaceae), May 1992, J. de Gruyter, CBS 248.92 = PD 79/141.

Plenodomus pimpinellae (Lowen & Sivan.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564759.

Basionym: *Leptosphaeria pimpinellae* Lowen & Sivan., Mycotaxon 35: 205. 1989.

= *Phoma pimpinellae* Boerema & Gruyter, Persoonia 17: 278. 1999.

Specimen examined: Israel, Mt Carmel near Kibbutz Oren, from dead stems of *Pimpinella anisum* (Apiaceae), 9 Dec. 1987, R. Rowen, 523-88 NY, **holotype** of *Leptosphaeria pimpinellae* Lowen & Sivan, culture ex-holotype CBS 101637 = PD 92/41.

Plenodomus tracheiphilus (Petri) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564760.

Basionym: *Deuterophoma tracheiphila* Petri, Boll. Staz. Patol. Veg. Roma 9: 396. 1929.

≡ *Bakerophoma tracheiphila* (Petri) Cif., Ist. Bot. Reale Univ. Reale Lab. Crittog. Pavia Atti Ser. 5, 5: 307. 1946.

≡ *Phoma tracheiphila* (Petri) L.A. Kantsch. & Gikaschvili, Trudy Inst. Zashch. Rast. Tbilisi 5: 20. 1948.

Specimens examined: Israel, from *Citrus limonium* (Rutaceae), Oct. 1993, J. de Gruyter, CBS 551.93 = PD 81/782. Italy, from *Citrus* sp. (Rutaceae), CBS 127250 = PD 09/04597141.

Note: The species produces a phialophora-like synanamorph.

Plenodomus visci (Moesz) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564761.

Basionym: *Plectophomella visci* Moesz, Magyar Bot. Lapok 21: 13. 1922.

= *Apocytospora visci* Höhn., Mitt. Bot. Lab. TH Wien 1: 43. 1924.

Specimen examined: Hungary, Tata-Tóváros, from leaves of *Viscum album* (*Viscaceae*), 22 Oct. 1911, G. von Moesz, BP, **holotype** of *Plectophomella visci* Moesz. **France**, from *Viscum album*, 1974, **epitype designated here** CBS H-20823, culture ex-epitype CBS 122783 = PD 74/1021.

Notes: *Plectophomella visci* is the type species of the genus *Plectophomella*. This genus was accepted by Sutton (1980) based on the eustromatic conidiomata; branched, septate conidiophores, phialidic conidiogenesis and small, hyaline conidia. However, the phylogenetic analyses clearly demonstrated the placement of *Plectophomella* grouping in the *Plenodomus* clade and therefore it is treated as a synonym.

Plenodomus wasabiae (Yokogi) J.F. White & P.V. Reddy, *Canad. J. Bot.* 76: 1920. 1999 (1998).

Basionym: *Phoma wasabiae* Yokogi, *Ann. Phytopathol. Soc. Japan* 2: 549. 1933.

Specimens examined: Taiwan, from *Wasabia japonica* (syn. *Eutrema wasabi*) (*Brassicaceae*), A. Rossman, CBS 120119 = FAU 559; from *Wasabia japonica*, A. Rossman, CBS 120120 = FAU 561.

Subplenodomus Gruyter, Verkley & Crous, **gen. nov.** MycoBank MB564769.

Etymology: Although the genus resembles *Plenodomus* in the production of thick-walled pycnidia, the pycnidial cell wall of *Subplenodomus* often remains pseudoparenchymatous, similar to the pycnidial wall of species of *Phoma*.

Conidiomata pycnidial, globose to papillate, or with an elongated neck, solitary or aggregated, thin-walled pseudoparenchymatous, or thick-walled scleroplectenchymatous, ostiolate, unilocular. *Conidiogenous cells* phialidic, ampulliform to doliiform. *Conidia* hyaline, aseptate, ellipsoid to cylindrical. *Chlamydospores* sometimes produced, olivaceous, unicellular in chains, or multicellular, dictyosporous-botryoid or forming pseudosclerotoid structures.

Type species: *Subplenodomus violicola* (P. Syd.) Gruyter, Aveskamp & Verkley (see below)

Subplenodomus apiicola (Kleb.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564770.

Basionym: *Phoma apiicola* Kleb., *Z. Pflanzenkrankh.* 20: 22. 1910.

Specimens examined: Germany, from tuber of *Apium graveolens* var. *rapaceum* (*Apiaceae*), Feb. 1972, Diercks, culture CBS 285.72. **Netherlands**, from stem base of *Apium graveolens*, 1978, J. de Gruyter, CBS 504.91 = PD 78/1073.

Subplenodomus drobnjacensis (Bubák) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564771.

Basionym: *Phoma drobnjacensis* Bubák, *Bot. Közlem.* 14: 63. 1915 = *Pyrenochaeta gentianae* Chevassut, *Bull. Soc. Mycol. France.* 81: 36. 1965.

Specimens examined: **Netherlands**, from stem base of *Gentiana makinoi* "Royal Blue" (*Gentianaceae*), 1983, M.M.J. Dorenbosch, CBS 270.92 = PD 83/650; Naaldwijk, from red-brown root of *Eustoma exaltatum* (*Gentianaceae*), 1988, M.M.J. Dorenbosch, CBS 269.92 = PD 88/896.

Subplenodomus valerianae (Henn.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564772.

Basionym: *Phoma valerianae* Henn., *Nyt Mag. Naturvidensk.* 42: 29. 1904.

= *Phyllosticta valerianae-tripteris* f. *minor* Unamuno, *Mem. Real Soc. Esp. Hist. Nat.* 15: 348. 1929.

Specimens examined: **Netherlands**, Arnhem, from dead stem of *Valeriana phu* (*Valerianaceae*), Sep. 1968, G.H. Boerema, CBS 630.68 = PD 68/141; Elburg, from stem base of *Valeriana officinalis*, 1973, M.M.J. Dorenbosch, culture CBS 499.91 = PD 73/672.

Subplenodomus violicola (P. Syd.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564774.

Basionym: *Phoma violicola* P. Syd., *Beibl. Hedwigia* 38: 137. 1899.

= *Phyllosticta violae* f. *violae-hirtae* Allesch. *Rabenh.-Fl.*, Ed. 2, *Pilze* 6: 156. 1898.

= *Phoma violae-tricoloris* Died., *Ann. Mycol.* 2: 179. 1904.

= *Phyllosticta violae* f. *violae-sylvaticae* Gonz. *Frag., Trab. Mus. Nac. Ci. Nat., Ser. Bot.* 7: 35. 1914.

Specimens examined: **Netherlands**, Baarn, from leaf spot in *Viola tricolor*, 10 Mar. 1968, H.A. van der Aa, CBS 306.68. **New Zealand**, Auckland, Henderson, from leaf spot in *Viola tricolor* (*Violaceae*), 1997, J. Jury, CBS 100272.

Coniothyriaceae W.B. Cooke. *Revista Biol. (Lisbon)* 12: 289. 1983.

Coniothyrium carteri (Gruyter & Boerema) Verkley & Gruyter, **comb. nov.** MycoBank MB564775.

Basionym: *Phoma carteri* Gruyter & Boerema, *Persoonia* 17(4): 547. 2002 ("2001"), nom. nov.

Replaced synonym: *Pyrenochaeta minuta* J.C. Carter, *Bull. Illinois Nat. Hist. Surv.* 21: 214. 1941 [not *Phoma minuta* Wehm., *Mycologia* 38: 318. 1946, nor *Phoma minuta* Alcalde, *Anales Inst. Bot. Cavanilles* 10: 235. 1952; not *Coniothyrium minutum* (Berl.) O. Kuntze, *Revis. Gen. Pl.* 3: 459. 1898 = *Phoma cava*, syn. of *Pyrenochaeta cava*; not *Coniothyrium minutum* (Died.) Petr. & Syd., *Feddes Repert. Spec. Nov. Regni Veg. Beih.* 42: 349. 1927].

Specimens examined: **Germany**, isolated from *Quercus robur* (*Fagaceae*), 1991, CBS 105.91. **Netherlands**, from shoot of *Quercus* sp. (*Fagaceae*), 1984, M.M.J. Dorenbosch, CBS 101633 = PD 84/74.

Coniothyrium dolichi (Mohanty) Verkley & Gruyter, **comb. nov.** MycoBank MB564776.

Basionym: *Pyrenochaeta dolichi* Mohanty, *Indian Phytopathol.* 11: 85. 1958.

Specimen examined: **India**, Nani Tal, Sarichuan, from leafspot of *Dolichos biflorus* (*Fabaceae*), 20 Oct. 1955, N.N. Mohanty, CBS 124140 = IMI 217262, CBS 124143 = IMI 217261.

Notes: A synanamorph was noted and described as a *Coniosporium* state based on the dark brown to black, dictyosporous conidia (Mohanty 1958). This synanamorph was considered later as monodictys-like (Grodona *et al.* 1997).

Coniothyrium glycines (R.B. Stewart) Verkley & Gruyter, **comb. nov.** MycoBank MB564777.

Basionym: *Pyrenochaeta glycines* R.B. Stewart, *Mycologia* 49: 115. 1957.

≡ *Phoma glycinicola* Gruyter & Boerema, *Persoonia* 17: 554. 2002 ("2001"), nom. nov., nom. inval. (not *Phoma glycines* Sawada, *Special. Publ. Coll. Agric., Natl. Taiwan Univ.* 8: 129. 1959, nom. inval.). ≡ *Phoma glycines* Sawada ex J.K. Bai & G.Z. Lu, *Fl. Fungorum Sin.* 15: 33. 2003.

Specimens examined: **Zambia**, on Mt. Makulu, from leaf of *Glycine max* (*Fabaceae*), Mar. 1985, J.M. Waller, CBS 124455 = IMI 294986. **Zimbabwe**, from a leaf of *Glycine max* (*Fabaceae*), 2001, C. Lavy, CBS 124141 = PG1.

Coniothyrium multiporum (V.H. Pawar, P.N. Mathur & Thirum.) Verkley & Gruyter, **comb. nov.** MycoBank MB564778.

Basionym: *Phoma multipora* V.H. Pawar, P.N. Mathur & Thirum., Trans. Brit. Mycol. Soc. 50: 260. 1967.

≡ *Phoma multipora* V.H. Pawar & Thirum., Nova Hedwigia 12: 501. 1966, nom. nud.

Specimens examined: **Egypt**, CBS 501.91 = PD 83/888. **India**, Bombay, Bandra, from saline soil, 15 Jan. 1958, M.J. Thirumalachar, **Isotype** CBS H-16492, culture ex-isotype CBS 353.65 = ATCC 16207 = HACC 164 = IMI 113689.

Coniothyrium palmarum Corda, Icon. Fungorum. (Corda) 4: 38. 1840.

≡ *Clisosporium palmarum* (Corda) Kuntze, Revis. Gen. Pl. 3: 458. 1898.
≡ *Microdiplodia palmarum* (Corda) Died., Ann. Mycol. 11: 47. 1913.

Specimens examined: **Italy**, Sardegna, near Dorgali, from a dead petiole of *Chamaerops humilis* (Arecaceae), Aug. 1970, W. Gams, CBS H-10891–10893, culture CBS 400.71.

Coniothyrium telephii (Allesch.) Verkley & Gruyter, **comb. nov.** MycoBank MB564779.

Basionym: *Pyrenochaeta telephii* Allesch., Ber. bayer. bot. Ges. 4: 33. 1896.

≡ *Phoma septicialis* Boerema, Versl. Meded. Plantenziektenk. Dienst Wageningen 153 (Jaarb. 1978): 20. 1979, nom. nov. [not *Phoma telephii* (Vestergr.) Kesteren, Netherlands J. Pl. Pathol. 78: 117. 1972].

Specimens examined: **Finland**, Helsinki, Asko Kahanpää, obtained from air, Jan. 1971, CBS H-16567, culture CBS 188.71; Oulu, from mineral wool between walls, Dec. 1996, K. Poldmaa, CBS 856.97. **Zimbabwe**, from leaf of *Glycine max* (Fabaceae), CBS 101636 = PD 86/1186.

Cucurbitariaceae G. Winter, Rabenh, Krypt.-Fl., Ed 2, 308. 1885.

Neophaeosphaeria filamentosa (Ellis & Everh.) Câmara, M.E. Palm & A.W. Ramaley, Mycol. Res. 107: 519. 2003.

Basionym: *Leptosphaeria filamentosa* Ellis & Everh., J. Mycol. 4: 76. 1888.

≡ *Paraphaeosphaeria filamentosa* (Ellis & Everh.) M.E. Barr, Mycotaxon 43: 392. 1992.

Specimen examined: **Mexico**, from *Yucca rostrata* (Asparagaceae), Stevens, CBS 102202 = BPI 802755.

Pyrenochaetopsis pratorum (P.R. Johnst. & Boerema) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564780.

Basionym: *Phoma pratorum* P.R. Johnst. & Boerema, New Zealand J. Bot. 19: 395. 1981.

Specimens examined: **New Zealand**, Rakura, near Hamilton, from a leaf of *Lolium perenne* (Poaceae), 1980, P.R. Johnston, isotype CBS H-7625, CBS H-7626, culture CBS 445.81 = PDDCC 7049 = PD 80/1254; *Dactylis glomerata* (Poaceae), 1980, CBS 286.93 = PD 80/1252.

Pleosporaceae Nitschke, Verh. Naturhist. Vereines Preuss. Rheinl. 26: 74. 1869.

Pleospora angustis Gruyter & Verkley, **nom. nov.** MycoBank MB564781.

≡ *Leptosphaeria clavata* A.L. Guyot, Revue Mycol. (Paris) 11: 62. 1946.
≡ *Massariosphaeria clavata* (A.L. Guyot) Shoemaker & C.E. Babc.,

Canad. J. Bot. 67: 1582.1989; not *Pleospora clavata* Gucevič ("as clavatis"), Novosti Sist. Nizsh. Rast. 7: 168. 1970.

Specimen examined: **Switzerland**, 1951, E. Müller, CBS 296.51.

Notes: The origin of the isolate deposited by E. Müller is unknown; however, it is likely that the isolate was obtained from *Poaceae*, *Triticum vulgare* or *Dactylis glomerata* (Müller 1950). *Pleospora clavata* Gucevič was obtained from *Lonicera alseuosmoides* and refers to a different species.

Pleospora betae (Berl.) Nevod., Grib. ross. Exs., No. 247. 1915.

Basionym: *Pyrenophora echinella* var. *betae* Berl. Nuovo Giorn. Bot. Ital. 20: 208. 1888.

= *Pleospora betae* Björl., Bot. Not. 1944: 218. 1944. (later homonym), nom. illeg.

≡ *Pleospora bjoerlingii* Byford, Trans. Brit. Mycol. Soc. 46: 614. 1963, nom. nov.

= *Phoma betae* A.B. Frank, Z. Rübenzucker-Ind. 42: 904, tab. 20. 1892.

= *Phyllosticta betae* Oudem., Ned. Kruidk. Arch. Ser. 2, 2: 181. 1877.

= *Gloeosporium betae* Dearn. & E.T. Barthol., Mycologia 9: 356. 1917.

Specimens examined: **Netherlands**, Wageningen, from *Beta vulgaris* (Chenopodiaceae), Sep. 1966, M.M.J. Dorenbosch, CBS H-16156, culture CBS 523.66 = IHEM 3915 = PD 66/270; from *Beta vulgaris*, 1977, G.H. Boerema, CBS 109410 = PD 77/113.

Note: The name *Phoma betae* A.B. Frank has been conserved against *Phyllosticta tabifica* and any combination based on that name (Shoemaker & Redhead 1999).

Pleospora calvescens (Fr.) Tul. & C. Tul., Selecta Fung. Carpol. (Paris) 2: 266. 1863.

Basionym: *Sphaeria calvescens* Fr., Ann. Sci. Nat., Bot. Ser. 2, 19: 353. 1843.

≡ *Leptosphaeria calvescens* (Fr.) Sacc., Syll. fung. 2: 24. 1883.

≡ *Pyrenophora calvescens* (Fr.) Sacc., Syll. fung. 2: 279. 1883.

= *Chaetodiplodia caulina* P. Karst., Hedwigia 23: 62. 1884.

≡ *Ascochyta caulina* (P. Karst.) v.d. Aa & Kesteren, Persoonia 10: 271. 1979.

= *Microdiplodia henningsii* Staritz, Hedwigia 53: 163. 1913.

Specimens examined: **Germany**, Munkmarsch, from leaf spots in *Atriplex hastata* (Chenopodiaceae), 20 July 1977, G.H. Boerema, CBS H-8980, culture CBS 246.79 = PD 77/655. **Netherlands**, Texel, from dead stem of *Atriplex hastata*, June 1978, H.A. van der Aa, CBS H-8976, culture CBS 343.78.

Note: For additional synonyms see Boerema *et al.* (1993).

Pleospora chenopodii Ellis & Kellerman, J. Mycol. 4: 26. 1888.

= *Diplodia hyalospora* Cooke & Ellis, Grevillea 7: 5. 1878 (not *Pleospora hyalospora* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia. 42: 238. 1890).

≡ *Ascochyta hyalospora* (Cooke & Ellis) Boerema, S.B. Mathur & Neerg., Netherlands J. Pl. Pathol. 83: 156. 1977.

= *Diplodina ellisii* Sacc., Syll. Fung. 3: 417. 1884

Specimens examined: **Bolivia**, isolated from *Chenopodium quinoa* (Chenopodiaceae), 1974, S.B. Mathur, CBS H-9051, CBS H-9052, culture CBS 206.80 = PD 74/1022. **Netherlands**, Zoutelande, from *Atriplex hastata* (Chenopodiaceae), Aug. 1968, H.A. van Kesteren, CBS 344.78 = PD 68/682.

Note: Isolate CBS 344.78 was originally identified as *Ascochyta caulina* but was identical to *Pleospora chenopodii* in the present study.

***Pleospora fallens* (Sacc.) Gruyter & Verkley, comb. nov.**

Mycobank MB564782.

Basionym: *Phoma fallens* Sacc., Syll. Fung. 10: 146. 1892.

- = *Phyllosticta glaucispora* Delacr., Bull. Soc. Mycol. France 9: 266. 1893.
 - ≡ *Phoma glaucispora* (Delacr.) Noordel. & Boerema, Versl. Meded. Plantenziektenk. Dienst Wageningen 166 (Jaarb. 1987): 108. 1989 ("1988").
- = *Phyllosticta oleandri* Gutner, Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 2, Sporov. Rast. 1: 306. 1933.

Specimens examined: **Italy**, Capri, Villa Jovis, from a leaf spot of *Nerium oleander* (*Apogynaceae*), CBS H-16639, culture CBS 284.70 = PD 97/2400. **New Zealand**, Levin, from leaf spot of *Olea europaea* (*Oleaceae*), 1978, G.F. Laundon, CBS 161.78 = LEV 1131.

***Pleospora flavigena* (Constantinou & Aa) Gruyter & Verkley, comb. nov. Mycobank MB564783.**Basionym: *Phoma flavigena* Constantinou & Aa, Trans. Brit. Mycol. Soc. 79: 343. 1982.

Specimen examined: **Romania**, Bucuresti, isolated from water, 1980, K. Fodor, CBS H-1418, **holotype** of *Phoma flavigena* Constantinou & Aa, culture ex-holotype CBS 314.80 = PD 91/1613.

***Pleospora halimiones* Gruyter & Verkley, nom. nov. Mycobank MB564784.**

- ≡ *Diplodina obiones* Jaap (as "*obionis*"), Verh. Bot. Vereins Prov. Brandenburg 47: 96. 1905 (not *Pleopora obiones* P. Crouan & H. Crouan, Fl. Finistère: 22. 1867).
- ≡ *Ascochyta obiones* (Jaap) Died., Ann. Mycol. 10: 141. 1912.
- ≡ *Ascochyta obiones* (Jaap) P.K. Buchanan, Mycol. Pap. 156: 28. 1987.
- = *Coniothyrium obiones* Jaap (as "*obionis*"), Schriften Naturwiss. Vereins Schleswig-Holstein 14: 29. 1907.

Specimens examined: **Netherlands**, Texel, from leaf spots in *Halimione portulacoides* (*Chenopodiaceae*), 27 Oct. 1968, H.A. van der Aa, CBS H-9127, CBS H-9129, culture CBS 786.68; Texel, De Cocksdorp, from dead stems of *Halimione portulacoides*, 6 July 1977, H.A. van der Aa, CBS H-9126, CBS H-9125, culture CBS 432.77 = IMI 282137.

Notes: Isolate CBS 453.68 preserved as *Chaetodiplodia* sp. and also isolated from dying stems and leaf sheaths of *Halimione portulacoides* on Texel, is not the same as *Pleo. halimiones* and is probably a different species.

***Pleospora herbarum* (Pers.) Rabenh., Bot. Zeitung (Berlin) 15: 428. 1857; Klotzschii Herb. Viv. Mycol. 2: no. 547 (1854.)**Basionym: *Sphaeria herbarum* Pers., Syn. Meth. Fung. 1: 78. 1801.
= *Stemphylium herbarum* E.G. Simmons, Sydowia 38: 291. 1986 (1985).

Specimen examined: **India**, Uttar Pradesh, from a leaf of *Medicago sativa* (*Fabaceae*), 1986 (isolated in 1983), E.G. Simmons, CBS 191.86 = IMI 276975.

Note: This isolate is the ex-type culture of *Stemphylium herbarum*.

***Pleospora incompta* (Sacc. & Martelli) Gruyter & Verkley, comb. nov. Mycobank MB564785.**Basionym: *Phoma incompta* Sacc. & Martelli, Syll. Fung. 10: 146. 1892.

Specimens examined: **Greece**, Crete, from branch of *Olea europaea* (*Oleaceae*), 1976, N. Malathrakis, CBS H-16394, culture CBS 467.76. **Italy**, from branch of *Olea europaea*, Mar. 1982, CBS H-16392, culture CBS 526.82.

***Pleospora typhicola* (Cooke) Sacc., Syll. Fung. 2: 264. 1883.**Basionym: *Sphaeria typhicola* Cooke, Grevillea 5: 121. 1877.

- ≡ *Clathrospora typhicola* (Cooke) Höhn., Ann. Mycol. 16: 88. 1918.
- ≡ *Pyrenophora typhicola* (Cooke) E. Müll., Sydowia 5: 256. 1951.
- ≡ *Macrospora typhicola* (Cooke) Shoemaker & C.E. Babco., Canad. J. Bot. 70: 1644. 1992.
- = *Phyllosticta typhina* Sacc. & Malbr., Sacc., Michelia 2: 88. 1880.
 - ≡ *Phoma typhina* (Sacc. & Malbr.) van der Aa & Vanev, A revision of the species described in *Phyllosticta*: 468. 2002.
- = *Phoma typharum* Sacc., Syll. Fung. 3: 163. 1884.

Specimens examined: **Netherlands**, Texel, from dead leaves of *Typha angustifolia* (*Typhaceae*), 1969, W. Gams, CBS H-16597, culture CBS 132.69; Staverden, from leaf spots of *Typha* sp., 24 June 1972, G.S. de Hoog, CBS H-16598, culture CBS 602.72.

Phoma-like anamorphs excluded from the suborder *Pleosporineae****Montagnulaceae*** M.E. Barr, Mycotaxon 77: 194. 2001.***Paraconiothyrium*** Verkley, Stud. Mycol. 50: 327. 2004.

Type species: *Paraconiothyrium estuarinum* Verkley & M. da Silva, Stud. Mycol. 50: 327. 2004.

***Paraconiothyrium flavescens* (Gruyter, Noordel. & Boerema) Verkley & Gruyter, comb. nov. Mycobank MB564786.**Basionym: *Phoma flavescens* Gruyter, Noordel. & Boerema, Persoonia 15(3): 375. 1993.

Specimen examined: **Netherlands**, Nagele, from soil, rhizosphere of *Solanum tuberosum* (*Solanaceae*), CBS 178.93 = PD 82/1062.

***Paraconiothyrium fuckelii* (Sacc.) Verkley & Gruyter, comb. nov. Mycobank MB564787.**Basionym: *Coniothyrium fuckelii* Sacc., Nuovo Giorn. Bot. Ital. 8: 200. 1876; Michelia 1: 207. 1878

- ≡ *Clisosporium fuckelii* (Sacc.) Kuntze, Revis. Gen. Pl. 3: 458. 1898.
- ≡ *Microsphaeropsis fuckelii* (Sacc.) Boerema, 2003, Persoonia 18: 160. 2003.

Specimen examined: **Denmark**, Geelskov, from a dead stem of *Rubus* sp. (*Rosaceae*), 1995, A.M. Dahl-Jensen, CBS 797.95.

Notes: *Coniothyrium fuckelii* var. *sporulosum* has been redispersed as *Paraconiothyrium sporulosum* (Verkley et al. 2004) and it is clearly different from *Paraconiothyrium fuckelii* (Damm et al. 2008).

***Paraconiothyrium fusco-maculans* (Sacc.) Verkley & Gruyter, comb. nov. Mycobank MB564788.**Basionym: *Phoma fusco-maculans* Sacc., Michelia 2: 275. 1881
= *Plenodomus fusco-maculans* (Sacc.) Coons, J. Agric. Res. 5: 714. 1916.

Specimens examined: **Italy**, Selva, from decorticated wood of *Malus pumila* (*Rosaceae*), Oct. 1880, PAD, **holotype** of *Phoma fusco-maculans* Sacc. **USA**, from wood of *Malus* sp. (*Rosaceae*), July 1916, G.H. Coons, **epitype designated here** CBS H-20825, culture ex-epitype CBS 116.16.

Notes: *Plenodomus fusco-maculans* was discussed by Boerema & Loerakker (1985) and de Gruyter et al. (2010). The holotype of the basionym *Aposphaeria fusco-maculans* was studied and considered to be *Aposphaeria pulviscula* (Boerema et al. 1996). However, the description of *A. fusco-maculans* given by Boerema et al. (1996) fits the generic concept of *Paraconiothyrium*, in congruence with the molecular phylogeny of the culture CBS 116.16.

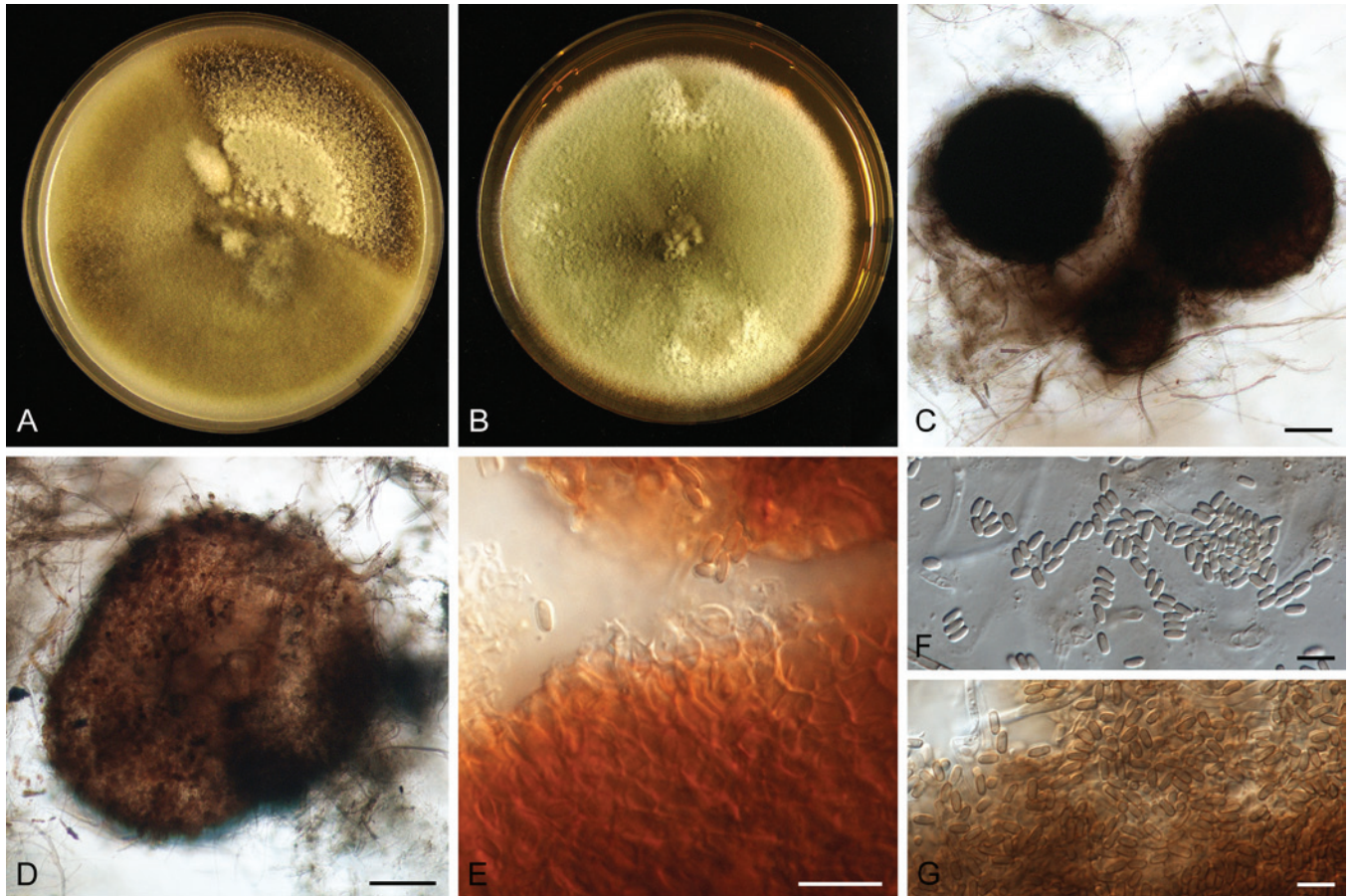


Fig. 6. *Paraconiothyrium maculicutis* sp. nov. CBS 101461. A–B. Fourteen day old cultures on OA (A) and MA (B). C–D. Pycnidia. E. Phoma-like conidiogenous cells. F–G. Conidia, initially hyaline to pale olivaceous (F), then becoming olivaceous (G). Scale bars: C–D = 20 μ m; E = 10 μ m; F–G = 5 μ m.

***Paraconiothyrium lini* (Pass.) Verkley & Gruyter, comb. nov.** MycoBank MB564789.

Basionym: *Phoma lini* Pass., Diagn. Funghi Nuovi 4, No. 81. 1890.

Specimen examined: Netherlands, from Wisconsin tank, 1970, CBS 253.92 = PD 70/998.

***Paraconiothyrium maculicutis* Verkley & Gruyter, sp. nov.** MycoBank MB564796. Fig. 6.

Etymology: Latin, cutis = skin; maculae = spots.

Pycnidia in vitro 50–125 μ m diam, globose to subglobose, glabrous or with mycelial outgrowth, scattered, non-ostiolate or ostiolate, pycnidial wall made up of 5–7 layers of cells. *Conidiogenous cells* 1.5–3 \times 0.5–2.5 μ m, indeterminate or ampulliform to filiform in a later state, up to 10 μ m in length. *Conidia* 1.5–2.5 \times 0.5–1.5 μ m, ellipsoidal, initially hyaline, then discolouring to olivaceous.

Description in vitro: Colonies on OA 50–52 mm diam after 7 d, margin entire; colony olivaceous buff to greenish olivaceous/grey olivaceous, with greenish olivaceous to pale olivaceous grey, finely floccose to woolly aerial mycelium; reverse smoke-grey to greenish olivaceous, with olivaceous patches. Colonies on MEA 43–44 mm diam after 7 d, margin entire; colony pale olivaceous grey to greenish olivaceous, with isabelline to cinnamon at centre, with compact pale olivaceous grey, finely floccose to woolly aerial mycelium; reverse buff to honey, isabelline to olivaceous near margin. *Pycnidia* globose to subglobose, olivaceous to brick, finally

olivaceous black, scattered, mainly on the agar, 50–125 μ m diam, glabrous or with mycelial outgrowth, non-ostiolate or ostiolate, pycnidial wall made up of 5–7 layers of cells. *Conidiogenous cells* 1.5–3 \times 0.5–2.5 μ m, ampulliform to filiform in a later state, up to 10 μ m in length. *Conidia* 1.5–2.5 \times 0.5–1.5 μ m, av. 1 \times 2 μ m, length/width ratio = 1.5–3.2, av. 2.2, ellipsoidal, initially hyaline, then discolouring to olivaceous. *Chlamydospores* absent. NaOH spot test: negative. *Crystals* absent.

Specimen examined: USA, Texas; San Antonio, Fort Sam Houston, from human, cutaneous lesions, 1989, D.P. Dooley, **holotype** CBS H-20824, culture ex-holotype CBS 101461 = IMI 320754 = UTHSC 87-144.

Notes: Isolate CBS 101461 was identified as *Pleurophoma pleurospora* (Dooley *et al.* 1989). However, *in vitro* data and the molecular phylogeny demonstrate that this isolate does not belong to *Pleurophoma pleurospora*, see below, and therefore is described as a new species in the genus *Paraconiothyrium*.

***Paraconiothyrium minitans* (W.A. Campb.) Verkley, Stud. Mycol. 50: 332. 2004.**

Basionym: *Coniothyrium minitans* W.A. Campb., Mycologia 39: 191. 1947.

Specimens examined: Netherlands, Boskoop, from stem of *Clematis* sp. (*Ranunculaceae*), 1999, J. de Gruyter, CBS 122786 = PD 99/1064-1. UK, CBS 122788 = PD 07/03486739.

***Paraconiothyrium tiliae* (F. Rudolphi) Verkley & Gruyter, comb. nov.** MycoBank MB564790.

Basionym: *Asteroma tiliae* F. Rudolphi, Linnaea 4: 514. 1829.

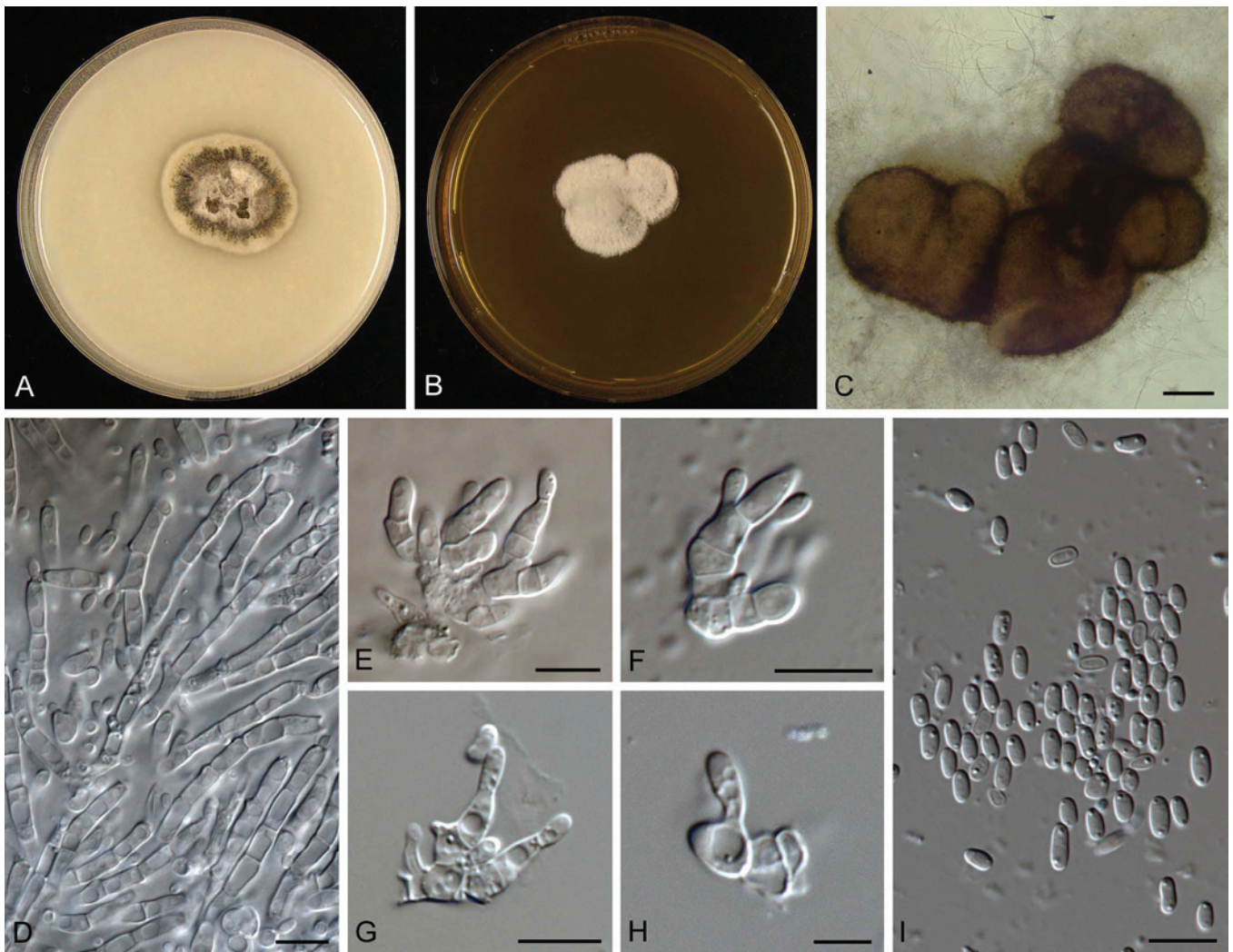


Fig. 7. *Pleurophoma pleurospora*. CBS 130329. A–B. Fourteen day old cultures on OA (A) and MA (B). C. Pycnidia. D–H. Conidiogenous cells, septate conidiophores with acropleurogenous conidiogenesis (D–G) or phoma-like (H). I. Conidia. Scale bars: C = 50 μ m; D–G, I = 10 μ m; H = 5 μ m.

\equiv *Asteromella tiliae* (F. Rudolphi) Butin & Kehr, Mycol. Res. 99: 1193. 1995, nom. inval., Art. 33.4.

Specimen examined: Austria, Amlach, from a leaf of *Tilia platyphyllos* (Tiliaceae), 10 Sep. 1993, H. Butin, **neotype** IMI 362854, **lectotype designated here** CBS H-20826, culture ex-lectotype CBS 265.94.

Pleurophoma pleurospora (Sacc.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 123: 117. 1914. Fig. 7.

Basionym: *Dendrophoma pleurospora* Sacc., *Michelia* 2: 97. 1880.

Description in vitro: Colonies on OA 14–18 mm diam after 7 d (18–28 mm after 14 d), margin entire to undulate; colony greenish olivaceous/olivaceous to rosy-buff and sepia, with white, felty aerial mycelium; reverse olivaceous grey to greenish olivaceous/olivaceous. Colonies on MEA 11–16 mm diam after 7 d (19–29 mm after 14 d), colony margin undulate; colony pale olivaceous grey/olivaceous grey to dark mouse-grey with rosy-buff tinges, with white, floccose, compact aerial mycelium, reverse umber/brown olivaceous to olivaceous/olivaceous black. *Pycnidia* globose to subglobose, olivaceous to olivaceous black, abundant, scattered, mainly on the agar, 30–120 μ m diam, solitary or aggregated, covered by mycelial outgrowths or setae-like hyphae, up to 50 μ m, non-papillated, without or with ostiole, walls made up of 2–5 layers of cells, outer layer(s) pigmented; conidial exudate not observed.

Conidiogenous cells of two types; ampulliform to doliiform, 4–6.5 \times 2–5.5 μ m, or filiform, septate, branched, acropleurogenous, up to 60 μ m long. *Conidia* 3.5–5.5 \times 1.5–2.5 μ m, av. 4.5 \times 2 μ m, length/width ratio = 1.5–3, av. 2.1, cylindrical to oblong, without or with some minute, polar orientated guttules. *Chlamydospores* absent. NaOH spot test: a weak reddish discolouring may occur on MA, not specific. *Crystals* absent.

Specimens examined: France, Perpignan, from leaf of *Laurus nobilis* (Lauraceae), PAD, **holotype** of *Dendrophoma pleurospora* Sacc. Netherlands, from wood of *Lonicera* sp. (Caprifoliaceae), **lectotype designated here** CBS H-20626, culture ex-lectotype CBS 130329 = PD 82/371; Molenhoek, Heumense Schans, from twig lesions of *Cytisus scoparius* (Fabaceae), 23 Aug. 2004, G. Verkley & M. Starink, CBS 116668.

Notes: A specimen derived from isolate CBS 130329 is assigned here as lectotype of *Pleurophoma pleurospora*, the type species of the genus (von Höhnelt 1914). The species is known from branches and bare wood of trees and shrubs (Sutton 1980, Boerema *et al.* 1996) and the isolate from *Cytisus scoparius* demonstrates that the species also may occur on green twigs. The isolates showed two types of conidiogenesis characteristic for the genus *Pleurophoma*; phoma-like, ampulliform to doliiform conidiogenous cells, as well as pyrenochaeta-like branched, filiform, septate, acropleurogenous. As a result, species of the genus *Pleurophoma* can easily be confused with taxa classified in the genera *Phoma*, *Paraphoma*, *Pyrenochaeta* and *Pyrenochaetopsis*.

Paraphaeosphaeria michotii (Westend.) O.E. Erikss., *Arkiv før Botanik* 6: 406. 1967.

Basionym: *Sphaeria michotii* Westend., *Bull. Acad. Roy. Sci. Belgique Ser. 2*, 7: 87. 1859.

Specimen examined: **Switzerland**, Kt. Obwalden, from *Typha latifolia* (*Typhaceae*), 18 May 1980, A. Leuchtmann, CBS 652.86 = ETH 9483.

Massarinaceae Munk, *Friesia* 5: 305. 1956.

Bysothecium circinans Fuckel, *Bot. Zeitung (Berlin)* 19: 251. 1861.

- ≡ *Leptosphaeria circinans* (Fuckel) Sacc., *Syll. Fung.* 2: 88. 1883.
- ≡ *Passeriniella circinans* (Fuckel) Sacc., *Syll. Fung.* 11: 326. 1895.
- ≡ *Trematosphaeria circinans* (Fuckel) G. Winter, *Rabenh. Krypt.-Fl.*, ed 1(2): 277. 1887.
- ≡ *Heptameria circinans* (Fuckel) Cooke, *Grevillea* 18: 30. 1889.
- = *Melanomma vindelicorum* Rehm, *Ber. Nat. Ver. Augsburg*: 116. 1881.
- ≡ *Trematosphaeria vindelicorum* (Rehm) Sacc., *Syll. Fung.* 2: 122. 1883.

Specimen examined: **USA**, South Dakota, from rotten crown of *Medicago sativa* (*Fabaceae*), G. Semeniuk, CBS 675.92 = ATCC 52767 = ATCC 52678 = IMI 266220.

Massarina eburnea (Tul. & C. Tul.) Sacc., *Syll. Fung.* 2: 153. 1883.

Basionym: *Massaria eburnea* Tul. & C. Tul., *Select. Fung. Carpol.* (Paris) 2: 239. 1863.

Specimens examined: **Switzerland**, Zürich, from *Fagus sylvatica* (*Fagaceae*), S.K. Bose, CBS 473.64 = ETH 2945. **UK**, Wales, isolated from dead branch of *Fagus sylvatica*, HHUF 26621, JCM 14422 = H3953.

Neottiosporina paspali (G.F. Atk.) B. Sutton & Alcorn, *Austral. J. Bot.* 22: 519. 1974.

Basionym: *Stagonospora paspali* G.F. Atk., *Bull. Cornell Univ. (Science)* 3: 33. 1897.

Specimen examined: **USA**, Florida, from *Paspalum notatum* (*Poaceae*), Oct. 1937, R.K. Voorhees, CBS 331.37.

Trematosphaeriaceae Suetrong *et al.* *Cryptogamie Mycol.* 32: 347. 2011.

Falciformispora lignatilis K.D. Hyde, *Mycol. Res.* 96: 27. 1992.

Specimen examined: **Thailand**, Pinruan Ban Bang, from *Elaeis guineensis* (*Arecaceae*), BCC 21118.

Medicopsis Gruyter, Verkley & Crous, **gen. nov.** MycoBank MB564791.

Etymology: refers to Medi- medica, Latin, -opsis, refers to, Greek. The description of the type species as the cause of a mycetoma suggest this is a human pathogen. However, the mycetoma described was secondary to a wound produced by a thorn of Palito blanco tree, and the species was found later on *Hordeum vulgare*.

Pycnidia solitary or confluent, on upper surface of the agar, globose to pyriform with elongated neck, setose, ostiolate, olivaceous to olivaceous-black, the wall with pseudoparenchymatal cells. *Conidiogenous cells* hyaline, phialidic, ampulliform to doliiform, to elongated. *Conidia* sub-hyaline to yellowish, ellipsoid, aseptate, catenulate.

Type species: *Medicopsis romeroi* (Borelli) Gruyter, Verkley & Crous (see below).

Medicopsis romeroi (Borelli) Gruyter, Verkley & Crous, **comb. nov.** MycoBank MB564792.

Basionym: *Pyrenochaeta romeroi* Borelli, *Dermatol. Venez.* 1: 326. 1959.

Specimens examined: **Venezuela**, from human, maduromycosis, no date, D. Borelli, UAMH 2892, **holotype** of *Pyrenochaeta romeroi* Borelli, culture ex-holotype CBS 252.60 = ATCC 13735 = FMC 151 = UAMH 10841. Country unknown, from *Hordeum vulgare* (*Poaceae*), 1984, M.M.J. Dorenbosch, CBS 122784 = PD 84/1022.

Notes: The species was described as a human pathogen of tropical origin, and it may cause suppurative subcutaneous or deep nonmycetomatous infections, or a subcutaneous phaeohyphomycotic cyst (Badali *et al.* 2010). However, the species also occurs in plant material.

Trematosphaeria pertusa (Pers.) Fuckel, *Jahrb. Nassauischen Vereins Naturk* 23–24: 161. 1870.

Basionym: *Sphaeria pertusa* Pers., *Syn. Meth. Fung.* 1: 83. 1801.

Specimen examined: **France**, Deux Sèvres, from bark of a dead stump of *Fraxinus excelsior* (*Oleaceae*), 25 Apr. 2004, Jacques Fournier, **epitype** IFRD 2002, culture ex-epitype CBS 122368.

Note: The epitype IFRD 2002 was designated by Zhang *et al.* (2008).

Lentitheciaceae Yin. Zhang, C.L. Schoch, J. Fourn., Crous & K.D. Hyde, *Stud. Mycol.* 64: 93. 2009.

Splanchnonema platani (Ces.) M.E. Barr, *Mycotaxon* 15: 364. 1982.

Basionym: *Sphaeria (Massaria) platani* Ces., in Rabenhorst, *Klotzschii Herb. Viv. Mycol.*: no. 1842. 1854.

Specimen examined: **USA**, from *Platanus occidentalis* (*Platanaceae*), Jan. 1937, C.L. Shear, CBS 221.37.

Note: This taxon was shown by Zhang *et al.* (2012) to cluster basal to the *Lentitheciaceae*.

Melanommataceae G. Winter, Rabenh. Krypt.-Fl., ed 1(2): 220 (1885) [as "*Melanommeae*"]

Aposphaeria corallinolutea Gruyter, Aveskamp & Verkley, **sp. nov.** MycoBank MB564798. Fig. 8.

Etymology: The name refers to the coral coloured colony on OA, and the luteous exudate diffusing into the agar medium.

Pycnidia in vitro 65–215 µm diam, solitary or aggregated to confluent, globose to subglobose, ostiolate or non-ostiolate. *Conidiogenous cells* 7–9 × 2–4 µm, ampulliform to filiform. *Conidia* 3–5 × 1–2 µm, ellipsoidal to allantoid, eguttulate or with some small, polar guttules.

Description in vitro: *Colonies* on OA 13–15 mm diam after 14 d, margin entire to somewhat lobated; colony vinaceous to brick, with white at centre, ochraceous near margin due to a diffusible pigment, with

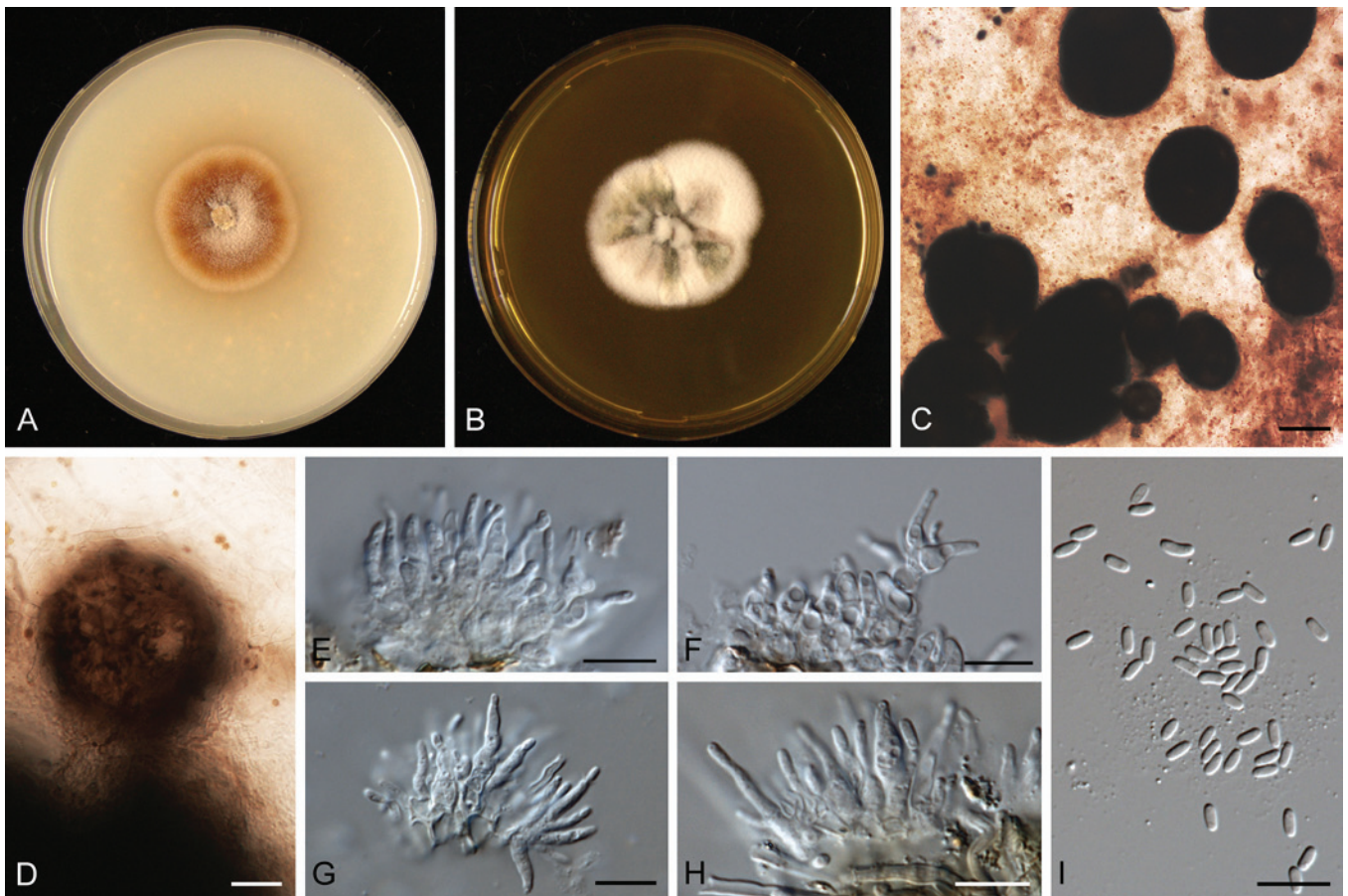


Fig. 8. *Aposphaeria corallinolutea* sp. nov. CBS 131287. A–B. Fourteen day old cultures on OA (A) and MA (B). C–D. Pycnidia. E–H. Conidiogenous cells. I. Conidia. Scale bars: C = 50 μ m; D = 20 μ m; E–I = 10 μ m.

white, felty or poorly developed aerial mycelium; reverse cinnamon to brick. Colonies on MEA 15–20 mm diam after 14 d, margin entire to somewhat lobated; colony white with dull green and grey olivaceous sectors and primrose tinges, with white, felty aerial mycelium; reverse sepia to brown olivaceous, greenish grey at centre, white near margin. *Pycnidia* globose to subglobose, olivaceous to brick, then olivaceous black, solitary or aggregated, 65–215 μ m diam, non-setose or with short setae-like outgrowths up to 25 μ m long, with or without distinct ostiole, pycnidial wall consisting of 3–5 layers of cells. *Conidiogenous cells* 7–9 \times 2–4 μ m, ampulliform to filiform. *Conidia* 3–5 \times 1–2 μ m, av. 4 \times 1.5 μ m, length/width ratio is 1.7–3.3, av. = 2.5, ellipsoidal to allantoid, eguttulate or with some small, polar guttules. *Chlamydozoospores* absent, NaOH test negative. *Crystals* produced in the agar, small, orange coloured.

Specimens examined: Netherlands, from wood of *Fraxinus excelsior* (Oleaceae), 1983, M.M.J. Dorenbosch, **holotype** CBS H-20625, culture ex-holotype CBS 131287 = PD 83/831; from wood of *Kerria japonica* (Rosaceae), 1983, M.M.J. Dorenbosch, CBS 131286 = PD 83/367.

Aposphaeria populina Died., Krypt.-Fl. Brandenburg 9: 206. 1912 (vol. dated "1915"). Fig. 9.

Description in vitro: Colonies on OA 21–24 mm diam after 7 d (32–37 mm diam after 14 d), margin entire to undulate; colony grey olivaceous/olivaceous to pale luteous/luteous, with white to pale olivaceous grey, finely felty to woolly aerial mycelium; reverse luteous to orange, greenish olivaceous to olivaceous or grey olivaceous/olivaceous grey to iron-grey, a rosy-buff discolouring near margin may occur. Colonies on MEA 16–20 mm diam after 7 d (30–37 mm diam after 14 d), margin entire to undulate; colony pale olivaceous grey

with rosy-vinaceous tinges to peach or olivaceous grey, with white, woolly aerial mycelium; reverse saffron to pale olivaceous/olivaceous grey, sometimes with dark vinaceous tinges, rosy-buff near margin. *Pycnidia* globose to subglobose, olivaceous to olivaceous black, scattered, 55–305 μ m diam, glabrous or with mycelial outgrowths, non-ostiolate or ostiolate, pycnidial wall composed of up to 10 layers of cells. *Conidiogenous cells* 5–11.5 \times 1.5–3 μ m, ampulliform to filiform. *Conidia* hyaline, subglobose to ellipsoidal, with 1–3 minute guttules, 1–2 \times 1–1.5 μ m, av. 1.5 \times 1 μ m, length/width ratio is 1.0–2.0, av. = 1.4. *Chlamydozoospores* and crystals absent, NaOH test negative.

Specimens examined: Germany, Triglitz, from twigs of *Populus canadensis* (Salicaceae), Mar. 1904. O. Jaap, B, **holotype**; from branch scars of *Picea abies*, (Pinaceae), Feb. 1982, H. von Aufess, CBS 350.82. Netherlands, Valkenswaard, from fallen twig of *Populus canadensis* (Salicaceae), 23 Mar. 1970, H.A. van der Aa, **epitype designated here** CBS H-9336, culture ex lectotype CBS 543.70; from wood of *Cornus mas* (Cornaceae), 1984, M.M.J. Dorenbosch, CBS 130330 = PD 84/221.

Beverwykella pulmonaria (Beverw.) Tubaki, Trans. Mycol. Soc. Japan 16: 139. 1975.

Basionym: *Papulaspora pulmonaria* Beverw., Antonie van Leeuwenhoek 20: 11. 1954.

Specimen examined: Netherlands, Baarn, from submerged leaf in rain water barrel of *Fagus sylvatica* (Fagaceae), Apr. 1953, A.L. van Beverwijk, culture CBS 283.53 = ATCC 32983 = IFO 6800.

Herpotrichia juniperi (Duby) Petr., Ann. Mycol. 23: 43. 1925.

Basionym: *Sphaeria juniperi* Duby, Klotzsch. Herb. Vivum Mycol. Systems Fungorum German., no. 1833. 1854.

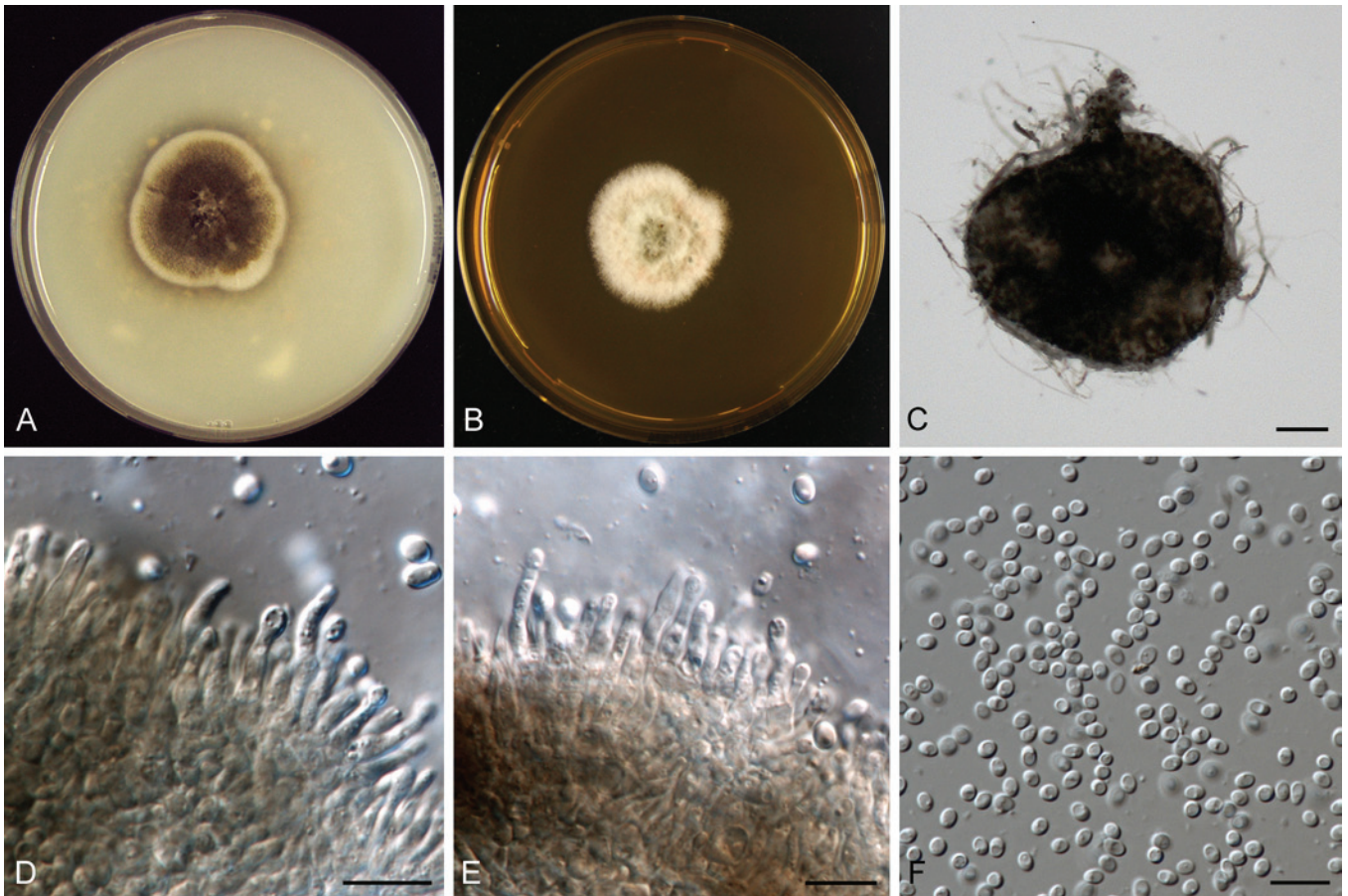


Fig. 9. *Aposphaeria populina*. CBS 543.70. A–B. Fourteen day old cultures on OA (A) and MA (B). C. Pycnidium with mycelial outgrowths (CBS 130330). D–E. Conidiogenous cells. F. Conidia. Scale bars: C = 20 µm; D–E = 10 µm; F = 5 µm.

Specimen examined: **Switzerland**, Andermatt, from *Juniperus nana* (Cupressaceae), Nov. 1931, E. Gäumann, CBS 200.31.

Melanomma pulvis-pyrius (Pers.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 160. 1870.

Basionym: *Sphaeria pulvis-pyrius* Pers., Syn. Meth. Fung. 1: 86. 1801.

Specimens examined: **Belgium**, from wood of *Fagus* sp. (Fagaceae), CBS 400.97. **France**, Vosges, Bot. Garden Le Chitelet, from unidentified decaying wood, CBS 371.75.

Notes: Phoma-like anamorphs have been reported by Chesters (1938) and Sivanesan (1984), but no anamorphic stage was observed in IFRDCC 2044, CBS 109.77 or CBS 371.75 after culturing 3 mo on PDA (Zhang *et al.* 2008). CBS 400.97 was preserved as *Trematosphaeria pertusa*.

Pleomassaria siparia (Berk. & Broome) Sacc., Syll. Fung. 2: 239. 1883.

Basionym: *Sphaeria siparia* Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 2(9): 321. 1852.

Specimen examined: **Netherlands**, Uden, from dead branch of *Betula verrucosa* (Betulaceae), 8 Dec. 1973, W.M. Loerakker, CBS H-258, CBS H-260, culture CBS 279.74.

Sporormiaceae Munk, Dansk Bot. Ark. 17(1): 450. 1957, nom. inval., Art. 36.1.

Preussia funiculata (Preuss) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 91. 1870 (1869–70).

Basionym: *Perisporium funiculatum* Preuss, Linnaea 24(1): 143. 1851.

Specimen examined: **Senegal**, from soil, CBS 659.74.

Sporormiella minima (Auersw.) S.I. Ahmed & Cain, Canad. J. Bot. 50: 449. 1972.

Basionym: *Sporormia minima* Auersw., Hedwigia 7: 66. 1868.

Specimen examined: **Panama**, from dung of goat, CBS 524.50.

Westerdykella Stolk, Trans. Brit. Mycol. Soc. 38: 422. 1955.

Type species: *Westerdykella ornata* Stolk, see below.

Westerdykella capitulum (V.H. Pawar, P.N. Mathur & Thirum) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564801.

Basionym: *Phoma capitulum* V.H. Pawar, P.N. Mathur & Thirum., Trans. Brit. Mycol. Soc. 50: 261. 1967.

≡ *Phoma capitulum* V.H. Pawar & Thirum., Nova Hedwigia 12: 502. 1966 (as "*capitula*"), nom. nud., nom. inval.

= *Phoma ostiolata* V.H. Pawar, P.N. Mathur & Thirum., Trans. Brit. Mycol. Soc. 50: 262. 1967, var. *ostiolata*.

≡ *Phoma ostiolata* V.H. Pawar & Thirum., Nova Hedwigia 12: 502. 1966, nom. nud., nom. inval.

= *Phoma ostiolata* var. *brunnea* V.H. Pawar, P.N. Mathur & Thirum., Trans. Brit. Mycol. Soc. 50: 263. 1967.

≡ *Phoma ostiolata* var. *brunnea* V.H. Pawar & Thirum., Nova Hedwigia 12: 502. 1966, nom. nud., nom. inval.

Specimen examined: India, Bandra, Bombay, from saline soil, 15 Jan. 1958, M.J. Thirumalachar, **Isotype** CBS H-7602, culture ex-isotype CBS 337.65 = ATCC 16195 = HACC 167 = IMI 113693 = PD 91/1614.

Westerdykella minutispora (P.N. Mathur ex Gruyter & Noordel.) Gruyter, Aveskamp & Verkley, **comb. nov.** MycoBank MB564793.

Basionym: *Phoma minutispora* P.N. Mathur ex Gruyter & Noordel., Persoonia 15: 75. 1992 (as "collection name" originally also referred to Thirumalachar; = depositor).

Replaced synonym: *Phoma oryzae* Cooke & Massee, Grevillea 16: 15. 1887 (not *Phoma oryzae* Catt., Arch. Triennale Bot. Crittog. Pavia 2–3: 118. 1879, nom. illeg).

≡ *Phyllosticta oryzae* (Cooke & Massee) I. Miyake. J. Coll. Agric. Imp. Univ. Tokyo 2: 252. 1910, nom. illeg.

Specimen examined: India, from saline soil, 1977, M.J. Thirumalachar, CBS H-5941, culture CBS 509.91 = PD 77/920.

Westerdykella ornata Stolk, Trans. Brit. Mycol. Soc. 38: 422. 1955.

Specimen examined: Mozambique, from mangrove mud, CBS 379.55.

Didymosphaeriaceae Munk, Dansk Bot. Ark. 15(2): 128. 1953.

Rousoella hysterooides (Ces.) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1. 128: 563. 1919.

Basionym: *Dothidea hysterooides* Ces., Atti Accad. Sci. Fis. 8: 24. 1879.

Specimen examined: Japan, Aomori, Shimokita Yagen, from culms of *Sasa kurilensis* (Poaceae), Y. Ooki, culture CBS 125434 = HH 26988.

Family *incertae sedis*

Nigrograna Gruyter, Verkley & Crous, **gen. nov.** MycoBank MB564794.

Etymology: refers to Nigro-, black, Latin, -grana, grains, Latin. The description refers to the black grains produced by the type species.

Pycnidia solitary or rarely confluent, on upper surface or submerged in agar, globose to subglobose or pyriform, with dark brown, septate mycelial outgrowths, with papillate ostioles, olivaceous to olivaceous-black, the wall with pseudoparenchymatous cells. *Conidiogenous cells* hyaline, phialidic, discrete. *Conidia* subhyaline, brown in mass, aseptate, ellipsoidal.

Type species: *Nigrograna mackinnonii* (Borelli) Gruyter, Verkley & Crous (see below).

Nigrograna mackinnonii (Borelli) Gruyter, Verkley & Crous, **comb. nov.** MycoBank MB564795.

Basionym: *Pyrenochaeta mackinnonii* Borelli, Castellania 4: 230. 1976.

Specimens examined: Mexico, from a mycetoma of a human, Feb. 2002, R. Arenas, CBS 110022; Venezuela, from a black grain mycetoma of human, Aug. 1975, D. Borelli, **holotype** FMC 270, culture ex-holotype CBS 674.75.

Thyridaria rubronotata (Berk. & Broome) Sacc., Syll. Fung. 2: 141. 1883.

Basionym: *Melogramma rubronotatum* Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 3(3): 20. 1859.

Specimen examined: Netherlands, Zuidelijk Flevoland, from a dead branch of *Acer pseudoplatanus* (Aceraceae), 13 Apr. 1985, N. Ernste, CBS H-18824, culture CBS 419.85.

DISCUSSION

The genus *Phoma* has been shown to be highly polyphyletic and *Phoma* is now restricted to taxa in the *Didymellaceae* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010). *Phoma* anamorphs and phoma-like species in *Coniothyriaceae*, *Leptosphaeriaceae*, *Melanommataceae*, *Montagnulaceae*, *Pleosporaceae*, *Sporormiaceae* and *Trematosphaeriaceae* are redisposed here as a result of this and previous studies.

The delimitation of *Leptosphaeriaceae* in *Pleosporineae* from *Cucurbitariaceae*, *Didymellaceae*, *Phaeosphaeriaceae* and *Pleosporaceae* agrees with recent studies of phoma-like species in *Pleosporales* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010, de Gruyter *et al.* 2010). *Cucurbitariaceae* is recognised as the fifth family in *Pleosporineae* in addition to the four families accepted by Zhang *et al.* (2009), which are *Didymellaceae*, *Leptosphaeriaceae*, *Phaeosphaeriaceae* and *Pleosporaceae*.

The genera *Leptosphaeria*, *Paraleptosphaeria*, *Plenodomus*, *Subplenodomus* and *Heterospora*

Plenodomus lingam and *L. doliolum*, the type species of *Plenodomus* and *Leptosphaeria* respectively, were found to be distant genetically, which agrees with findings of previous molecular phylogenetic studies (Jasalavic *et al.* 1995, Morales *et al.* 1995, Dong *et al.* 1998, Câmara *et al.* 2002, Eriksson & Hawksworth 2003, Wunsch & Bergstrom 2011). In our study the generic type species grouped in sister clades, which represent *Leptosphaeria* and *Plenodomus*. Species of *Leptosphaeria* produce dark brown, 3-septate ascospores, which have been considered the primitive state with more recently evolved species producing ascospores that are paler in colour, longer and narrower, and more than 3-septate (Wehmeyer 1946). This hypothesis is supported by the results obtained in our study. *Paraleptosphaeria* is distinct but seems to be most closely related to *Leptosphaeria* producing 3(–5)-septate, yellow/brown or hyaline ascospores. Both genera include only necrotrophic species. *Plenodomus* and *Subplenodomus* include necrotrophs and plant pathogens. Ascospores in *Plenodomus* are 3–7-septate, whereas in *Subplenodomus* no sexual state has thus far been recorded. The scleropectenchymatous pycnidial cell wall is typical for *Plenodomus*, whereas in *Subplenodomus* the pycnidial cell wall is pseudoparenchymatous. *Heterospora* is closely allied to *Subplenodomus* and no sexual state has been recorded for this genus either. The distinctive characteristics of the genera *Heterospora*, *Leptosphaeria*, *Paraleptosphaeria*, *Plenodomus* and *Subplenodomus* are summarised in Table 2. A blast search in GenBank using ITS sequences of five selected species of the *Leptosphaeriaceae*, namely *L. doliolum*, *L. etheridgei*, *Plen. lingam*, *H. dimorphospora* and *Subplen. drobnjacensis*, did not reveal close matches to other

Table 2. Characteristics of ascospores, mitosporic state and pathogenicity of *Leptosphaeria*, *Paraleptosphaeria*, *Plenodomus* and *Subplenodomus* *in vivo*.

Genus	Ascospores	Mitosporic state	Pathogenicity
<i>Leptosphaeria</i>	Ascospores 3-septate, (dark) brown	Mitosporic state common, pycnidial cell wall usually directly scleroplectenchymatous, conidia mostly aseptate	Necrotrophic
<i>Paraleptosphaeria</i>	Ascospores 3–5-septate, hyaline to yellow/brown	Mitosporic state rare, pycnidial cell wall directly scleroplectenchymatous, conidia aseptate	Necrotrophic
<i>Plenodomus</i>	Ascospores 3–7-septate, pale yellow to brown	Mitosporic state common, pycnidial cell wall initially pseudoparenchymatous, later scleroplectenchymatous, conidia aseptate	Necrotrophic or plant pathogenic
<i>Subplenodomus</i>	No known sexual state	Mitosporic state common, pycnidial cell wall mainly pseudoparenchymatous, conidia aseptate	Necrotrophic or plant pathogenic
<i>Heterospora</i>	No known sexual state	Mitosporic state common, pycnidial cell wall pseudoparenchymatous, conidia of two types: small aseptate and large septate	Plant pathogenic

teleomorphic or anamorphic genera.

Plectophomella visci grouped in *Plenodomus* in this study and in the *Leptosphaeriaceae* in a previous molecular phylogeny of *Phoma* and allied anamorph genera (de Gruyter *et al.* 2009). *Plectophomella visci* is the type species of *Plectophomella* (Moesz 1922) and three additional species have been described in the genus. Two species were described from the bark of *Ulmus* spp., viz. *Plectophomella ulmi* (basonym *Dothiorella ulmi*) and *Plectophomella concentrica* (Redfern & Sutton 1981). *Dothiorella ulmi* is considered the appropriate name for *Plectophomella ulmi* (Crous *et al.* 2004). A third species, *Plectophomella nypae*, was described from *Nypa fruticans* (*Arecaceae*) (Hyde & Sutton 1992). As a result of the transfer of the type species *Plectophomella visci* to *Plenodomus*, the taxonomy of both *Plectophomella concentrica* and *P. nypae* needs to be reconsidered based on the outcome of a molecular study.

Plenodomus chrysanthemi could not be differentiated from *Plen. tracheiphilus* based on comparison of their LSU and ITS sequences. *Plenodomus vasinfecta* was proposed by Boerema *et al.* (1994) for the species originally described as *Phoma tracheiphila* f. sp. *chrysanthemi* (Baker *et al.* 1985). Because these are part of the *Plenodomus* clade the name *Plenodomus chrysanthemi* is proposed with *P. tracheiphila* f. sp. *chrysanthemi* and *P. vasinfecta* as synonyms. *Plenodomus chrysanthemi* and *Plen. tracheiphilus* are host specific (*Chrysanthemum* and *Citrus*, respectively) and the scleroplectenchymatous conidiomatal wall of *Plen. tracheiphilus* differentiates this species from *Plen. chrysanthemi*, where only a parenchymatous wall has been observed (Boerema *et al.* 1994). The results of this molecular study and the production of a *Phialophora* synanamorph by both species demonstrate the close relationship of both taxa.

Plenodomus enteroleucus and *Plen. inflorescens* have a similar ecological niche as opportunistic pathogens on woody plants in Europe. Both taxa were formerly described as varieties of *Ph. enteroleuca*, vars. *enteroleuca* and *inflorescens*, and could be differentiated only by the fluorescence of var. *enteroleuca* under black light. However, the molecular phylogeny demonstrates the two varieties are only distantly related and they are raised from varietal status to species rank. The close relation of *Plen. wasabiae* with *Plen. biglobosus* agrees with the results of a previous study on the production of Phomaligin A and other yellow pigments, as well as ITS sequence analyses (Pedras *et al.* 1995).

Subplenodomus apiicola, *Subplen. drobnjacensis*, *Subplen. valerianae* and *Subplen. violicola* all produce pycnidia with an elongated neck, resembling *Plenodomus*. The pycnidial wall remains usually pseudoparenchymatous. Pycnidia with

a scleroplectenchymatous wall are only observed in *Subplen. drobnjacensis*. *Subplenodomus apiicolus*, *Subplen. drobnjacensis* and *Subplen. valerianae* produce relatively small conidia, up to 4.5 × 2 µm (de Gruyter & Noordeloos 1992) in congruence with many of the *Plenodomus* species described; however, in contrast *Subplen. violicola* produces relatively large conidia, up to 11 × 3 µm (Boerema 1993).

The grouping of species of *Phoma* section *Plenodomus* based on the host being either herbaceous plants or wood of trees and shrubs (Boerema 1982, Boerema *et al.* 1994) is not supported by the molecular phylogeny. The grouping of the species into two categories based on the production of pseudoparenchymatous pycnidia that become scleroplectenchymatous pycnidia (type 1), versus always scleroplectenchymatous pycnidia (type 2) (Boerema *et al.* 1981), is partly supported by the molecular phylogeny. In the *Leptosphaeria* clade most species directly develop scleroplectenchymatous pycnidia, whereas in the *Plenodomus* clade the pycnidia generally are pseudoparenchymatous and become scleroplectenchymatous.

Heterospora is established for two species of *Phoma* sect. *Heterospora* that cluster in the *Leptosphaeriaceae*, viz. *H. chenopodii* and *H. dimorphospora*. All other species of *Phoma* sect. *Heterospora* are in the *Didymellaceae* (Aveskamp *et al.* 2010).

The *Leptosphaeria doliolum* species complex

The taxonomy of the generic type species *Leptosphaeria doliolum* and *Phoma* anamorphs is complex with a number of subspecies and varieties described in literature. *Leptosphaeria doliolum* subsp. *doliolum* and *L. doliolum* subsp. *errabunda* are morphologically very similar, as well as the anamorphs *Ph. acuta* subsp. *errabunda* and *Ph. acuta* subsp. *acuta*. It has been suggested that both taxa represent originally American and European counterparts (Boerema *et al.* 1994). Both subspecies of *L. doliolum* proved to be closely related in a phylogenetic analysis utilising LSU and ITS. A detailed multilocus phylogenetic study including the ITS, ACT, TUB and CHS genes, however, demonstrated that both subspecies could be clearly differentiated, and represent two subclades in the *L. doliolum* complex. All species allied with *L. doliolum* and *L. errabunda* are necrotrophic species. Surprisingly, *L. macrocapsa* grouped with the *L. errabunda* isolates. *Leptosphaeria macrocapsa* is described as a host-specialised necrotroph on *Mercurialis perennis* (*Euphorbiaceae*) in Europe (Boerema *et al.* 1994). The species is characterised by large pycnidia (Grove, 1935), with a conspicuously broad, long cylindrical neck (Boerema *et al.* 1994). This is different to the sharply delimited papilla or neck of variable

length of the pycnidia of *L. errabunda*. *Leptosphaeria sydowii*, a necrotroph on *Senecio* spp. in particular (*Asteraceae*), proved to be closely related to *L. errabunda*. It can be concluded that the *Leptosphaeria doliolum* complex includes several necrotrophic species, with adapted host specificity.

The genus *Coniothyrium*

Coniothyrium palmarum is the type species of the genus *Coniothyrium*. *Coniothyrium* is characterised by ostiolate pycnidial conidiomata, annellidic conidiogenous cells, the absence of conidiophores, and brown, thick-walled, 0- or 1-septate, verrucose conidia. *Coniothyrium* is similar morphologically to some species in the genus *Microsphaeropsis*. However, *Microsphaeropsis* is characterised by the production of phialidic conidiogenous cells with periclinal thickening, and thin-walled, pale greenish brown conidia.

Coniothyrium, *Microsphaeropsis* and *Paraconiothyrium* clearly grouped in different clades in a study of the partial SSU nrDNA (Verkley *et al.* 2004). In a subsequent study utilising SSU and LSU sequences, the generic type species *Microsphaeropsis olivacea* grouped in *Didymellaceae*, whereas *Coniothyrium palmarum* clustered with the genus *Leptosphaeria* in *Leptosphaeriaceae* (de Gruyter *et al.* 2009). In the present study *C. palmarum* and its relatives grouped in a distinct clade, which represents *Coniothyriaceae*. *Phoma carteri*, *Ph. glycinicola*, *Ph. septicialis* and *Pyrenochaeta dolichi* grouped in this clade and are transferred to the genus *Coniothyrium*. The inclusion of these species with setose pycnidia and conidiogenesis with elongated conidiophores expands the morphological circumscription of *Coniothyrium*. Species with those characters are also found in other genera treated in this paper in the *Cucurbitariaceae*, *Didymellaceae*, *Phaeosphaeriaceae*, *Leptosphaeriaceae*, *Montagnulaceae* and *Sporormiaceae*, indicating convergent evolution.

The *Coniothyrium* species included here are plurivorous or soil-borne, such as *C. palmarum*, *C. septicialis* and *C. multiporum*, or are associated with a specific host such as *C. carteri* on *Quercus* spp. (*Fagaceae*), *C. glycinicola* on *Glycine max* (*Fabaceae*) and *C. dolichii* on *Dolichos biflorus* (*Fabaceae*). The species also are diverse geographically.

Coniothyrium palmarum was frequently found associated with leaf spots on *Phoenix dactylifera* (*Arecaceae*) in India and Cyprus (Sutton 1980). The *C. palmarum* isolates regularly used in phylogenetic studies are CBS 758.73, from leaf spots on *Phoenix dactylifera* in Israel, and CBS 400.71, from a dead petiole of *Chaemeropsis humulis* (*Arecaceae*) in Italy. The subtropical distribution of these species is similar to that of the most closely allied *C. dolichi* and *C. glycinicola*. *Coniothyrium multiporum*, recorded from marine soil, also is found in warm regions. *Coniothyrium carteri*, in contrast, is reported from North America and Europe.

Coniothyrium dolichi produces setose pycnidia with hyaline conidia (Mohanty 1958). The conidiogenesis was studied in detail later. phoma-like ampulliform conidiogenous cells as well as conidiogenous cells on filiform, septate conidiophores were found in the same pycnidia leading to confusion regarding the classification of this species in *Phoma* or *Pyrenochaeta* (Grodona *et al.* 1997). This study clearly supports the classification in *Coniothyrium*. *Coniothyrium glycinicola* was originally placed in the genus *Pyrenochaeta* as *Py. glycines* due to its setose pycnidia (Stewart 1957). The conidiogenesis and hyaline

conidia are phoma-like and therefore, it was reclassified as *Ph. glycinicola* in *Phoma* sect. *Paraphoma* (de Gruyter & Boerema 2002). However, in the original description it was noted that the conidia were greenish-yellow in mass (Stewart 1957), resembling *Microsphaeropsis* or coniothyrium-like conidia. This study clearly supports the classification in *Coniothyrium*. *Coniothyrium carteri* produces setose pycnidia with hyaline conidia and therefore, the species was classified in *Phoma* section *Paraphoma* (de Gruyter & Boerema 2002). In spite of this similarity, *C. carteri* was determined to be only distantly related to the generic type species *Paraphoma radicina* (de Gruyter *et al.* 2010). *Coniothyrium multiporum* was described in *Phoma* section *Phoma*; however, it proved to be unrelated to *Phoma* in *Didymellaceae* (Aveskamp *et al.* 2010). The conidiogenesis may comprise elongated conidiophores (Pawar *et al.* 1967). Two isolates originally described as *Ph. septicialis* are placed here in *Coniothyrium telephii*. Other strains deposited as *Ph. septicialis* proved to be *Pyrenochaeta unguis-hominis* (de Gruyter *et al.* 2010).

The anamorph of the genus *Neophaeosphaeria* was described as coniothyrium-like, producing pigmented, aseptate conidia from holoblastic, percurrently proliferating conidiogenous cells with conspicuous annellations (Câmara *et al.* 2003). Although *Neophaeosphaeria* is related to *Coniothyrium* based on the molecular data, *Neophaeosphaeria* probably belongs to a separate phylogenetic clade. The grouping of *N. filamentosa* with the *Coniothyrium* species included in this study was poorly supported and *N. filamentosa* proved to be more distantly related in previous molecular phylogenetic studies (Verkley *et al.* 2004, Damm *et al.* 2008, de Gruyter *et al.* 2010).

Both anamorph genera *Cyclothyrium* and *Cytoplea* were considered to be related to *Coniothyrium* and *Microsphaeropsis* (Sutton 1980) based on morphological similarities. *Cyclothyrium* also resembles *Paraconiothyrium* but produces conidiogenous cells that are more elongated than in most species of *Paraconiothyrium* and the conidia are almost truncate at the base, or at least they are much less rounded at the base than the conidia of *Paraconiothyrium* (Verkley *et al.* 2004). The generic type species *Cyclothyrium juglandis*, the anamorph of *Thyridaria rubronotata*, proved to be related to *Roussoella hysterooides*, teleomorph of *Cytoplea* (Verkley *et al.* 2004). Based on present results *R. hysterooides* could not be assigned to familial rank. The clustering of this species in *Massariaceae* (Zhang *et al.* 2009) could not be confirmed. Moreover, *Roussoella* probably is not a monophyletic genus (Tanaka *et al.* 2009). *Thyridaria rubronotata*, the teleomorph of *Cyclothyrium juglandis*, proved to be related to *Massariosphaeria phaeospora* but was not assigned to familial rank (Schoch *et al.* 2009).

Coniothyrium-like anamorphs also have been linked to *Mycosphaerella* in the past. However, these species were subsequently accommodated in *Colletogloeopsis* (Cortinas *et al.* 2006), *Readeriella/Kirramyces* (Crous *et al.* 2007) and are now known to be species of *Teratosphaeria* (Crous *et al.* 2009b).

The genus *Pleospora*

Pleospora is a large genus in *Pleosporaceae*, *Pleosporales*, and includes important pathogens that occur on both monocotyledons and dicotyledons. Anamorphs of *Pleospora* s. lat. have been described in various genera of coelomycetes and hyphomycetes as summarised by Zhang *et al.* (2009, 2012). A delimitation of *Pleospora* into two sections, *Pyrenophora* and *Eu-Pleospora* was made based

on the size of fruiting bodies and ascospore septation and colour (Munk 1957). The genus *Pyrenophora* (*Drechslera* anamorphs) is recognised at the generic rank. However, *Pleospora* remains heterogenous (Wehmeyer 1961, Berbee 1996) and molecular phylogenetic studies demonstrated that *Pleospora* is polyphyletic in *Pleosporaceae* (Kodsueb *et al.* 2006, Wang *et al.* 2007, Inderbitzin *et al.* 2009). Taxa with a *Stemphylium* anamorph such as *Pleospora sedicola* and *Pleo. tomatonis*, as well as *Pleo. halophola* with no known anamorph, are closely related to *Cochliobolus*, whereas *Pleo. herbarum* and *Pleo. ambigua* were more distantly related in the *Pleosporaceae* (Kodsueb *et al.* 2006, Wang *et al.* 2007). A phylogenetic study of the genus *Massariosphaeria* demonstrated the polyphyly in the genera *Pleospora*, *Kirschsteiniethelia*, *Massarina*, *Melanomma*, *Trematosphaeria* and *Massariosphaeria* in the *Loculoascomycetes* (Wang *et al.* 2007) and the paraphyletic character of the genus *Cochliobolus* was demonstrated (Kodsueb *et al.* 2006, Mugambi & Huhndorf 2009). These findings support the previous speculation by several authors that ascomatal and ascospore morphologies have undergone convergent evolution among *Pleosporales* (Wang *et al.* 2007).

Pleospora betae groups ambiguously in *Pleosporaceae* (Dong *et al.* 1998). SSU nrDNA sequence data supported the affinity of *P. betae* to *Leptosphaeriaceae*. Partial LSU nrDNA data supported the affinity of *P. betae* to *Pleosporaceae* (Dong *et al.* 1998), but bootstrap support values in that study were low. In a multigene phylogenetic study *Pleo. betae* was found as being basal to *Pleosporaceae* (Zhang *et al.* 2009). Our results demonstrate the sister group relationship of *Pleo. betae* and its relatives to the generic type species *Pleo. herbarum*.

Pleospora betae has been often confused with *Pleo. calvescens* as was discussed by Boerema *et al.* (1987). Both species are pathogens of *Chenopodiaceae* and are morphologically rather similar and therefore, a phylogenetic relation of both species was inferred (Boerema 1984). In addition *Ascochyta hyalospora*, originally found on the American continent on *Chenopodiaceae*, also was supposed to be closely related. Our results demonstrate that *Pleo. betae* and *Pleo. calvescens* could be recognised at species rank and confirmed that *A. hyalospora* is related supporting our transfer to *Pleospora* as *Pleo. chenopodii*. The delimitation of both halophytic species *Pleo. chenopodii* and *Pleo. calvescens* needs further study; both species could not be clearly differentiated based on the ACT sequences alone. Additional studies are underway to elucidate these species boundaries, in which also the recently described halophyte, *Ascochyta manawaorae* (Verkley *et al.* 2010), will be included. *Pleospora fallens* and *Pleo. incompta*, formerly described in *Phoma* sect. *Phoma* and producing mainly glabrous pycnidia, grouped in the *Pleo. herbarum* clade. *Pleospora typhicola*, producing pilose pycnidia, also grouped in this clade.

Phoma-like species excluded from the *Pleosporineae*

The genus *Paraconiothyrium* was introduced by Verkley *et al.* (2004) as the anamorph of *Paraphaeosphaeria*. The morphological characters of *Paraconiothyrium* are variable. The conidiomata can be eustromatic to pycnidial, the phialidic conidiogenous cells are discrete or integrated, and the thin-walled conidia are aseptate or septate, smooth-walled or minutely warted, and hyaline to brown in a later stage (Verkley *et al.* 2004). The morphological characters of *Ph. lini* and *Asteromella tilliae*, redisposed here in *Paraconiothyrium*, fit this description.

Paraconiothyrium fuckelii is a serious plant pathogen of *Rosaceae* (Horst & Cloyd 2007), but it also is recorded as an opportunistic human pathogen as summarised by de Hoog *et al.* (2000). The teleomorph is currently known as *Leptosphaeria coniothyrium*, but this is not likely considering the phylogeny of *Leptosphaeriaceae* in *Pleosporales* (Fig 1). The species was also described as *Melanomma coniothyrium* (Holm 1957); however, *Melanomma* is more distantly related in *Melanommataceae*.

Neottiosporina paspali proved to be related to *Paraconiothyrium*. However, this species is characterised by conidia with an apical appendage (Sutton 1980) and resembles members of *Massariaceae*. *Pyrenochaeta romeroi* is redescribed in the new genus *Medicopsis*, and its taxonomic position is most close to *Trematosphaeriaceae*.

Aposphaeria corallinolutea could be recognised as a new species in *Melanommataceae*. *Phoma capitulum* and *Ph. minutispora* (*Phoma* section *Phoma*) clustered in the *Sporormiaceae*, most closely related to the holotype isolate of *Westerdykella ornata*. Other phoma-like anamorphs have been recorded in *Sporormiaceae*, such as anamorphs of *Sporormia aemulans* (\equiv *Preussia aemulans*) and *Westerdykella dispersa* (\equiv *Pycnidiphora dispersa*) (von Arx & Storm 1967). The *in vitro* characters of *W. capitulum* and *W. oryzae* agree with the *in vitro* characters of phoma-like anamorphs in the *Sporormiaceae* summarised by Boerema *et al.* (2004). The conidia produced are small, mostly 2–3 \times 1–2 μ m, arising from undifferentiated cells, but sometimes also elongated conidiogenous cells are observed. The colonies, often with a pink-yellow-red discolouration on OA, usually produce little aerial mycelium, whereas pycnidia are often produced in abundance. No matching sequences were found in a blast search in GenBank using the partial LSU sequences of *W. capitulum* and *W. minutispora*. *Westerdykella minutispora* from India was most similar to a sequence of *Westerdykella nigra*, isolate CBS 416.72, obtained from soil in Pakistan, and *W. capitulum* was most similar to a sequence of *W. dispersa*, isolate CBS 297.56, obtained from a seedling of *Phlox drummondii*, USA. These blast results support the redisposition of both species in the genus *Westerdykella*.

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