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

Maikel Aveskamp, Hans de Gruyter, Joyce Woudenberg, Gerard Verkley and Pedro W. Crous
Studies in Mycology

The Studies in Mycology is an international journal which publishes systematic monographs of filamentous fungi and yeasts, and in rare occasions the proceedings of special meetings related to all fields of mycology, biotechnology, ecology, molecular biology, pathology and systematics. For instructions for authors see www.cbs.knaw.nl.

EXECUTIVE EDITOR
Prof. dr hc Robert A. Samson, CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.
E-mail: r.samson@bios.knaw.nl

LAYOUT EDITOR
Manon van den Hoeven-Verweij, CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.
E-mail: m.verweij@bios.knaw.nl

SCIENTIFIC EDITORS
Prof. dr Uwe Begerow, Lehrstuhl für Evolution und Biodiversität der Pflanzen, Ruhr-Universität Bochum, Universitätsstr. 150, Gebäude ND 44780, Bochum, Germany.
E-mail: dominik.begerow@rub.de

Prof. dr Martin-Luther-Universität, Institut für Biologie, Geobotanik und Botanischer Garten, Herbarium, Neuerkow, D-06099 Halle, Germany.
E-mail: uwe.braun@botanik.uni-halle.de

Dr Paul Cannon, CABI and Royal Botanic Gardens, Kew, Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, U.K.
E-mail: p.cannon@kew.org

Prof. dr Lori Carris, Associate Professor, Department of Plant Pathology, Washington State University, Pullman, WA 99164-6340, U.S.A.
E-mail: carris@mail.wsu.edu

Prof. dr Pedro W. Crous, CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.
E-mail: p.crous@bios.knaw.nl

Prof. dr David M. Geiser, Department of Plant Pathology, 121 Buckhout Laboratory, Pennsylvania State University, University Park, PA, U.S.A. 16802.
E-mail: dgeiser@psu.edu

Dr Johannes Z. Groenewald, CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.
E-mail: e.groenewald@bios.knaw.nl

Prof. dr David S. Hibbett, Department of Biology, Clark University, 950 Main Street, Worcester, Massachusetts, 01610-1477, U.S.A.
E-mail: dhibbett@clarku.edu

Prof. dr Hyeon-Dong Shin, Division of Environmental Science & Ecological Engineering, Korea University, Seoul 136-701, Korea.
E-mail: hdshin@korea.ac.kr

E-mail: lnorvell@pnnw-ms.com

Dr Ernst Parmasto, Institute of Zoology & Botany, 181 Riia Street, Tartu, Estonia EE-51014.
E-mail: e.parmasto@obi.ee

Prof. Dr Alan J.L. Phillips, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Quinta de Torre, 2829-516 Caparica, Portugal.
E-mail: aljp@fct.unl.pt

Dr Amy Y. Rossman, Rm 304, Bidg 011A, Systematic Botany & Mycology Laboratory, Beltsville, MD, U.S.A. 20705.
E-mail: amy@ntars-grn.gov

Dr Keith A. Seifert, Research Scientist / Biodiversity (Mycology and Botany), Agriculture & Agri-Food Canada, KW Neatby Bldg, 960 Carling Avenue, Ottawa, ON, Canada K1A OC6.
E-mail: seifertk@agr.gc.ca

Dr Roger Shivas, Plant Pathology Herbarium, Agri-Science Queensland, Indooroopilly, Qld 4068, Australia.
E-mail: roger.shivas@deoq.qld.gov.au

Prof. dr Jeffrey K. Stone, Department of Botany and Plant Pathology, Cordley 2082, Oregon State University, Corvallis, OR, U.S.A. 97331-2902.
E-mail: stonej@brc.orst.edu

Dr Richard C. Summerbell, 27 Hillcrest Park, Toronto, Ont. M4X 1E3, Canada.
E-mail: summerbell@aol.com

Prof. dr Brett Summerrell, Royal Botanic Gardens and Domain Trust, Mrs. Macquaries Road, Sydney, NSW 2000, Australia.
E-mail: brett.summerrell@rbgsyd.nsw.gov.au

Prof. dr Ulf Thane, Department of Systems Biology, Center for Microbial Biotechnology, Technical University of Denmark, Center for Mikrobiel Bioteknologi, Salltofs Plads 221, Building 221, room 210, 2800 Kgs. Lyngby, Denmark.
E-mail: ut@bio.dtu.dk

Copyright 2010 CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.

You are free to share — to copy, distribute and transmit the work, under the following conditions:

Attribution: You must attribute the work in the manner specified by the author or licensor (but not in any way that suggests that they endorse you or your use of the work).
Non-commercial: You may not use this work for commercial purposes.
No derivative works: You may not alter, transform, or build upon this work.

For any reuse or distribution, you must make clear to others the license terms of this work, which can be found at http://creativecommons.org/licenses/by-nc-nd/3.0/legalcode. Any of the above conditions can be waived if you get permission from the copyright holder. Nothing in this license impairs or restricts the author’s moral rights.

Publication date: 15 March 2010
Published and distributed by CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands. Internet: www.cbs.knaw.nl.
E-mail: info@cbs.knaw.nl.

Online ISSN: 1872-9797
Print ISSN: 0166-0616

Cover: Top from left to right: Boeremia exigua var. gilvescens, conidia. Proma ductifila, pycnidia. Didymella clematidis, peritheciun with ascii. Bottom from left to right: D. clematidis, ascii with ascospores. D. clematidis, pycnidial wall with conidigenous cells. B. exigua var. exigua, ostiole configuration.
CONTENTS

INTRODUCTION ........................................................................................................................................... 2

Phoma ......................................................................................................................................................... 2

MATERIALS AND METHODS ....................................................................................................................... 4

Strain selection ............................................................................................................................................. 4

DNA extraction, amplification and sequence analysis .............................................................................. 4

Morphology ............................................................................................................................................... 5

RESULTS ..................................................................................................................................................... 5

Systematics of the genus Phoma .................................................................................................................. 5

DNA phylogenetical analysis ...................................................................................................................... 5

Treatment of the clades .............................................................................................................................. 16

Clade 1, Outgroup ...................................................................................................................................... 16

Clade 2, Sporomycetaceae ........................................................................................................................ 16

Clade 3, Melanomataceae ........................................................................................................................ 16

Clade 4 ........................................................................................................................................................ 16

Clade 5, Cucurbitariaceae ........................................................................................................................ 16

Clade 6, Phaeosphaeriaceae ...................................................................................................................... 16

Clade 7, Leptosphaeriaceae and Pleosporaceae ...................................................................................... 17

Clade 8, Didymellaceae ............................................................................................................................ 20

Systematics of the Didymellaceae ............................................................................................................ 22

DNA phylogenetic analysis ....................................................................................................................... 22

Systematics: treatment of clades ............................................................................................................... 22

Group A – outgroup and basal lineages ................................................................................................. 23

Group B ...................................................................................................................................................... 24

Group C ...................................................................................................................................................... 25

Groups D & E – Leptosphaerulina and Macroventuria ........................................................................... 25

Group F ...................................................................................................................................................... 26

Group G ...................................................................................................................................................... 27

Group H ...................................................................................................................................................... 27

Group I ...................................................................................................................................................... 28

Group J ...................................................................................................................................................... 29

Group K – Peyronellae ............................................................................................................................. 30

Group L ...................................................................................................................................................... 33

Group M – Epicoccum ............................................................................................................................. 35

Group N – Boeremia gen. nov ................................................................................................................. 36

Group O ...................................................................................................................................................... 40

Group P ...................................................................................................................................................... 41

Group Q ...................................................................................................................................................... 41

Group R ...................................................................................................................................................... 42

Group S – Stagonosporopsis ..................................................................................................................... 42

Residual species in the Didymellaceae .................................................................................................... 46

DISCUSSION ............................................................................................................................................... 51

What is Phoma? .......................................................................................................................................... 51

Taxonomic revisions .................................................................................................................................. 52

Teleomorph relations ............................................................................................................................... 52

Can the sections be maintained? ............................................................................................................ 53

Section Helerospora .................................................................................................................................. 53

Section Macrospora .................................................................................................................................. 53

Section Paraphoma .................................................................................................................................. 53

Section Peyronellae .................................................................................................................................. 54

Section Phoma .......................................................................................................................................... 54

Section Phyllostictoides .......................................................................................................................... 54

Section Pilosa ............................................................................................................................................. 54

Section Plenodomus .................................................................................................................................. 54

Section Sclerophomella ........................................................................................................................... 55

DNA Barcoding ......................................................................................................................................... 55

ACKNOWLEDGEMENTS .......................................................................................................................... 55

REFERENCES ............................................................................................................................................. 55

INDEX ....................................................................................................................................................... 61
Highlights of the Didymellaceae: A polyphasic approach to characterise Phoma and related pleosporalean genera

M.M. Aveskamp1,2, J. de Gruyter1,2, J.H.C. Woudenberg, G.J.M. Verkley1 and P.W. Crous1,3

1CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; 2Dutch Plant Protection Service (PD), Geeritweg 15, 6706 EA Wageningen, The Netherlands; 3Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands

*Correspondence: Maikel M. Aveskamp, m.aveskamp@cbs.knaw.nl
*Current address: Mycolim BV, Veld Oostenrijk 13, 5961 NV Horst, The Netherlands

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

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

INTRODUCTION

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

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

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

Phoma

The genus Phoma Sacc. emend. Boerema & G.J. Bollen (Pleosporales) is a good example of a coelomycetous genus made fascinating by its great ecological diversity, but taxing investigators with profound difficulties in making identifications. The majority of the taxa within this mitosporic genus have been found in association with land plants, causing mainly leaf and stem spots (Aveskamp et al. 2008, Zhang et al. 2009). Approximately 50 % of the Phoma taxa that were redescribed by Boerema et al. (2004) are recognised as relevant phytopathogenic fungi, including a series of pathogens with quarantine status (Boerema et al. 2004, Aveskamp et al. 2008). Although most taxa are continuously present in the environment as saprobic soil organisms, many species switch to a pathogenic lifestyle when a suitable host is encountered (Aveskamp et al. 2008). The genus further comprises several species and varieties that are recognised as endophytic, fungicolous and lichenicolous (Hawksworth & Cole 2004, Torres et al. 2005a, b, De Gruyter et al. 2009). In Table 1, a list is provided with the main characters of every section (Boerema 1997). This subdivision into sections has led to an identification system that is considered to be extremely helpful in morphological identification (Boerema et al. 2004). However, as was hypothesised by Boerema et al. (2004), the classification has proved to be artificial. Molecular evidence has shown that the sections are linked to phylogenetically distinct teleomorph genera (Reddy et al. 1998, Torres et al. 2005b, De Gruyter et al. 2009). Even these teleomorph genera are not always monophyletic (Morales et al. 1995, Câmara et al. 2002, Kodsueb et al. 2006, Inderbitzin et al. 2009). In addition, characters that are thought to be specific for a certain section appeared to be polyphyletic, as is illustrated for dictyochlamydospores and setose pycnidia, the main characters for the sections Peyronellaeae (Aveskamp et al. 2009a and Paraphoma (Grondona et al. 1997, De Gruyter et al. 2010) respectively. Furthermore, Phoma section Phoma, a group of species which is characterised by the absence of chlamydospores, septate conidia, and pycnidial ornamentation or wall thickening, is
considered to be a repository for degenerated and insufficiently understood species that could not be placed elsewhere.

The genus *Phoma* is typified by *Phoma herbarum* (Boerema 1984). This species has thus far not been linked to any teleomorph, but several other species that are currently accommodated in *Phoma* do have a sexual state. The species in the section *Pilosa* are linked to the teleomorph genus *Pleospora*, while many species in the section *Plenodomus* have a sexual state in *Leptosphaeria*. As mentioned above, *Leptosphaeria* is para- or possibly polyphyletic (Morales et al. 1995, Câmara et al. 2002). A teleomorph in the poorly studied genus *Didymella* is associated with approximately 40 *Phoma* species placed in sections *Phoma*, *Phylllostictoides* and *Sclerophomella* (Boerema et al. 2004). Moreover, *Phoma* has been linked in literature to several other teleomorph genera, such as *Mycosphaerella* (Corlett 1991, De Gruyter 2002, Crous et al. 2009a, b), *Beliziana* (Kohlmeyer & Volkmann-Kohlmeyer 1987), *Atradiomyella* (Davey & Currah 2009) and *Fenestella*, *Cucurbitaria*, *Preussia*, and *Westendyckella* (von Arx 1981, Zhang et al. 2009). None of these hypothesised teleomorph-anamorph linkages is supported by molecular evidence. All must be investigated by study of type material. However, these associations are unlikely as the mentioned teleomorph genera are not linked to the teleomorph genus *Pleospora*, although these genera are morphologically clearly distinct from *Didymella* (Van der Aa 1971, Von Arx 1981, Zhang et al. 2009). The genetic similarity between those two genera has been observed before by Kotsueb et al. (2006), but the phylogenetic relationship with the genus *Didymella* was not noted in their study. Members of these two genera have therefore also been included in this study.

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

Three genes have in recent years been proposed as standard loci for use in DNA barcoding in fungi. These comprise the internal transcribed spacers (ITS) of the rDNA operon ITS region (Druzhinina et al. 2005), actin (ACT, Aveskamp et al. 2009b), and cytochrome c oxidase subunit I (COI, Seifert et al. 2007). The last locus was successfully applied in DNA Barcoding of *Pennisetum* (Seifert et al. 2007, Chen et al. 2009). However, COI analysis applied to a subset of *Ph. exigua* related strains, did not reveal taxon-specific conserved SNPs (Aveskamp et al. 2009b), whilst in an attempt to barcode *Aspergillus*, COI was found to have limited value (Geiser et al. 2007). Although ACT has proven helpful in resolving the phylogeny of *Phoma exigua* below species level (Aveskamp et al. 2009b), it could not be applied in the present study, as interspecific variation proved to be too high to align the obtained sequences properly. The use of ITS as fungal barcode locus is most popular (Seifert 2009) and has been applied in several taxonomic groups, such as *Trichoderma* and *Hypocrea* (Druzhinina et al. 2005), and *Trichophyton* (Summerbell et al. 2007) and in ecological groups such as wood-inhabiting fungi (Naumann et al. 2007). The power of this locus for barcoding lies in the multiple copies that are present within each cell; this phenomenon results in lower detection frequency.
thresholds than can be obtained with single-copy loci. Despite the general practicality of using ITS in barcoding, the locus is relatively conservative and may oversimplify species delimitations or blur generic boundaries in some groups (Nilsson et al. 2008). In the present study, a combination of four loci is therefore applied. These include two loci that are renowned for their capacity to resolve phylogenies above family level, namely parts of the LSU (Large Subunit – 28S) and SSU (Small Subunit – 18S) rDNA. Additionally two loci were applied that mainly provide resolution at species level – or even below. In addition to the abovementioned ITS regions, also part of the β-tubulin gene was utilised, which was successfully applied in a preliminary study on Phoma species of the section Peyronellaea (Aveskamp et al. 2009a).

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

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

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

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

MATERIALS AND METHODS

Strain selection

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

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

DNA extraction, amplification and sequence analysis

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

For nucleotide sequence comparisons fragments of four loci were analysed: LSU, SSU, ITS, and TUB. Amplification of LSU and SSU was conducted utilising the primer combination LROR (Rehner & Samuels 1994) and LR7 (Vilgalys & Hester 1990) for LSU sequencing and the primer pair NS1 and NS4 (White et al. 1990) for SSU. The PCRs were performed in a 2720 Thermal Cycler (Applied Biosystems, Foster City, California) in a total volume of 12.5 μL. The PCR mixture contained 0.5 μL 10 × diluted genomic DNA, 0.2 μM of each primer, 0.5 Unit Taq polymerase E (Genaxxon Bioscience), 12.5 μL. The PCR mixture contained 0.5 μL 10 × diluted genomic DNA, 0.2 μM of each primer, 0.5 Unit Taq polymerase E (Genaxxon Bioscience), 0.04 mM (SSU) or 0.06 mM (LSU) of each of the dNTP, 2 mM MgCl₂, and 1 × PCR buffer E incomplete (Genaxxon Bioscience). Conditions for amplification for both regions were an initial denaturation step of 5 min at 94 °C, followed by 35 cycles of denaturation, annealing and elongation and a final elongation step of 7 min at 72 °C. For the LSU amplification, the 35 cycles consisted of 30 s at 94 °C, 50 s at 48 °C and 90 s at 72 °C; for the LSU 45 s at 94 °C, 45 s at 48 °C and 2 min at 72 °C. The loci ITS and TUB were amplified as described by Aveskamp et al. (2009a), using the primer pairs V9G (De Hoog & Gerrits van den Ende 1998) and ITS4 (White et al. 1990) for ITS sequencing and the BT2Fw and BT4Rd primer pair (Aveskamp et al. 2009a) for sequencing of the TUB locus. PCR products were analysed by electrophoresis in a 1.0 % (w/v) agarose gel containing 0.1 ugl/ml ethidium bromide in 1 × TAE buffer (0.4 M Tris, 0.05 M glacial acetic acid 0.01 M ethylenediamine tetraacetic acid [EDTA], pH 7.85). The amplicons were visualised under UV light. Hyperladder I (Bioline, Luckenwalde, Germany) was applied as size standard.

The obtained amplicons were sequenced in both directions using the same primer combinations, except for LSU, where an additional primer, LRS (White et al. 1990) was further required
to assure complete coverage of the locus. Sequencing reactions were prepared with the BigDye terminator chemistry v. 3.1 (Applied Biosystems) according to the manufacturer’s recommendations. Sequence products were purified with Sephadex G-50 Fine (Amersham Biosciences, Roosendaal, the Netherlands) and subsequently separated and analysed on an ABI Prism 3730 DNA Sequencer (Applied Biosystems). Consensus sequences were computed from the forward and reverse sequences using the BioNumerics v. 4.61 software package (Applied Maths, St-Martens-Latem, Belgium). The consensus sequences are deposited in GenBank (For GenBank accession numbers see Tables 2, 3).

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

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

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

Morphology

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

RESULTS

Systematics of the genus Phoma

DNA phylogenetical analysis

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

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

Species that were ascribed to the Phoma section Phoma by Boerema et al. (2004) appear to be genetically highly heterogeneous, as these species are recovered in almost every clade. Species that were ascribed to Phoma section Heterospora appear to be linked to at least three distinct clades. Also polymorphism is observed for sections Paraphoma, Peyronellaea and Sclerophomella, as well as for Conidiethyum and Ascosypha. The type species of this latter genus, A. pisi, is not included in the present tree, but is genetically similar to the Didymellaceae.
<table>
<thead>
<tr>
<th>Strain no.</th>
<th>Holomorph$^2$</th>
<th>SSU GenBank no.</th>
<th>LSU GenBank no.</th>
<th>Original substrate</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>CBS 129.79</td>
<td>Ampelomyces quetequalis</td>
<td>EU754029</td>
<td>EU754128</td>
<td>Mildew on Cucumis sativus</td>
<td>Canada</td>
</tr>
<tr>
<td>CBS 543.70</td>
<td>Apothesphaeria populina</td>
<td>EU754031</td>
<td>EU754130</td>
<td>Populus canadensis</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 246.79, PD 77/655</td>
<td>Ascochyta caulina T</td>
<td>EU754032</td>
<td>EU754131</td>
<td>Atriplex hastata</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 544.74</td>
<td>Ascochyta hordei var. hordaei</td>
<td>EU754035</td>
<td>EU754134</td>
<td>Triticum aestivum</td>
<td>South Africa</td>
</tr>
<tr>
<td>CBS 117477</td>
<td>Ascochyta sp.</td>
<td>GU238202</td>
<td>GU237926</td>
<td>Salicornia australis</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 265.94</td>
<td>Asterosella tiliae</td>
<td>EU754040</td>
<td>EU754139</td>
<td>Tilia platyphyllos</td>
<td>Austria</td>
</tr>
<tr>
<td>CBS 431.74; PD 74/2447</td>
<td>Boeremia exigua var. exigua B</td>
<td>EU754084</td>
<td>EU754183</td>
<td>Solanum tuberosum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 341.67; CECT 20055; IMI 331912</td>
<td>Boeremia foveata B</td>
<td>GU238203</td>
<td>GU237947</td>
<td>Solanum tuberosum</td>
<td>U.K.</td>
</tr>
<tr>
<td>CBS 149.94</td>
<td>Chaetasbolisia erysiphoides</td>
<td>EU754041</td>
<td>EU754140</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 216.75; PD 71/1030</td>
<td>Chaetosphaerella homophila T</td>
<td>EU754045</td>
<td>EU754144</td>
<td>Anthyllis vulneraria</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 589.79</td>
<td>Coniothyrium concentricum</td>
<td>EU754053</td>
<td>EU754152</td>
<td>Yucca sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 797.95</td>
<td>Coniothyrium fuckelii</td>
<td>GU238204</td>
<td>GU237960</td>
<td>Rubus sp.</td>
<td>Denmark</td>
</tr>
<tr>
<td>CBS 400.71</td>
<td>Coniothyrium palmarum</td>
<td>EU754054</td>
<td>EU754153</td>
<td>Chamaeops humilis</td>
<td>Italy</td>
</tr>
<tr>
<td>CBS 122787; PD 0346691</td>
<td>Coniothyrium sp.</td>
<td>EU754052</td>
<td>EU754151</td>
<td>Unknown</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 183.55</td>
<td>Didymella exigua T</td>
<td>EU754056</td>
<td>EU754155</td>
<td>Rumex anilloides</td>
<td>France</td>
</tr>
<tr>
<td>CBS 524.77</td>
<td>Didymella fabae</td>
<td>EU754053</td>
<td>EU754133</td>
<td>Phaseolus vulgaris</td>
<td>Belgium</td>
</tr>
<tr>
<td>CBS 581.83A</td>
<td>Didymella rabeii</td>
<td>GU238205</td>
<td>GU237970</td>
<td>Cicer aritinum</td>
<td>Syria</td>
</tr>
<tr>
<td>CBS 173.73; ATCC 24428; IMI 164070</td>
<td>Epicoccum nigrum T</td>
<td>GU238206</td>
<td>GU237975</td>
<td>Dactylis glomerata</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 298.36</td>
<td>Leptosphaeria biglobosa</td>
<td>GU238207</td>
<td>GU237980</td>
<td>Brassica napus var. napobrassica</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 127.23; MUCL 9930</td>
<td>Leptosphaeria maculans</td>
<td>EU754090</td>
<td>EU754189</td>
<td>Brassica sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 939.69</td>
<td>Leptosphaerulina australis</td>
<td>EU754088</td>
<td>EU754167</td>
<td>Soil</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 525.71</td>
<td>Macroventuria anomaehaeta T</td>
<td>GU238208</td>
<td>GU237984</td>
<td>Decayed canvas</td>
<td>South Africa</td>
</tr>
<tr>
<td>CBS 442.83</td>
<td>Microsphaeropsis olivacea</td>
<td>EU754072</td>
<td>EU754171</td>
<td>Taxus baccata</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 331.37</td>
<td>Neoditosporina paspali</td>
<td>EU754073</td>
<td>EU754172</td>
<td>Paspalum notatum</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 122788; PD 99/1064-1</td>
<td>Paraconiothyrium minitans</td>
<td>EU754075</td>
<td>EU754174</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 626.68; IMI 108771</td>
<td>Peyronellaea gardiniae T</td>
<td>GQ387534</td>
<td>GQ387595</td>
<td>Gardenia jasminoides</td>
<td>India</td>
</tr>
<tr>
<td>CBS 528.66; PD 63/590</td>
<td>Peyronellaea glomerata B</td>
<td>EU754085</td>
<td>EU754184</td>
<td>Chrysanthemum sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 531.66</td>
<td>Peyronellaea pinodella B</td>
<td>GU238209</td>
<td>GU238017</td>
<td>Triolium pratense</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 235.55</td>
<td>Peyronellaea pinodes</td>
<td>GU238210</td>
<td>GU238021</td>
<td>Unknown</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 588.69</td>
<td>Peyronellaea zeae-maydis T</td>
<td>EU754093</td>
<td>EU754192</td>
<td>Zea mays</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 110110</td>
<td>Phaeosphaeria oryzae</td>
<td>GQ387530</td>
<td>GQ387591</td>
<td>Oryza sativa</td>
<td>South Korea</td>
</tr>
<tr>
<td>CBS 297.74</td>
<td>Phialophoropsis litoralis</td>
<td>EU754078</td>
<td>EU754177</td>
<td>Sea water</td>
<td>Montenegro</td>
</tr>
<tr>
<td>CBS 285.72</td>
<td>Phoma apiicola B</td>
<td>GU238211</td>
<td>GU238040</td>
<td>Apium graveolens var. rapaceum</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 337.65; ATCC 16195; IMI 116393</td>
<td>Phoma capitulum B</td>
<td>GU238212</td>
<td>GU238054</td>
<td>Soil</td>
<td>India</td>
</tr>
<tr>
<td>CBS 522.66</td>
<td>Phoma chrysanthemicola T</td>
<td>GQ387521</td>
<td>GQ387582</td>
<td>Chrysanthemum montifolium</td>
<td>U.K.</td>
</tr>
<tr>
<td>CBS 100311</td>
<td>Phoma complanata</td>
<td>EU754082</td>
<td>EU754181</td>
<td>Heracleum sphondylum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 345.78; PD 76/1015</td>
<td>Phoma dimorphospora</td>
<td>GU238213</td>
<td>GU238069</td>
<td>Chenopodium quinoa</td>
<td>Peru</td>
</tr>
<tr>
<td>CBS 527.66</td>
<td>Phoma eupyrena B</td>
<td>GU238214</td>
<td>GU238072</td>
<td>Soil</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 161.78</td>
<td>Phoma fallens B</td>
<td>GU238215</td>
<td>GU238074</td>
<td>Olea europaea</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 170.70; ATCC 22770; CECT 20011; IMI 163514; PD 70/Ak</td>
<td>Phoma fimeti T</td>
<td>GQ387523</td>
<td>GQ387584</td>
<td>Apium graveolens</td>
<td>Netherlands</td>
</tr>
</tbody>
</table>
### Table 2. (Continued).

<table>
<thead>
<tr>
<th>Strain no.¹</th>
<th>Holomorph²</th>
<th>GenBank no.</th>
<th>Original substrate</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>CBS 178.93; PD 82/1062</td>
<td>Phoma flavescens T</td>
<td>GU238216 GU238075</td>
<td>Soil</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 314.80</td>
<td>Phoma flavigena T</td>
<td>GU238217 GU238076</td>
<td>Water</td>
<td>Romania</td>
</tr>
<tr>
<td>CBS 633.92; ATCC 36786; VKM MF-325</td>
<td>Phoma fusicola</td>
<td>EU754028 EU754127</td>
<td>Microsphaera alphoides on Quercus sp.</td>
<td>Ukraine</td>
</tr>
<tr>
<td>CBS 284.70</td>
<td>Phoma glaucispora B</td>
<td>GU238218 GU238078</td>
<td>Nerium oleander</td>
<td>Italy</td>
</tr>
<tr>
<td>CBS 175.93; PD 92/370</td>
<td>Phoma haematocycla T</td>
<td>GU238219 GU238080</td>
<td>Phormium tenax</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 615.75; PD 73/865, IMI 199779</td>
<td>Phoma herbarum B</td>
<td>EU754087 EU754186</td>
<td>Rosa multiflora</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 448.68</td>
<td>Phoma heteromorphospora B</td>
<td>EU754088 EU754187</td>
<td>Chenopodium album</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 467.76</td>
<td>Phoma incompta B</td>
<td>GU238220 GU238087</td>
<td>Olea europaea</td>
<td>Greece</td>
</tr>
<tr>
<td>CBS 253.92; PD 70/998</td>
<td>Phoma lini T</td>
<td>GU238221 GU238093</td>
<td>Water</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 529.66; PD 66/521</td>
<td>Phoma macrostoma var. macrostoma B</td>
<td>GU238222 GU238098</td>
<td>Malus sylvestris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 316.90</td>
<td>Phoma medicaginis var. medicaginis</td>
<td>GU238223 GU238103</td>
<td>Medicago sativa</td>
<td>Czech Republic</td>
</tr>
<tr>
<td>CBS 509.91; PD 77/920</td>
<td>Phoma minutispora</td>
<td>GU238224 GU238108</td>
<td>Saline soil</td>
<td>India</td>
</tr>
<tr>
<td>CBS 501.91; PD 83/888</td>
<td>Phoma multipora B</td>
<td>GU238225 GU238109</td>
<td>Unknown</td>
<td>Egypt</td>
</tr>
<tr>
<td>CBS 376.91; PD 328.78, PD 77/177</td>
<td>Phoma opuntiae T</td>
<td>GU238226 GU238123</td>
<td>Opuntia ficus-indica</td>
<td>Peru</td>
</tr>
<tr>
<td>CBS 560.81; PD 92/1569; PDCC 6614</td>
<td>Phoma paspali T</td>
<td>GU238227 GU238124</td>
<td>Paspalum dilatatum</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 445.81; PDCC 7049</td>
<td>Phoma praturnor T</td>
<td>GU238228 GU238126</td>
<td>Lolium perenne</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 111.79; PD 76/437; IMI 386094</td>
<td>Phoma radicina B</td>
<td>EU754092 EU754191</td>
<td>Malus sylvestris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 138.96; PD 82/653</td>
<td>Phoma samarorum B</td>
<td>GU387517 GU387578</td>
<td>Phlox paniculata</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 343.85; IMI 366007</td>
<td>Phoma tenuicola T</td>
<td>GU387563 GU387624</td>
<td>Globodera pallida</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 630.68; PD 68/141</td>
<td>Phoma valerianae B</td>
<td>GU238229 GU238150</td>
<td>Valeriana officinalis</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 539.63</td>
<td>Phoma vaesuncta T</td>
<td>GU238230 GU238151</td>
<td>Chrysanthemum sp.</td>
<td>Greece</td>
</tr>
<tr>
<td>CBS 306.68</td>
<td>Phoma violicola B</td>
<td>GU238231 GU238152</td>
<td>Viola tricolor</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 523.66; PD 66/270</td>
<td>Plesospora betae B</td>
<td>EU754080 EU754179</td>
<td>Beta vulgaris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 191.86; IMI 276975</td>
<td>Plesospora herbarum T</td>
<td>GU238232 GU238160</td>
<td>Medicago sativa</td>
<td>India</td>
</tr>
<tr>
<td>CBS 257.68; IMI 331911</td>
<td>Pleurophoma cava</td>
<td>EU754100 EU754199</td>
<td>Soil</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 398.61; IMI 070678</td>
<td>Pseudobiddaria phragmites T</td>
<td>EU754104 EU754203</td>
<td>Phragmites australis</td>
<td>U.K.</td>
</tr>
<tr>
<td>CBS 122789; PD 0346800</td>
<td>Pyrenochaeta acicola</td>
<td>EU754105 EU754204</td>
<td>Hordeum vulgare</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 306.65</td>
<td>Pyrenochaeta lycopersici T</td>
<td>EU754106 EU754205</td>
<td>Lycopersicon esculentum</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 407.76</td>
<td>Pyrenochaeta nubilis T</td>
<td>EU754107 EU754206</td>
<td>Laurus nobilis</td>
<td>Italy</td>
</tr>
<tr>
<td>CBS 252.60; ATCC 13735</td>
<td>Pyrenochaeta romeri T</td>
<td>EU754108 EU754209</td>
<td>Man</td>
<td>Venezuela</td>
</tr>
<tr>
<td>CBS 524.50</td>
<td>Pyrenochaeta sp.</td>
<td>EU754110 EU754206</td>
<td>Solarium sp.</td>
<td>Peru</td>
</tr>
<tr>
<td>CBS 343.86</td>
<td>Stagonospora neglecta var. colorata</td>
<td>EU754119 EU754218</td>
<td>Phragmites australis</td>
<td>France</td>
</tr>
<tr>
<td>CBS 101.80; PD 75/909; IMI 366090</td>
<td>Stagonosporopsis andigena B</td>
<td>GU238233 GU238169</td>
<td>Solarium sp.</td>
<td>Peru</td>
</tr>
<tr>
<td>CBS 133.96; PD 79/127</td>
<td>Stagonosporopsis cucurbitacearum</td>
<td>GU238234 GU238181</td>
<td>Cucurbita sp.</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 631.68; PD 68/147</td>
<td>Stagonosporopsis terricola B</td>
<td>GU238235 GU238182</td>
<td>Solidago floribunda</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 164.31</td>
<td>Stenocarpella macrospora</td>
<td>EU754121 EU754220</td>
<td>Zea mays</td>
<td>Unknown</td>
</tr>
</tbody>
</table>

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

²T: Ex-type strain; B: Reference strain according to Boerema et al. (2004).
### Table 3. Strains from the Didymellaceae used for DNA analyses. The GenBank accession numbers in bold have been obtained from other studies.

<table>
<thead>
<tr>
<th>Strain no.¹</th>
<th>Holomorph²</th>
<th>GenBank no.</th>
<th>Original substrate</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>CBS 544.74</td>
<td>Ascochyta hordei var. hordei</td>
<td>EU754134 GU237887 GU237488</td>
<td>Triticum aestivum</td>
<td>South Africa</td>
</tr>
<tr>
<td>CBS 109.79; PD 77/747</td>
<td>Boeremia crinicola B</td>
<td>GU237927 GU237737 GU237489</td>
<td>Cannabis sativa</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 118.93; PD 70/195</td>
<td>Boeremia crinicola</td>
<td>GU237928 GU237759 GU237490</td>
<td>Cannabis sativa</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 101194; PD 79/687; IMI 373349</td>
<td>Boeremia diversispora</td>
<td>GU237929 GU237716 GU237491</td>
<td>Phaseolus vulgaris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 102.80; PD 79/61; CECT 20049; IMI 331907</td>
<td>Boeremia diversispora B</td>
<td>GU237930 GU237725 GU237492</td>
<td>Phaseolus vulgaris</td>
<td>Kenya</td>
</tr>
<tr>
<td>CBS 119730</td>
<td>Boeremia exigua var. coaffeae</td>
<td>GU237942 GU237759 GU237504</td>
<td>Coffea arabica</td>
<td>Brazil</td>
</tr>
<tr>
<td>CBS 109183; IMI 300060; PD 2000/10506</td>
<td>Boeremia exigua var. coaffeae B</td>
<td>GU237943 GU237748 GU237505</td>
<td>Coffea arabica</td>
<td>Cameroon</td>
</tr>
<tr>
<td>CBS 431.74; PD 74/2447</td>
<td>Boeremia exigua var. exigua B</td>
<td>EU754183 FJ427001 FJ427112</td>
<td>Solanum tuberosum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 101150; PD 79/118</td>
<td>Boeremia exigua var. exigua</td>
<td>GU237933 GU237715 GU237495</td>
<td>Cichorium intybus</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 101197; PD 95/721</td>
<td>Boeremia exigua var. forsythiae</td>
<td>GU237931 GU237718 GU237493</td>
<td>Forsythia sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 101213; PD 92/959</td>
<td>Boeremia exigua var. forsythiae B</td>
<td>GU237932 GU237723 GU237494</td>
<td>Forsythia sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 101196; PD 79/176</td>
<td>Boeremia exigua var. heteromorpha</td>
<td>GU237934 GU237717 GU237496</td>
<td>Nerium oleander</td>
<td>France</td>
</tr>
<tr>
<td>CBS 443.94</td>
<td>Boeremia exigua var. heteromorpha B</td>
<td>GU237935 GU237866 GU237497</td>
<td>Nerium oleander</td>
<td>Italy</td>
</tr>
<tr>
<td>CBS 569.79; PD 72/741</td>
<td>Boeremia exigua var. lilacis</td>
<td>GU237936 GU237892 GU237498</td>
<td>Syringa vulgaris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 100167; ATCC 33233; CECT 20022; CECT 200023; IMI 197074</td>
<td>Boeremia exigua var. lonicola</td>
<td>GU237937 GU237752 GU237499</td>
<td>Linum usitatissimum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 101202; PD 82/942</td>
<td>Boeremia foveata B</td>
<td>GU237939 GU237707 GU237501</td>
<td>Populus (x) euramerica</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 101207; PD 94/614</td>
<td>Boeremia foveata var. populii T</td>
<td>GU237940 GU237719 GU237502</td>
<td>Salix sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 100354; PD 84/448</td>
<td>Boeremia foveata var. pseudotrichetis T</td>
<td>GU237941 GU237721 GU237503</td>
<td>Syringa vulgaris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 102121; PD 93/838</td>
<td>Boeremia foveata var. virbuni B</td>
<td>GU237944 GU237711 GU237506</td>
<td>Viburnum opulus</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 100976; CECT 2828; PD 94/1394</td>
<td>Boeremia foveata B</td>
<td>GU237946 GU237742 GU237508</td>
<td>Solanum tuberosum</td>
<td>Bulgaria</td>
</tr>
<tr>
<td>CBS 341.67; CECT 20055; IMI 331912</td>
<td>Boeremia foveata B</td>
<td>GU237947 GU237834 GU237509</td>
<td>Solanum tuberosum</td>
<td>U.K.</td>
</tr>
<tr>
<td>CBS 369.91; PD 70/811</td>
<td>Boeremia hedericola</td>
<td>GU237948 GU237841 GU237510</td>
<td>Hedera helix</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 367.91; PD 87/229</td>
<td>Boeremia hedericola B</td>
<td>GU237949 GU237842 GU237511</td>
<td>Hedera helix</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 378.67; PD 76/276</td>
<td>Boeremia lycopersici B</td>
<td>GU237950 GU237848 GU237512</td>
<td>Lycopersicon esculentum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 109972; PD 84/143</td>
<td>Boeremia lycopersici</td>
<td>GU237951 GU237739 GU237513</td>
<td>Lycopersicon esculentum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 100353; PD 87/718</td>
<td>Boeremia noackiana B</td>
<td>GU237952 GU237710 GU237514</td>
<td>Phaseolus vulgaris</td>
<td>Guatemala</td>
</tr>
<tr>
<td>CBS 101203; PD 79/1114</td>
<td>Boeremia noackiana</td>
<td>GU237953 GU237720 GU237515</td>
<td>Phaseolus vulgaris</td>
<td>Colombia</td>
</tr>
<tr>
<td>CBS 109170; PD 75/796</td>
<td>Boeremia sambuci-nigrae</td>
<td>GU237954 GU237738 GU237516</td>
<td>Sambucus nigra</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 629.68; CECT 20048; IMI 331913; PD 67/753</td>
<td>Boeremia sambuci-nigrae T</td>
<td>GU237955 GU237897 GU237517</td>
<td>Sambucus nigra</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 126.93; PD 73/642</td>
<td>Boeremia strasseri</td>
<td>GU237956 GU237773 GU237518</td>
<td>Mentha sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 261.92; ATCC 244146; PD 92/318</td>
<td>Boeremia strasseri</td>
<td>GU237957 GU237812 GU237519</td>
<td>Mentha piperita</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 109175; PD 79/524</td>
<td>Boeremia telephi B</td>
<td>GU237958 GU237874 GU237520</td>
<td>Sedum spectabile</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 760.73; PD 71/1616</td>
<td>Boeremia telephi B</td>
<td>GU237959 GU237905 GU237521</td>
<td>Sedum spectabile</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 149.94</td>
<td>Chaetasbolisia euryphoides</td>
<td>EU75410 GU237785 GU237522</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 187.83; PD 82/128</td>
<td>Didymella adianticola B</td>
<td>GU238035 GU237796 GU237576</td>
<td>Polystichum adiantiforme</td>
<td>Costa Rica</td>
</tr>
<tr>
<td>CBS 259.92; PD 89/1887</td>
<td>Didymella adianticola</td>
<td>GU238036 GU237811 GU237577</td>
<td>Polystichum adiantiforme</td>
<td>Costa Rica</td>
</tr>
<tr>
<td>CBS 102654; PD 75/248</td>
<td>Didymella aplanata</td>
<td>GU237997 GU237726 GU237555</td>
<td>Rubus idaeus</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 205.63</td>
<td>Didymella aplanata T</td>
<td>GU237998 GU237798 GU237556</td>
<td>Rubus idaeus</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 234.37</td>
<td>Didymella cannabis</td>
<td>GU237961 GU237804 GU237523</td>
<td>Cannabis sativa</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 102653; PD 77/1131</td>
<td>Didymella catariae</td>
<td>GU237962 GU237727 GU237524</td>
<td>Nepeta cataria</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 183.55</td>
<td>Didymella exigua T</td>
<td>EU754155 GU237794 GU237525</td>
<td>Rumex arifolius</td>
<td>France</td>
</tr>
<tr>
<td>CBS 524.77</td>
<td>Didymella fabae</td>
<td>GU237963 GU237880 GU237526</td>
<td>Phaseolus vulgaris</td>
<td>Belgium</td>
</tr>
<tr>
<td>CBS 649.71</td>
<td>Didymella fabae</td>
<td>GU237964 GU237902 GU237527</td>
<td>Vicia faba</td>
<td>Netherlands</td>
</tr>
</tbody>
</table>
Table 3. (Continued).

<table>
<thead>
<tr>
<th>Strain no.</th>
<th>Holomorph</th>
<th>GenBank no.</th>
<th>Original substrate</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>PD 83/492</td>
<td>Didymella fabae</td>
<td>GU237975</td>
<td>Phaseolus vulgaris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>PD 84/512</td>
<td>Didymella macropodi</td>
<td>GU237966</td>
<td>Crucifer</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 100190; PD 82/736</td>
<td>Didymella macropodi</td>
<td>GU237967</td>
<td>Brassica napus</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 126.54</td>
<td>Didymella pisi</td>
<td>GU237968</td>
<td>Pisum sativum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 122785; PD 78/517</td>
<td>Didymella pisi</td>
<td>GU237969</td>
<td>Pisum sativum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 534.65</td>
<td>Didymella rabeii</td>
<td>GU237970</td>
<td>Cicer arrietinum</td>
<td>India</td>
</tr>
<tr>
<td>CBS 581.83a</td>
<td>Didymella rabeii</td>
<td>GU237971</td>
<td>Cicer arrietinum</td>
<td>Syria</td>
</tr>
<tr>
<td>CBS 121.75; ATCC 32164; IHEM 3403; IMI 194767; PD 73/584</td>
<td>Didymella urticicola T</td>
<td>GU237972</td>
<td>Urtica dioica</td>
<td>Netherlands</td>
</tr>
<tr>
<td>PD 73/570</td>
<td>Didymella urticicola</td>
<td>GU237973</td>
<td>Urtica dioica</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 454.64</td>
<td>Didymella vitатаbina</td>
<td>FJ515646</td>
<td>Cenpas vilatba</td>
<td>France</td>
</tr>
<tr>
<td>CBS 138.25</td>
<td>Diplodina coloradensis</td>
<td>EU754158</td>
<td>Senecio sp.</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 172.34</td>
<td>“Dothiora ulmi”</td>
<td>EU754160</td>
<td>Ustus sp.</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 125.82; IMI 1331914; CECT 20044</td>
<td>Epicoccum nigrum</td>
<td>GU237974</td>
<td>Human</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 173.73; ATCC 24428; IMI 164070</td>
<td>Epicoccum nigrum T</td>
<td>GU237975</td>
<td>Dactylis glomerata</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 246.60; ATCC 22237; ATCC 16652; IMI 081601</td>
<td>Epicoccum piniprum T</td>
<td>GU237976</td>
<td>Soil</td>
<td>India</td>
</tr>
<tr>
<td>PD 77/1028</td>
<td>Epicoccum piniprum</td>
<td>GU237977</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 179.80; PD 76/1018</td>
<td>Epicoccum sorghi</td>
<td>GU237978</td>
<td>Sorghum vulgare</td>
<td>Puerto Rico</td>
</tr>
<tr>
<td>CBS 627.68; PD 66/926</td>
<td>Epicoccum sorghi</td>
<td>GU237979</td>
<td>Citrus sp.</td>
<td>France</td>
</tr>
<tr>
<td>CBS 213.55</td>
<td>Leptosphaeria americana</td>
<td>GU237981</td>
<td>Trifolium pretense</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 275.59; ATCC 13446</td>
<td>Leptosphaeria arachidicola</td>
<td>GU237983</td>
<td>Arachis hypochaera</td>
<td>Taiwan</td>
</tr>
<tr>
<td>CBS 317.83</td>
<td>Leptosphaeria australis</td>
<td>EU754166</td>
<td>Eugenia aromatica</td>
<td>Indonesia</td>
</tr>
<tr>
<td>CBS 939.69</td>
<td>Leptosphaeria australis</td>
<td>EU754167</td>
<td>Soil</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 235.58</td>
<td>Leptosphaeria trifoli</td>
<td>GU237982</td>
<td>Trifolium sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 525.71</td>
<td>Macroventuria anomochaeta T</td>
<td>GU237984</td>
<td>decayed canvas</td>
<td>South Africa</td>
</tr>
<tr>
<td>CBS 502.72</td>
<td>Macroventuria anomochaeta</td>
<td>GU237985</td>
<td>Medicago sativa</td>
<td>South Africa</td>
</tr>
<tr>
<td>CBS 526.71</td>
<td>Macroventuria wentii</td>
<td>GU237986</td>
<td>Unidentified plant material</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 432.71</td>
<td>Microsphaeropsis olivacea</td>
<td>GU237987</td>
<td>Sororamus sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 233.77</td>
<td>Microsphaeropsis olivacea</td>
<td>GU237988</td>
<td>Pinus lario</td>
<td>France</td>
</tr>
<tr>
<td>CBS 442.83</td>
<td>Microsphaeropsis olivacea</td>
<td>EU754171</td>
<td>Taxus baccata</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 132.96; PD 93/853</td>
<td>Peyronellaeae eletorolophi T</td>
<td>GU237989</td>
<td>Rhinanthus major</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 185.85; PD 80/1191</td>
<td>Peyronellaeae americana B</td>
<td>GU237990</td>
<td>Zea mays</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 568.97; PD 94/1544; ATCC 44494</td>
<td>Peyronellaeae americana</td>
<td>GU237991</td>
<td>Glycine max</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>PD 82/1059</td>
<td>Peyronellaeae americana</td>
<td>GU237992</td>
<td>Nematoide cyst</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 360.84</td>
<td>Peyronellaeae anserina B</td>
<td>GU237993</td>
<td>Potatoflour</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 363.91; PD 79/712</td>
<td>Peyronellaeae anserina</td>
<td>GU237994</td>
<td>Pisum sativum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 315.90; PD 80/1190</td>
<td>Peyronellaeae arachidica</td>
<td>GU237995</td>
<td>Arachis hypogaea</td>
<td>Zimbabwe</td>
</tr>
<tr>
<td>CBS 333.75; ATCC 28333; IMI 386092; PREM 44889</td>
<td>Peyronellaeae arachidica T</td>
<td>GU237996</td>
<td>Arachis hypogaea</td>
<td>South Africa</td>
</tr>
<tr>
<td>CBS 269.93; PD 78/1087</td>
<td>Peyronellaeae aurea B</td>
<td>GU237999</td>
<td>Medicago polymorpha</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 444.81; PDDCC 6546</td>
<td>Peyronellaeae australis T</td>
<td>GU238000</td>
<td>Actinidia chinensis</td>
<td>New Zealand</td>
</tr>
<tr>
<td>PD 77/919</td>
<td>Peyronellaeae australis</td>
<td>GU238001</td>
<td>Actinidea chinensis</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 109.92; PD 73/1405</td>
<td>Peyronellaeae calopreferens T</td>
<td>GU238002</td>
<td>Undefined food material</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 630.97; ATCC 96683; IMI 361196; PD 90/2022</td>
<td>Peyronellaeae calopreferens</td>
<td>GU238004</td>
<td>Heteroderma glycines</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 875.97; PD 93/1503</td>
<td>Peyronellaeae calopreferens</td>
<td>GU238003</td>
<td>Indoor environment</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 123380; PD 84/1013</td>
<td>Peyronellaeae coffeae-arabicacae T</td>
<td>GU238005</td>
<td>Coffea arabica</td>
<td>Ethiopia</td>
</tr>
</tbody>
</table>
Table 3. (Continued).

<table>
<thead>
<tr>
<th>Strain no.</th>
<th>Holomorph¹</th>
<th>GenBank no.</th>
<th>Original substrate</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>CBS 123398; PD 84/1014</td>
<td>Peyronellaea coffeae-arabicae</td>
<td>GU238006 FJ426994 FJ427105</td>
<td>Coffea arabica</td>
<td>Ethiopia</td>
</tr>
<tr>
<td>PD 92/1460</td>
<td>Peyronellaea curtisi</td>
<td>GU238012 FJ427041 FJ427151</td>
<td>Sprekelia</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 251.92; PD 86/1145</td>
<td>Peyronellaea curtisi B</td>
<td>GU238013 FJ427038 FJ427148</td>
<td>Nerine sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 377.91; PD 79/210</td>
<td>Peyronellaea eucalyptica B</td>
<td>GU238007 GU237846 GU237562</td>
<td>Eucalyptus sp.</td>
<td>Australia</td>
</tr>
<tr>
<td>CBS 508.91; PD 73/1413</td>
<td>Peyronellaea eucalyptica</td>
<td>GU238008 GU237878 GU237563</td>
<td>Water</td>
<td>Croatia</td>
</tr>
<tr>
<td>CBS 302.79; PD 79/1156</td>
<td>Peyronellaea gardeniae</td>
<td>GQ387596 FJ427002 FJ427113</td>
<td>Air</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 626.68; IMI 108771</td>
<td>Peyronellaea gardeniae T</td>
<td>GQ387595 FJ427003 FJ427114</td>
<td>Gardenia jasminoides</td>
<td>India</td>
</tr>
<tr>
<td>CBS 469.97; MUCL 9882</td>
<td>Peyronellaea pinodella</td>
<td>GU238009 FJ427012 FJ427123</td>
<td>Indoor environment</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 528.66; PD 63/590</td>
<td>Peyronellaea pinodella B</td>
<td>EU754184 FJ427013 FJ427124</td>
<td>Chrysanthemum sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 103.25</td>
<td>Peyronellaea lethalis</td>
<td>GU238010 GU237729 GU237564</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 463.69</td>
<td>Peyronellaea musae B</td>
<td>GU238011 FJ427026 FJ427136</td>
<td>Mangifera indica</td>
<td>India</td>
</tr>
<tr>
<td>CBS 377.93; PD 80/976</td>
<td>Peyronellaea obtusa B</td>
<td>GU238014 GU237847 GU237565</td>
<td>Daucus carota</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 391.93; PD 80/87</td>
<td>Peyronellaea obtusa B</td>
<td>GU238015 GU237858 GU237566</td>
<td>Spinacia oleracea</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 318.90; PD 81/729</td>
<td>Peyronellaea pinodella</td>
<td>GU238016 FJ427051 FJ427161</td>
<td>Pisum sativum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 531.66</td>
<td>Peyronellaea pinodella B</td>
<td>GU238017 FJ427052 FJ427162</td>
<td>Trifolium pratense</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 100580; PD 98/1135</td>
<td>Peyronellaea pinodella</td>
<td>GU238018 GU237713 GU237567</td>
<td>Glycine max</td>
<td>Hungary</td>
</tr>
<tr>
<td>CBS 567.97; PD 97/2160</td>
<td>Peyronellaea pinodella</td>
<td>GU238019 GU237891 GU237568</td>
<td>Glycine max</td>
<td>Hungary</td>
</tr>
<tr>
<td>CBS 159.78b</td>
<td>Peyronellaea pinodes</td>
<td>GU238020 GU237786 GU237569</td>
<td>Pisum sativum</td>
<td>Iraq</td>
</tr>
<tr>
<td>CBS 265.49</td>
<td>Peyronellaea pinodes</td>
<td>GU238022 GU237823 GU237571</td>
<td>Primula auricula</td>
<td>Switzerland</td>
</tr>
<tr>
<td>CBS 235.55</td>
<td>Peyronellaea pinodes</td>
<td>GU238021 GU237805 GU237570</td>
<td>Unknown</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 525.77</td>
<td>Peyronellaea pinodes</td>
<td>GU238023 GU237883 GU237572</td>
<td>Pisum sativum</td>
<td>Belgium</td>
</tr>
<tr>
<td>CBS 525.77a</td>
<td>Peyronellaea pinodes</td>
<td>GU238024 GU237882 GU237573</td>
<td>Pisum sativum</td>
<td>Belgium</td>
</tr>
<tr>
<td>CBS 533.66; ATCC 16791; IMI 122266; PD 64/914</td>
<td>Peyronellaea pomorum var. pomorum B</td>
<td>GU238028 FJ427056 FJ427166</td>
<td>Polygonum tataricum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 265.76; ATCC 26241; IMI 176742; VKM F-1843</td>
<td>Peyronellaea pomorum var. cibinata T</td>
<td>GU238025 FJ427053 FJ427163</td>
<td>Heracleum dissectum</td>
<td>Russia</td>
</tr>
<tr>
<td>CBS 286.76; ATCC 26242; IMI 176743; VKM F-1844</td>
<td>Peyronellaea pomorum var. cibinata T</td>
<td>GU238026 FJ427054 FJ427164</td>
<td>Allium nutans</td>
<td>Russia</td>
</tr>
<tr>
<td>CBS 388.80; PREM 45736</td>
<td>Peyronellaea pomorum var. cyanea T</td>
<td>GU238027 FJ427055 FJ427165</td>
<td>Triticum sp.</td>
<td>South Africa</td>
</tr>
<tr>
<td>CBS 381.96; PD 71/706</td>
<td>Peyronellaea protuberans B</td>
<td>GU238029 GU237853 GU237574</td>
<td>Lycium halifolium</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 281.83</td>
<td>Peyronellaea sancta T</td>
<td>GU238030 FJ427063 FJ427170</td>
<td>Alantus allisissma</td>
<td>South Africa</td>
</tr>
<tr>
<td>LEV 15292</td>
<td>Peyronellaea sancta</td>
<td>GU238031 FJ427065 FJ427172</td>
<td>Gleditsia triacanthan</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 110.92; PD 76/1010</td>
<td>Peyronellaea subglomerata B</td>
<td>GU238032 FJ427080 FJ427186</td>
<td>Triticum sp.</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>PD 78/1090</td>
<td>Peyronellaea subglomerata</td>
<td>GU238033 FJ427081 FJ427187</td>
<td>Zea mays</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 588.69</td>
<td>Peyronellaea zeae-maydis T</td>
<td>EU754186 FJ427086 FJ427190</td>
<td>Zea mays</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 179.97</td>
<td>Phoma acetoceallae</td>
<td>GU238034 GU237793 GU237575</td>
<td>Rumex hydrolapathum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 379.93; PD 82/945</td>
<td>Phoma aliena</td>
<td>GU238037 GU237851 GU237578</td>
<td>Berberis sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 877.97; PD 94/1401</td>
<td>Phoma aliena</td>
<td>GU238038 GU237910 GU237579</td>
<td>Buxus sempervivens</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 381.91; PD 79/1110</td>
<td>Phoma anigozanthi B</td>
<td>GU238039 GU237852 GU237580</td>
<td>Anigozanthus maugleisi</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 107.96; PD 73/598</td>
<td>Phoma aquilegicola B</td>
<td>GU238041 GU237735 GU237582</td>
<td>Aconitum pyramidale</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 108.96; PD 79/611</td>
<td>Phoma aquilegicola B</td>
<td>GU238042 GU237736 GU237583</td>
<td>Aquilegia sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 125.93; PD 77/1029</td>
<td>Phoma arachidis-hypogaeae B</td>
<td>GU238043 GU237771 GU237584</td>
<td>Arachis hypogaea</td>
<td>India</td>
</tr>
<tr>
<td>CBS 383.67; PD 65/223</td>
<td>Phoma aurietiae B</td>
<td>GU238044 GU237854 GU237585</td>
<td>Aubrietia hybrida cv. Superbissima</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 627.97; PD 70/714</td>
<td>Phoma aurietiae B</td>
<td>GU238045 GU237895 GU237586</td>
<td>Aubrietia sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 714.85; PD 74/265</td>
<td>Phoma bellidis B</td>
<td>GU238046 GU237904 GU237587</td>
<td>Bellis perennis</td>
<td>Netherlands</td>
</tr>
<tr>
<td>PD 94/886</td>
<td>Phoma bellidis</td>
<td>GU238047 GU237923 GU237581</td>
<td>Bellis sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>Strain no.</td>
<td>Holomorph</td>
<td>GenBank no.</td>
<td>Original substrate</td>
<td>Locality</td>
</tr>
<tr>
<td>-----------</td>
<td>-----------</td>
<td>-------------</td>
<td>--------------------</td>
<td>----------</td>
</tr>
<tr>
<td>CBS 109942; PD 84/402</td>
<td>Phoma boeremae T</td>
<td>GU238084</td>
<td>FJ426982</td>
<td>Medicago littoralis cv. Harbinger</td>
</tr>
<tr>
<td>CBS 120105</td>
<td>Phoma brasiliensis T</td>
<td>GU238049</td>
<td>GU237760</td>
<td>Amaranthus sp.</td>
</tr>
<tr>
<td>CBS 357.84</td>
<td>Phoma bulgarica T</td>
<td>GU238050</td>
<td>GU237387</td>
<td>Trachystemon orientale</td>
</tr>
<tr>
<td>CBS 124515; PD 82/1058</td>
<td>Phoma bulgarica</td>
<td>GU238051</td>
<td>GU237768</td>
<td>Trachystemon orientale</td>
</tr>
<tr>
<td>CBS 448.83</td>
<td>Phoma calidophila T</td>
<td>GU238052</td>
<td>FJ427059</td>
<td>Soil</td>
</tr>
<tr>
<td>PD 84/109</td>
<td>Phoma calidophila</td>
<td>GU238053</td>
<td>FJ427060</td>
<td>Cucumis sativus</td>
</tr>
<tr>
<td>CBS 128.93; PD 79/140</td>
<td>Phoma chenopodiicola B</td>
<td>GU238055</td>
<td>GU237775</td>
<td>Chenopodium quinoa cv. Saiana</td>
</tr>
<tr>
<td>CBS 129.93; PD 89/803</td>
<td>Phoma chenopodiicola</td>
<td>GU238056</td>
<td>GU237776</td>
<td>Chenopodium quinoa cv. Saiana</td>
</tr>
<tr>
<td>CBS 102.66</td>
<td>Phoma clematidina</td>
<td>FJS15630</td>
<td>FJ426988</td>
<td>Clematis sp.</td>
</tr>
<tr>
<td>CBS 108.79; PD 78/522; PD 91/876</td>
<td>Phoma clematidina T</td>
<td>FJS15632</td>
<td>FJ426999</td>
<td>Clematis sp.</td>
</tr>
<tr>
<td>CBS 507.63; MUCL 9574; PD 07/03486747</td>
<td>Phoma clematidis-rectae</td>
<td>FJS15647</td>
<td>FJS15606</td>
<td>Clematis sp.</td>
</tr>
<tr>
<td>PD 95/1958</td>
<td>Phoma clematidis-rectae</td>
<td>FJS15648</td>
<td>FJS15607</td>
<td>Clematis sp.</td>
</tr>
<tr>
<td>CBS 100409</td>
<td>Phoma commelinicicola B</td>
<td>GU238057</td>
<td>GU237712</td>
<td>Tradescantia sp.</td>
</tr>
<tr>
<td>CBS 100311</td>
<td>Phoma complanata</td>
<td>EUT54181</td>
<td>GU237709</td>
<td>Heracleum sphonolymph</td>
</tr>
<tr>
<td>CBS 268.92; PD 75/3</td>
<td>Phoma complanata</td>
<td>EUT54180</td>
<td>GU237815</td>
<td>Angelica sylvestris</td>
</tr>
<tr>
<td>CBS 506.91; IMI 215222; PD 91/876</td>
<td>Phoma costarricensis B</td>
<td>GU238058</td>
<td>GU237876</td>
<td>Coffea sp.</td>
</tr>
<tr>
<td>CBS 497.91; PD 79/209</td>
<td>Phoma costarricensis</td>
<td>GU238059</td>
<td>GU237870</td>
<td>Coffea arabica</td>
</tr>
<tr>
<td>CBS 193.82</td>
<td>Phoma crystallifera T</td>
<td>GU238060</td>
<td>GU237797</td>
<td>Chamaespradium sagittale</td>
</tr>
<tr>
<td>CBS 124513; PD 73/1414</td>
<td>Phoma dactylidis T</td>
<td>GU238061</td>
<td>GU237766</td>
<td>Dactylis glomerata</td>
</tr>
<tr>
<td>CBS 133.93; PD 88/961; IMI 173142</td>
<td>Phoma destructiva var. destructiva</td>
<td>GU238064</td>
<td>GU237779</td>
<td>Solarium lyopersicum</td>
</tr>
<tr>
<td>CBS 378.73; CECT 2877</td>
<td>Phoma destructiva var. destructiva B</td>
<td>GU238063</td>
<td>GU237849</td>
<td>Lycopersicon esculentum</td>
</tr>
<tr>
<td>CBS 162.78; PD 77/725</td>
<td>Phoma destructiva var. diversispora</td>
<td>GU238062</td>
<td>GU237788</td>
<td>Lycopersicon esculentum</td>
</tr>
<tr>
<td>CBS 507.91; PD 74/148</td>
<td>Phoma dictamnicicola B</td>
<td>GU238065</td>
<td>GU237877</td>
<td>Dictamus albus</td>
</tr>
<tr>
<td>CBS 109179; PD 90/835-1</td>
<td>Phoma digitals</td>
<td>GU238066</td>
<td>GU237744</td>
<td>Digitals sp.</td>
</tr>
<tr>
<td>CBS 229.79; LEV 7660</td>
<td>Phoma digitals B</td>
<td>GU238067</td>
<td>GU237802</td>
<td>Digitalis purpurea</td>
</tr>
<tr>
<td>CBS 346.82</td>
<td>Phoma dimorpha T</td>
<td>GU238068</td>
<td>GU237835</td>
<td>Opuntia sp.</td>
</tr>
<tr>
<td>CBS 186.83; PD 82/47</td>
<td>Phoma dracconis B</td>
<td>GU238070</td>
<td>GU237795</td>
<td>Dracaena sp.</td>
</tr>
<tr>
<td>CBS 123.93; PD 77/1148</td>
<td>Phoma eupatoni B</td>
<td>GU238071</td>
<td>GU237764</td>
<td>Eupatorium cannabinum</td>
</tr>
<tr>
<td>CBS 374.91; PD 78/391</td>
<td>Phoma eupreva B</td>
<td>GU238072</td>
<td>FJ426999</td>
<td>Solarium tuberosum</td>
</tr>
<tr>
<td>CBS 527.66; ATCC 22238</td>
<td>Phoma eupreva B</td>
<td>GU238073</td>
<td>FJ427000</td>
<td>Soil</td>
</tr>
<tr>
<td>CBS 633.92; ATCC 36786; VKM MF-325</td>
<td>Phoma fungicola</td>
<td>EUT54127</td>
<td>GU237900</td>
<td>Microspora alpillicoides on Quercus sp.</td>
</tr>
<tr>
<td>CBS 112.96</td>
<td>Phoma glauci</td>
<td>GU238077</td>
<td>GU237750</td>
<td>Dicentra sp.</td>
</tr>
<tr>
<td>CBS 114.96; PD 94/888</td>
<td>Phoma glauci B</td>
<td>FJS15649</td>
<td>FJS15609</td>
<td>Chelidonium majus</td>
</tr>
<tr>
<td>CBS 377.67</td>
<td>Phoma gossypiicola B</td>
<td>GU238079</td>
<td>GU237845</td>
<td>Gossypium hirsutum</td>
</tr>
<tr>
<td>CBS 104.80; PD 74/1017</td>
<td>Phoma henningsii B</td>
<td>GU238081</td>
<td>GU237731</td>
<td>Acacia mearnsii</td>
</tr>
<tr>
<td>CBS 502.91; PD 86/276</td>
<td>Phoma herbarum</td>
<td>GU238082</td>
<td>GU237874</td>
<td>Nerium sp.</td>
</tr>
<tr>
<td>CBS 615.75; PD 73/665; IMI 199779</td>
<td>Phoma herbarum B</td>
<td>EU880896</td>
<td>FJ427022</td>
<td>Rosa multiflora</td>
</tr>
<tr>
<td>CBS 629.97; PD 76/1017</td>
<td>Phoma herbicola B</td>
<td>GU238083</td>
<td>GU237898</td>
<td>Water</td>
</tr>
<tr>
<td>CBS 105.80; PD 75/908</td>
<td>Phoma huancayensis T</td>
<td>GU238084</td>
<td>GU237732</td>
<td>Solarium sp.</td>
</tr>
<tr>
<td>CBS 390.93; PD 77/1173</td>
<td>Phoma huancayensis</td>
<td>GU238085</td>
<td>GU237857</td>
<td>Chenopodium quinoa</td>
</tr>
<tr>
<td>CBS 220.85</td>
<td>Phoma humicola B</td>
<td>GU238086</td>
<td>GU237800</td>
<td>Franseria sp.</td>
</tr>
<tr>
<td>CBS 123394</td>
<td>Phoma infossa</td>
<td>GU238088</td>
<td>FJ427024</td>
<td>Fraxinus pennsylvanica</td>
</tr>
<tr>
<td>CBS 123395</td>
<td>Phoma infossa T</td>
<td>GU238089</td>
<td>FJ427025</td>
<td>Fraxinus pennsylvanica</td>
</tr>
<tr>
<td>CBS 252.92; PD 80/1144</td>
<td>Phoma insulana B</td>
<td>GU238090</td>
<td>GU237810</td>
<td>Olea europaea</td>
</tr>
<tr>
<td>Strain no.¹</td>
<td>Holomorph²</td>
<td>GenBank no.</td>
<td>Original substrate</td>
<td>Locality</td>
</tr>
<tr>
<td>-------------</td>
<td>------------</td>
<td>-------------</td>
<td>-------------------</td>
<td>----------</td>
</tr>
<tr>
<td>CBS 124.93; PD 87/269</td>
<td>Phoma labilis B</td>
<td>GU283091; GU237665; GU237619</td>
<td>Solanum lycopersicum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 479.93; PD 70/93</td>
<td>Phoma labilis</td>
<td>GU283092; GU237688; GU237620</td>
<td>Rosa sp.</td>
<td>Israel</td>
</tr>
<tr>
<td>CBS 347.82</td>
<td>Phoma longicolla</td>
<td>GU283094; GU237836; GU237621</td>
<td>Opuntiae sp.</td>
<td>Spain</td>
</tr>
<tr>
<td>CBS 124514; PD 80/1189; VPRI 1239</td>
<td>Phoma longicolla T</td>
<td>GU283095; GU237767; GU237622</td>
<td>Opuntiae sp.</td>
<td>Spain</td>
</tr>
<tr>
<td>CBS 223.69</td>
<td>Phoma macrostoma var. incolorata B</td>
<td>GU283096; GU237801; GU237623</td>
<td>Acer pseudoplatanus</td>
<td>Switzerland</td>
</tr>
<tr>
<td>CBS 109173; PD 83/908</td>
<td>Phoma macrostoma var. incolorata B</td>
<td>GU283097; GU237740; GU237624</td>
<td>Malus sylvestris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 529.66; PD 66/521</td>
<td>Phoma macrostoma var. macrostoma B</td>
<td>GU283098; GU237885; GU237625</td>
<td>Malus sylvestris</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 482.95</td>
<td>Phoma macrostoma var. macrostoma</td>
<td>GU283099; GU237869; GU237626</td>
<td>Larix decidua</td>
<td>Germany</td>
</tr>
<tr>
<td>CBS 259.92; IMI 286996; PD 91/272</td>
<td>Phoma matteucicola B</td>
<td>GU283100; GU237812; GU237627</td>
<td>Matteuccia struthiopteris</td>
<td>Canada</td>
</tr>
<tr>
<td>CBS 112.53</td>
<td>Phoma medicaginis</td>
<td>GU283101; GU237749; GU237628</td>
<td>Medicago sativa</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 404.65; IMI 116999</td>
<td>Phoma medicaginis var. macrospora B</td>
<td>GU283102; GU237859; GU237629</td>
<td>Medicago sativa</td>
<td>Canada</td>
</tr>
<tr>
<td>CBS 316.90</td>
<td>Phoma medicaginis var. medicaginis</td>
<td>GU283103; GU237829</td>
<td>Medicago sativa</td>
<td>Czech Republic</td>
</tr>
<tr>
<td>CBS 105.95</td>
<td>Phoma microchlamydospora T</td>
<td>GU283104</td>
<td>Eucalyptus sp.</td>
<td>U.K.</td>
</tr>
<tr>
<td>CBS 491.90</td>
<td>Phoma microchlamydospora</td>
<td>GU283105; GU237829; GU237631</td>
<td>Uidentifed vegetable</td>
<td>U.K.</td>
</tr>
<tr>
<td>CBS 315.83</td>
<td>Phoma minor</td>
<td>GU283106; GU237826; GU237631</td>
<td>Syzygium aromaticum</td>
<td>Indonesia</td>
</tr>
<tr>
<td>CBS 325.82</td>
<td>Phoma minor T</td>
<td>GU283107; GU237831; GU237632</td>
<td>Syzygium aromaticum</td>
<td>Indonesia</td>
</tr>
<tr>
<td>CBS 110.79; PD 65/8875; MUCL 8247</td>
<td>Phoma multirostrata</td>
<td>GU283110; FJ427030; FJ427140</td>
<td>Cucumis sativus</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 274.60; IMI 081598</td>
<td>Phoma multirostrata T</td>
<td>GU283111; FJ427031; FJ427141</td>
<td>Soil</td>
<td>India</td>
</tr>
<tr>
<td>CBS 368.65; PD 92/1757; HACC 154</td>
<td>Phoma multirostrata</td>
<td>GU283112; FJ427033; FJ427143</td>
<td>Soil</td>
<td>India</td>
</tr>
<tr>
<td>PD 83/48</td>
<td>Phoma multirostrata</td>
<td>GU283113</td>
<td>FJ427037; FJ427147</td>
<td>Cucumis sativus</td>
</tr>
<tr>
<td>CBS 117.93; PD 83/90</td>
<td>Phoma nebulosa</td>
<td>GU283114; GU237757; GU237633</td>
<td>Mercurialis perennis</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 503.75; ATCC 32163; DSM 63391; IMI 194766; PD 75/4</td>
<td>Phoma nebulosa B</td>
<td>GU283115; GU237875; GU237634</td>
<td>Urtica dioica</td>
<td>Austria</td>
</tr>
<tr>
<td>CBS 358.71</td>
<td>Phoma negriana B</td>
<td>GU283116; GU237838; GU237635</td>
<td>Vitis vinifera</td>
<td>Germany</td>
</tr>
<tr>
<td>PD 79/74</td>
<td>Phoma negriana</td>
<td>GU283117; GU237916; GU237636</td>
<td>Vitis vinifera</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 116.96; PD 95/7930</td>
<td>Phoma nigripycnidia B</td>
<td>GU283118; GU237756; GU237637</td>
<td>Vicia cracca</td>
<td>Russia</td>
</tr>
<tr>
<td>CBS 114.93; PD 74/228</td>
<td>Phoma novae-verbascicola</td>
<td>GU283119; GU237753; GU237638</td>
<td>Verbascum sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 127.93; PD 92/347</td>
<td>Phoma novae-verbascicola B</td>
<td>GU283120; GU237774; GU237639</td>
<td>Verbascum densiflorum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 654.77</td>
<td>Phoma omnivirens</td>
<td>GU283122</td>
<td>FJ427043; FJ427153</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 991.95</td>
<td>Phoma omnivirens</td>
<td>GU283121</td>
<td>FJ427044; FJ427154</td>
<td>Soil</td>
</tr>
<tr>
<td>CBS 560.81; PD 92/1569; PDDCC 6614</td>
<td>Phoma paspaë T</td>
<td>GU283124</td>
<td>FJ427048; FJ427158</td>
<td>Paspalum dilatatum</td>
</tr>
<tr>
<td>CBS 561.81; PDDCC 6615</td>
<td>Phoma paspaë</td>
<td>GU283125; GU237889; GU237640</td>
<td>Lolium perenne</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 124516; PD 84/453</td>
<td>Phoma pedeia</td>
<td>GU283126; GU237769; GU237641</td>
<td>Orchidaceae</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 124517; PD 92/612A</td>
<td>Phoma pedeia T</td>
<td>GU283127; GU237770; GU237642</td>
<td>Schefflera elegantissima</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 267.92; PD 76/1014</td>
<td>Phoma pereyprena T</td>
<td>GU283128; GU237814; GU237643</td>
<td>Coffea arabica</td>
<td>India</td>
</tr>
<tr>
<td>CBS 268.93; CBS 108.93; PD 88/720</td>
<td>Phoma piperis B</td>
<td>GU283129; GU237816; GU237644</td>
<td>Peperomia perekopifolia</td>
<td>Netherlands</td>
</tr>
<tr>
<td>PD 90/2011</td>
<td>Phoma piperis</td>
<td>GU283130; GU237921; GU237645</td>
<td>Peperomia sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 284.93; PD 75/907</td>
<td>Phoma plurivora</td>
<td>GU283131; GU237822; GU237646</td>
<td>Medicago sativa</td>
<td>Australia</td>
</tr>
<tr>
<td>CBS 558.81; PDDCC 6873</td>
<td>Phoma plurivora T</td>
<td>GU283132; GU237888; GU237647</td>
<td>Setana sp.</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 109181; PD 83/757</td>
<td>Phoma polemonii B</td>
<td>GU283133; GU237746; GU237648</td>
<td>Polemonium caeruleum</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 116.93; PD 71/884</td>
<td>Phoma poolensis B</td>
<td>GU283134; GU237755; GU237649</td>
<td>Antirrhinum majus</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 113.20; PD 92/774</td>
<td>Phoma poolensis</td>
<td>GU283135; GU237751; GU237650</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 372.91; PD 75/690</td>
<td>Phoma putaminum B</td>
<td>GU283137; GU237843; GU237651</td>
<td>Ulnus sp.</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 130.69; CECT 20054; IMI 331916</td>
<td>Phoma putaminum B</td>
<td>GU283138; GU237777; GU237652</td>
<td>Malus sylvestris</td>
<td>Denmark</td>
</tr>
<tr>
<td>CBS 109177; LEV 15165; PD 2000/9941</td>
<td>Phoma rhei B</td>
<td>GU283139; GU237743; GU237653</td>
<td>Rheum rhaponticum</td>
<td>New Zealand</td>
</tr>
<tr>
<td>CBS 298.89</td>
<td>Phoma saxea</td>
<td>GU283140; GU237824; GU237654</td>
<td>Limestone</td>
<td>Germany</td>
</tr>
<tr>
<td>Strain no.¹</td>
<td>Holomorph²</td>
<td>GenBank no.</td>
<td>Original substrate</td>
<td>Locality</td>
</tr>
<tr>
<td>------------</td>
<td>------------</td>
<td>-------------</td>
<td>--------------------</td>
<td>----------------</td>
</tr>
<tr>
<td>CBS 419.92</td>
<td>Phoma saxea T</td>
<td>GU238141</td>
<td>GU237860</td>
<td>Corroded mediterranean marble</td>
</tr>
<tr>
<td>CBS 122.93</td>
<td>Phoma selagineicola B</td>
<td>GU238142</td>
<td>GU237762</td>
<td>Selagineicola sp.</td>
</tr>
<tr>
<td>CBS 160.78</td>
<td>Phoma selagineicola B</td>
<td>GU238143</td>
<td>GU237787</td>
<td>Senecio jacobaea</td>
</tr>
<tr>
<td>CBS 249.92</td>
<td>Phoma subberbarum</td>
<td>GU238144</td>
<td>GU237780</td>
<td>Solanum sp.</td>
</tr>
<tr>
<td>CBS 250.92</td>
<td>Phoma subberbarum B</td>
<td>GU238145</td>
<td>GU237809</td>
<td>Solanum sp.</td>
</tr>
<tr>
<td>CBS 305.79A</td>
<td>Phoma subberbarum</td>
<td>GU238146</td>
<td>GU237825</td>
<td>Zea mays</td>
</tr>
<tr>
<td>CBS 135.93</td>
<td>Phoma sylvetica B</td>
<td>GU238147</td>
<td>GU237781</td>
<td>Melampyrum pratense</td>
</tr>
<tr>
<td>CBS 874.97</td>
<td>Phoma sylvetica B</td>
<td>GU238148</td>
<td>GU237907</td>
<td>Melampyrum pratense</td>
</tr>
<tr>
<td>CBS 436.75</td>
<td>Phoma tropica T</td>
<td>GU238149</td>
<td>GU237864</td>
<td>Saintpaulia ionantha</td>
</tr>
<tr>
<td>CBS 876.97</td>
<td>Phoma versabilis B</td>
<td>GU238152</td>
<td>GU237909</td>
<td>Silene sp.</td>
</tr>
<tr>
<td>PD 2000/1379</td>
<td>Phoma versabilis</td>
<td>GU238153</td>
<td>GU237913</td>
<td>Stellania media</td>
</tr>
<tr>
<td>CBS 500.91</td>
<td>Phoma viburnicola B</td>
<td>GU238154</td>
<td>GU237871</td>
<td>Ilex aquifolium</td>
</tr>
<tr>
<td>CBS 523.73</td>
<td>Phoma viburnicola B</td>
<td>GU238155</td>
<td>GU237879</td>
<td>Viburnum cassinoides</td>
</tr>
<tr>
<td>CBS 383.68</td>
<td>Phoma xanthina B</td>
<td>GU238157</td>
<td>GU237855</td>
<td>Delphinium sp.</td>
</tr>
<tr>
<td>PD 84/407</td>
<td>Phoma xanthina</td>
<td>GU238158</td>
<td>GU237918</td>
<td>Delphinium sp.</td>
</tr>
<tr>
<td>CBS 131.93</td>
<td>Phoma zantedeschiae</td>
<td>GU238159</td>
<td>FJ427084</td>
<td>Calla sp.</td>
</tr>
<tr>
<td>CBS 105.96</td>
<td>Stagonosporopsis actaeae B</td>
<td>GU238165</td>
<td>GU237733</td>
<td>Cimicifuga simplex</td>
</tr>
<tr>
<td>CBS 106.96</td>
<td>Stagonosporopsis actaeae T</td>
<td>GU238166</td>
<td>GU237734</td>
<td>Actaea spicata</td>
</tr>
<tr>
<td>CBS 176.93</td>
<td>Stagonosporopsis ajacis</td>
<td>GU238167</td>
<td>GU237790</td>
<td>Delphinium sp.</td>
</tr>
<tr>
<td>CBS 177.93</td>
<td>Stagonosporopsis ajacis T</td>
<td>GU238168</td>
<td>GU237791</td>
<td>Delphinium sp.</td>
</tr>
<tr>
<td>CBS 101.80</td>
<td>Stagonosporopsis andigena B</td>
<td>GU238169</td>
<td>GU237714</td>
<td>Solanum sp.</td>
</tr>
<tr>
<td>CBS 269.80</td>
<td>Stagonosporopsis andigena</td>
<td>GU238170</td>
<td>GU237817</td>
<td>Solanum sp.</td>
</tr>
<tr>
<td>CBS 102836</td>
<td>Stagonosporopsis artemisicola B</td>
<td>GU238171</td>
<td>GU237728</td>
<td>Artemisia dracunculus</td>
</tr>
<tr>
<td>CBS 178.25</td>
<td>Stagonosporopsis astragal B</td>
<td>GU238172</td>
<td>GU237792</td>
<td>Astragalus sp.</td>
</tr>
<tr>
<td>CBS 248.90</td>
<td>Stagonosporopsis canicae</td>
<td>GU238175</td>
<td>GU237807</td>
<td>Carica papaya</td>
</tr>
<tr>
<td>PD 06/0302531</td>
<td>Stagonosporopsis canicae</td>
<td>GU238176</td>
<td>GU237912</td>
<td>Carica papaya</td>
</tr>
<tr>
<td>CBS 282.76</td>
<td>Stagonosporopsis canicae</td>
<td>GU238177</td>
<td>GU237821</td>
<td>Brassica sp.</td>
</tr>
<tr>
<td>CBS 713.85</td>
<td>Stagonosporopsis crystalliniformis T</td>
<td>GU238178</td>
<td>GU237903</td>
<td>Lycopericon eouslentum</td>
</tr>
<tr>
<td>CBS 771.85</td>
<td>Stagonosporopsis crystalliniformis</td>
<td>GU238179</td>
<td>GU237906</td>
<td>Solanum tuberosum</td>
</tr>
<tr>
<td>CBS 109171</td>
<td>Stagonosporopsis cucurbitacearum</td>
<td>GU238180</td>
<td>GU237922</td>
<td>Cucurbita sp.</td>
</tr>
<tr>
<td>CBS 133.96</td>
<td>Stagonosporopsis dennisii B</td>
<td>GU238181</td>
<td>GU237780</td>
<td>Cucurbita sp.</td>
</tr>
<tr>
<td>CBS 631.68</td>
<td>Stagonosporopsis dennisii</td>
<td>GU238182</td>
<td>GU237899</td>
<td>Solidago floribunda</td>
</tr>
<tr>
<td>CBS 135.96</td>
<td>Stagonosporopsis dennisii</td>
<td>GU238183</td>
<td>GU237872</td>
<td>Solidago canadensis</td>
</tr>
<tr>
<td>CBS 320.90</td>
<td>Stagonosporopsis dorenboschii B</td>
<td>GU238184</td>
<td>GU237830</td>
<td>Physostegia virginiana</td>
</tr>
<tr>
<td>CBS 426.90</td>
<td>Stagonosporopsis dorenboschi T</td>
<td>GU238185</td>
<td>GU237862</td>
<td>Physostegia virginiana</td>
</tr>
<tr>
<td>CBS 109182</td>
<td>Stagonosporopsis helioptidis B</td>
<td>GU238186</td>
<td>GU237747</td>
<td>Heliotis patula</td>
</tr>
<tr>
<td>PD 95/6189</td>
<td>Stagonosporopsis helioptidis</td>
<td>GU238187</td>
<td>GU237924</td>
<td>Ambrosia artemisiifolia</td>
</tr>
<tr>
<td>CBS 104.42</td>
<td>Stagonosporopsis hortensis B</td>
<td>GU238198</td>
<td>GU237730</td>
<td>Unknown</td>
</tr>
<tr>
<td>CBS 572.85</td>
<td>Stagonosporopsis hortensis B</td>
<td>GU238199</td>
<td>GU237704</td>
<td>Phaseolus vulgaris</td>
</tr>
<tr>
<td>CBS 425.90</td>
<td>Stagonosporopsis liguicola var. inoxydabilis T</td>
<td>GU238188</td>
<td>GU237861</td>
<td>Chrysanthemum parthenii</td>
</tr>
<tr>
<td>PD 85/259</td>
<td>Stagonosporopsis liguicola var. inoxydabilis</td>
<td>GU238189</td>
<td>GU237920</td>
<td>Matricaria sp.</td>
</tr>
<tr>
<td>CBS 500.63</td>
<td>Stagonosporopsis liguicola var. liguicola B</td>
<td>GU238190</td>
<td>GU237872</td>
<td>Chrysanthemum indicum</td>
</tr>
<tr>
<td>CBS 137.96</td>
<td>Stagonosporopsis liguicola var. liguicola B</td>
<td>GU238191</td>
<td>GU237866</td>
<td>Chrysanthemum indicum</td>
</tr>
<tr>
<td>CBS 562.81</td>
<td>Stagonosporopsis loticola T</td>
<td>GU238192</td>
<td>GU237890</td>
<td>Loto pedunculatus</td>
</tr>
<tr>
<td>CBS 628.97</td>
<td>Stagonosporopsis loticola</td>
<td>GU238193</td>
<td>GU237896</td>
<td>Loto tenuis</td>
</tr>
<tr>
<td>Strain no.</td>
<td>Holomorph¹</td>
<td>GenBank no.</td>
<td>Original substrate</td>
<td>Locality</td>
</tr>
<tr>
<td>------------</td>
<td>------------</td>
<td>-------------</td>
<td>-------------------</td>
<td>----------</td>
</tr>
<tr>
<td>CBS 101494; PD 98/5247</td>
<td>Stagonosporopsis lupini B</td>
<td>GU238194 GU237724 GU237699</td>
<td>Lupinus albus</td>
<td>U.K.</td>
</tr>
<tr>
<td>CBS 375.84; PD 80/1250</td>
<td>Stagonosporopsis lupini</td>
<td>GU238195 GU237844 GU237700</td>
<td>Lupinus mutabilis</td>
<td>Peru</td>
</tr>
<tr>
<td>CBS 634.92; IMI 193307</td>
<td>Stagonosporopsis oculo-hominis T</td>
<td>GU238196 GU237901 GU237701</td>
<td>Human</td>
<td>U.S.A.</td>
</tr>
<tr>
<td>CBS 103180; PD 79/175</td>
<td>Stagonosporopsis rudbeckiae B</td>
<td>GU238197 GU237745 GU237702</td>
<td>Rudbeckia bicolor</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 379.91; PD 77/675</td>
<td>Stagonosporopsis tracheli B</td>
<td>GU238173 GU237850 GU237678</td>
<td>Campanula isophylla</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 384.68</td>
<td>Stagonosporopsis tracheli B</td>
<td>GU238174 GU237856 GU237679</td>
<td>Campanula isophylla</td>
<td>Sweden</td>
</tr>
<tr>
<td>CBS 273.92; PD 76/1019</td>
<td>Stagonosporopsis valerianellae B</td>
<td>GU238200 GU237819 GU237705</td>
<td>Valerianella locusta</td>
<td>Netherlands</td>
</tr>
<tr>
<td>CBS 329.67; PD 66/302</td>
<td>Stagonosporopsis valerianellae B</td>
<td>GU238201 GU237832 GU237706</td>
<td>Valerianella locusta var. oleracea</td>
<td>Netherlands</td>
</tr>
</tbody>
</table>

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

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

---

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

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

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

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

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

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

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

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

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

*Phoma fimeti* forms a subclade with *Ph. samarorum* and a strain that was previously identified as *Stenocarpella macrospora* (BPP = 0.98; RBS = 67 %), but that is probably misidentified (De
Gruyter et al. 2009). Especially the finding of Ph. samarorum is noteworthy, as it is found rather distinct from two clusters of other species belonging to the section Heterospora, which are retrieved among the Leptosphaeriaceae and Didymellaceae (clades 7 and 8). In contrast to these other Heterospora species, the large conidia of Ph. samarorum that can be observed in planta are clearly distinct by the subulate top cells, and measures up to 17 × 3.5 μm (Boerema et al. 1997). The strain identified as Stenocarpella macrospora is now sterile and therefore not studied morphologically. This species is known to produce similar-shaped, septate conidia, which are however pigmented and considerably larger, 44–82 × 7.5–11.5 μm (Sutton 1980). The close association with Ph. fimeti is therefore remarkable as this species is known to produce only minute, aseptate conidia, measuring (2–)2.5–4–(5) × (1.5–)2–2.5–(3) μm (De Gruyter & Noordeloos 1992).

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

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

**Clade 7, Leptosphaeriaceae and Pleosporaceae:**

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

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

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

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

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

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

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

This clade also accommodates Pleospora betae, a notorious leaf and seed pathogen of beet (Beta vulgaris, Bugbee & Cole 1981), and Pl. herbarum, which is the type species of the genus Pleospora. The genetic distance between the two species was already observed in a study utilising SSU nrDNA sequences (Dong et al. 1998). Also three Phoma species that are found in close association with these “true” Pleosporaceae and that are found basal to this clade, Ph. fallens, Ph. flavigena and Ph. glaucispora...
Fig. 2. Fifty percent majority rule consensus tree from a BI analysis of LSU, ITS and TUB sequences of Didymellaceae (n = 274). At the nodes the BI Posterior Probabilities are presented above the branch, and bootstrap percentages of the analysis are given below the branch. Branches that were less than 50 % supported in the ML analyses are indicated with a hyphen. The bar indicates the number of substitutions per site. The tree is rooted with Ascochyta hordei var. hordei (CBS 544.74) and Phoma paspali (CBS 560.81 & CBS 561.81).
Fig. 2. (Continued).
Heterospora have glabrous pycnidia and, like Ph. betae, aseptate conidia, hence their link to Phoma. Absence of an ostiole is only recorded in Ph. glaucispora (De Gruyter et al. 1998).

Pleospora is linked to the anamorph genus Stemphylium (Simmons 1969), Alternaria and Dendryphon (Von Arx 1981). The pluriform nature of the Pleospora anamorphs strongly contrasts with the relatively uniform morphology of the teleomorphic structures (Holm 1962, Kodsuëb et al. 2006, Inderbitzin et al. 2009). The polyphyletic nature of Pleospora has been hypothesised by Holm (1982) and Berbee (1996), but only recently have molecular studies confirmed its taxonomic complexity (Dong et al. 1998, Kodsuëb et al. 2006, Inderbitzin et al. 2009).

Clade 8, Didymellaceae:
The major cluster observed in the generic phylogeny is the top clade in Fig. 1, which represents the Didymellaceae clade. This clade is well supported (BPP = 0.99, RBS = 94 %), but with the loci used, a high level of basal polytomy is recorded within the clade. The ancestral species in this clade are the Gramineae-pathogens, Ascochyta hordei and Ph. paspali. The latter species has been considered to be an indigenous pathogen of grasses in Australia and New Zealand (Johnston 1981, Boerema et al. 2004), but based on sequence comparisons this species is probably also present in Europe (Wirsel et al. 2001, C. Gueidan pers. comm.).

Clade 8 comprises most Phoma species, including CBS 615.75, the representative strain of Ph. herbarum (Boerema et al. 2009).
Fig. 2. (Continued).
2004), which is type species of the genus (Boerema 1964). This clade also includes the type species of the Phoma sections Phoma, Peyronellaea, Phylllostictoides, Soloraphomella and Macrospora. Some phytopathologically and medically relevant species of the section Heterospora are also associated with this clade, although some of these species of this section are found in other clades, such as Ph. samarorum (clade 6) and Ph. dimorphospora, and the sectional type Ph. heteromorphospora (clade 7). Finally, a single species of the setose section Paraphoma, Ph. gardeniea, is found in the Didymellaceae. Based on the sequence data obtained in this study, it is estimated that approximately 70% of the species recognised by Boerema et al. (2004) can be associated with the Didymellaceae.

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

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

Where a sexual state is known for the Phoma and Ascochyta species in clade 8, it is Didymella. The type species of this teleomorph genus, D. exigua, is also found within this clade, although it is not associated with a Phoma anamorph state. The family Didymellaceae was introduced for this group by De Gruyter et al. (2009). However, type species of two other teleomorph genera have also been found within this clade. DNA sequences of Leptosphaerulina australiensis resemble a high level of similarity with those of the various Phoma and Didymella strains, although none are identical. Also sequences of LSU and ITS sequence data obtained from GenBank of L. americana, L. argentensis, L. charantarum, L. crassiasca and L. trifolii (GenBank accession no. AY273818, AY849949, EU272493, U79485,AY831558 respectively) were highly similar or even identical to the Didymellaceae sequences obtained in the present study (data not shown). These observations are in congruence with the results obtained by Silva-Hanlin & Hanlin (1999), who found that D. bryoniae (anam. Ph. cucurbitacearum) was closely related with L. charantarum and L. crassiasca. Also Macroventuria anomochaeta, which represents the genus Macroventuria (Van der Aa 1971) groups in Didymellaceae. The close genetical resemblance of Macroventuria and Leptosphaerulina found in the present study is in congruence with the results of Kofsuw et al. (2006).

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

Systematics of the Didymellaceae

DNA phylogenetic analysis

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

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

Systematics: treatment of clades

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

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

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

Several well-supported clusters are recognised within this family that are treated here as novel groups of the Didymellaceae. In this section these separate groups are treated. However, although multiple genes were employed in this study to generate a phylogenetic reconstruction of the family, high levels of basal polytomy were observed as well (Fig. 2). Application of general nrDNA loci alone did not reduce this high level of polytomy, whilst interspecies variation in several well-supported clades was reduced drastically.
Group A – outgroup and basal lineages:
The tree presented in Fig. 2 is rooted to Ascochyta hordei and Ph. paspali, which proved to be ancestral to the Didymellaceae in Fig. 1. The latter species was described by Johnston (1981) as a species from grasses in New Zealand and Australia, but in recent years, isolates with similar genotypes were isolated from iron-rich volcanic soil from France (C. Gueidan, pers. comm.), and from common reed (Phragmites australis) in Germany (Wüstem et al. 2001). These isolates were, however, never studied morphologically.

Another species used as outgroup is Ascochyta hordei var. hordei (CBS 544.74), which was obtained from a South African Triticum aestivum, indicating that also within the Didymellaceae, species that are ascribed to Ascochyta do not form a monophyletic group. Also CBS 259.92, the isolate of Ph. matteucicola, proved to be basal to most other Phoma species. Phoma matteucicola is commonly known as a pathogen of many fern species (De Gruyter et al. 2002). Within the basal lineages, also a group comprising Ph. humicola and the novel species Ph. saxea is found, although this group is only supported by BI analysis (BPP = 0.92, RBS < 50 %).

Although Phoma humicola is known as a saprotic soil fungus, it is sometimes mistaken for the notorious potato pathogen Ph. humicola (Group N), due to a similar biochemical reaction to NaOH and the formation of citrine green crystals (De Gruyter et al. 1998). However, conidia of Ph. humicola are always eguttulatate in contrast to those of Ph. foveata. Phoma saxea has been found twice in Germany on rock material, and will be further described below.


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


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

Conidia dimorpha, intra idem pycnidia formata. Conidia typus 1 (sub)globosa, glabra, hyalina, continua, (3–)3.5–5.5 μm diam., (0–)3–10(–15) guttulæ praeditæ. Conidia typus 2 cylindrica vel ellipsoidea, glabra, hyalina, continua, (3.5–)4.5–7(–7.5) × 2.5–3.5(–4) μm, plerumque eguttulata, vel 1–3 guttulas praeditæ. Matrix conidiorum salmonea. Chlamydosporeae continuae, globosae, vinidulae, in catenas usque 35 positæ, (8.5–)10.5–16.5(–17.5) × (6–)8–12.5(–14) μm.

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

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

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

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

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

Both strains of this species have been isolated from stone material, such as limestone (CBS 298.89) and corroded Mediterranean marble (CBS 419.92). Although the genus is known from all kinds of substrates, the number of rock-inhabiting Phoma isolates is relatively low. Selbmann et al. (2002) report on Ph. herbarum from Antarctic rock, and Boerema et al. (2004) list several species from rock-like materials, such as cement (Ph. herbarum), wall-plaster (Ph. heteroderae – here recombined into Ph. coloripherens) and crockery (Ph. pomorum). In addition, multiple species are recorded from rock-inhabiting lichens (Nelson et al. 2009, Ruibal et al. 2009). These species, listed by Hawksworth & Cole (2004) are, however, unculturable and could therefore not be compared with Ph. saxea in vitro. However, the morphological descriptions suggest that the mentioned species and Ph. saxea are different taxonomic entities.
Group B:
Four of the six species clustering in Group B produce a Didymella teleomorph. Only Ph. polemonii and Ph. xanthina presently have no known sexual state. The species in this clade are collected from a wide variety of dicots, although all individual taxa appear to be host-specific (Boerema et al. 2004). Also the micromorphological features of these species are highly variable.

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


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

**Didymella catariae** (Cooke & Ellis) Sacc., Syll. Fung. 1: 557. 1882.
Basionym: Sphaeria catariae Cooke & Ellis, Grevillea 5: 96. 1876.
Specimen examined: The Netherlands, from the stem of Nepeta catenaria, 1977, M.M.J Dorenbosch, CBS 102635 = PD 77/1131.


\[fig. 3. Phoma saxea\] (CBS 419.92). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D. Pycnidia. E–F. Conidiogenous cells. G. Conidia. H. Chain of unicellular chlamydospores. Scale bars: D = 100 μm; E–G = 5 μm; H = 20 μm.
Phoma polemnonii Cooke, Grevillea 13(68): 94. 1885.


**Group C**

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

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


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

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


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


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

Groups D & E – Leptosphaerulina and Macroventuria:

The most remarkable findings in the Didymellaceae are the Leptosphaerulina and Macroventuria (clade E) teleomorph genera. The species belonging to these teleomorphs are found amidst the Leptosphaerulina, Macroventuria, and Didymella, although all three genera are known for their hyaline ascospores (Van der Aa 1971, Von Arx 1981). Leptosphaerulina
produces large, longitudinally and transversely septated ascospores, resembling those of Pleospora and Cucurbitaria, although the ascospores of these genera are pigmentless. The major difference between Didymella and Macroventuria is the presence of setae on the pseudothecia of the latter genus, whereas Didymella ascomata are commonly glabrous. According to the original description (Van der Aa 1971), Macroventuria strains resemble Venturia by their setose pycnidia, but differ in their restricted number of the asci.


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

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

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


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


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

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

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


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

*Pycnidia* always solitary, produced on the agar surface, globose, peroblate to suboblate, glabrous, measuring (50–)65–130(–150) ×
Phoma pedeiae Aveskamp, Gruyter & Verkley, sp. nov. MycoBank MB515594. Fig. 4.

Conidia ellipsoidal vel cylindrical, glabra, hyalina, continua, 3–4.5 × 1.5–2.5 μm, 0–2(–3) guttulias praedita. Matrix conidiornis cremeo-alba.

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

Pycnidia solitaria or confluent, produced on the agar surface, globose to ellipsoidal, glabrous, (90–)100–230(–255) × (75–)90–15(–165) μm with 1–2 conspicuous, non-papillate ostioles. Pycnidial wall pseudoparenchymatous, composed of oblong to isodiametric cells, 3–5 layers, 11–17 μm thick. Conidiogenous cells phalidic, hyaline, simple, smooth, doliform to ampulliform, variable in size, ca. (3–)3.5–5 × 3–4(–5) μm. Conidia variable in shape and size, subglobulose to oval or oblate, thin-walled, smooth, aseptate, measuring (5–)5.5–7.5(–8.5) × 3–4.5(–5) μm, with 0–2(–3) minute guttules, initially hyaline, but brown at maturity. Conidial exudates not recorded.

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

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

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

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


Group G:

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

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

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


Specimens examined: Canada, from Zea mays, holotype L 992.177.439, culture ex-holotype CBS 250.9292 = DAOM 171914 = PD 92/171; from Zea mays, May 1978, G.A. Neish, CBS 305.79A = DAOM 170848; Peru, from Solanum sp., CBS 249.92 = PD 78/1088.

Group H: Phoma bellidis and Ph. senecionis are found in association with two plant genera from the Compositae family: Bellis spp. and Senecio spp. respectively (De Gruyter et al. 1993). The distantly related Ph. digitalis is a pathogen of Digitalis spp. (Scrophulariaceae), but shares the feature with Ph. bellidis that it is also recorded as a seed-pathogen (Boerema & Dorenbosch 1979). In contrast, Ph. senecionis is only known as a necrophyte.
**Phoma bellidis** Neerg., Friesia 4: 74. 1950.


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

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


**Group I**

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


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


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

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

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

Etymology: The epithet refers to the two different conidial types that are observed.
Species examined: Spain, Canary Isles, Gran Canaria, from phyllocladium of *Opuntia* sp., June 1982, H.A. Van der Aa, **holotype designated here** CBS H-20234, culture ex-holotype CBS 346.82.

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

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

**Group K – Peyronellaeae:**

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

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

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

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

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

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

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

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

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

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


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

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

**Peyronellaea alectorolophi** (Rehm.) Aveskamp, Gruyter & Verkley, *comb. nov.* MycoBank MB515997

*Basionym:* Didymella alectorolophi Rehm, apud Ade, Hedwigia 64: 294. 1923.


**Peyronellaea americana** (Morgan-Jones & J.F. White) Aveskamp, Gruyter & Verkley, *comb. nov.* MycoBank MB515996


**Peyronellaea anserina** (Marchal) Aveskamp, Gruyter & Verkley, *comb. nov.* MycoBank MB515998

*Basionym:* Phoma anserina Marchal, Champignon Copr. 11: 1891.


**Peyronellaea arachidicola** (Kohkr.) Aveskamp, Gruyter & Verkley, *comb. nov.* MycoBank MB515999


**Peyronellaea australis** Aveskamp, Gruyter & Verkley, nom. nov. pro Phoma nigricans P.R. Johnst. & Boerema, MycoBank MB516001.


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


**Peyronellaea calorigreferens** (Boerema, Gruyter & Noordel.) Aveskamp, Gruyter & Verkley, *comb. nov.* MycoBank MB516002


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

**Peyronellaea calorreferens** (Boerema, Gruyter & Noordel.) Aveskamp, Gruyter & Verkley, *comb. nov.* MycoBank MB516002

of 1(–4) slightly papillate ostioles, measuring (70–)100–200(–250) μm diam. *Pyrnidial wall* pseudoparenchymatous, composed of isodiametric cells, 2–5 layers thick, with many hyphal outgrowths, some setae-like. *Conidiogenous cells* phialidic, hyaline, simple, smooth, flask-shaped, ca. 3–5.5 × 3–6.5 μm. *Conidia* broadly ellipsoidal to ovoid to cylindrical, thin-walled, smooth, hyaline, (3.5–)4–8.5(–12) × 2.3–5.5(–4.5) μm, aseptate, with (1–)2–5(–8) polar guttules. Conidial matrix pale pink. *Chlamydoconidia* highly variable in shape and size, mostly unicellular but also multicellular. Where unicellular, pale brown to brown, guttulate, intercalary, solitary or in chains, globose, 7.5–19(–26) μm, thick-walled and often with a distinct "envelope". Where multicellular dicytosporous alternarioide or botryoid, brown to brown, guttulate, intercalary, solitary or in chains, globose, 8.5(–12) × 2–3.5(–4.5) μm, aseptate, with (1–)2–5(–8) polar guttules.

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

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


**Peyronellaea obtusa** (Fuckel) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515608.


**Peyronellaea pinodella** (L.K. Jones) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515609.

**Basionym:** *Ascochyta pinodella* L.K. Jones, Bull. New York State Agric. Exp. Sta. 54: 10. 1927.


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

**Peyronellaea pinodes** (Berk. & A. Bloxam) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515610.


**Peyronellaea pomorum** var. *circinata* (Kusnezzowa) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515612.


**Peyronellaea pomorum** var. *cyanea* (Jooste & Papendorf) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515614.

**Basionym:** *Phoma cyanea* Jooste & Papendorf, Mycotaxon 12: 444. 1981.


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

**Peyronellaea pomorum** var. *pomorum* (Thüm.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515611.

**Basionym:** *Phoma pomorum* var. *pomorum* Thüm., Fungi Pompilici: 105. 1879.

Specimen examined: The Netherlands, Wageningen, from Polygonum tataricum, 1964, M.M.J. Dorenbosch, CBS H-16540, culture CBS 539.66 = ATCC 16791 = IMI 122266 = PD 84/914.

**Peyronellaea protuberans** (Lév.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515613.


Specimen examined: The Netherlands, from a leaf of *Lycium halifolium*, 1971, CBS 361.96 = PD 71/706.

**Peyronellaea sancta** (Aveskamp, Gruyter & Verkley) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515615.


**Peyronellaea subglomerata** (Boerema, Gruyter & Noordel.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515616.


**Peyronellaea zeae-maydis** (Mukunya & Boothr.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515617.


**Group L:**

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

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

Conidia cylindrica, glabra, hyalina, continua, 6–9(–10) × 2–3(–3.5) μm, (3)4–6(–8) guttulatis parvis praedita. Matrix conidiornia alba.
**Etymology:** Epithet refers to the country of origin, Brazil.

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

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

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

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


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

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


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

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

Conidiomata pycnidial, globose to subglobose, measuring 50–250 μm diam, on agar surface or immersed, mostly solitary but incidentally confluent. Ostioles papillate or on pronounced necks. *Pycnidal wall* pseudoparenchymatous, counting 2–8 cell layers of which the outer 1–3 are brown-olivaceous pigmented. *Conidiogenous cells* phialidic, hyaline, simple, smooth, ampulliform, ca. 3–7 × 3–7 μm. *Conidia* variable in shape, initially hyaline but in later stages a slight brownish pigmentation may be found, thin-walled, smooth, always aseptate 3–8.5(–10) × 1.5–4(–4.5) μm. *Chlamydospores* unicellular or multicellular, intercalary or terminal, smooth, verrucose or incidentally turbinate, subhyaline to dark brown, where unicellular globose, measuring 5–15 μm diam, where multicellular globose or irregular shaped, smooth, verrucose or incidentally turbinate, measuring 6–35 μm.

Type species: *Epicoccum nigrum* Link.


**Epicoccum pimprinum** (P.N. Mathur, S.K. Menon & Thirum.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515619.

Specimens examined: India, Poona, Pimpri, from soil, Mar. 1959, S.K. Menon, ex-isotype culture CBS 246.60 = ATCC 22237 = ATCC 16652 = IMI 81601; from soil, 1977, PD 77/1028.
**Epicoccum sorghi** (Sacc.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515620.


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


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

**Group N – Boeremia gen. nov.:**

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

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

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

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

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

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


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

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

**Etymology:** Named after Gerhard H. Boerema, who made great contributions to our understanding of the taxonomy of phomoid fungi.
**Boeremia crincola** (Siemasko) Aveskamp, Gruyter & Verkley, *comb. nov.* MycoBank MB515622.


**Boeremia diversispora** (Bubák) Aveskamp, Gruyter & Verkley, *comb. nov.* MycoBank MB515623.

*Basionym:* *Phoma diversispora* Bubák, Oest. Bot. Z. 55: 78. 1905

≡ *Phoma exigua* var. *diversispora* (Bubák) Boerema apud Boerema & van Kesteren, Gewasbescherming 11: 122. 1980

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


For a complete description see De Gruyter et al. (2002).

Specimens examined: *Brazil,* Patrocinio, from leaf of *Coffee arabica,* L.H. Pfenning, CBS 119730.

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


Specimens examined: *Germany,* Artern, from *Foeniculum vulgare,* Apr. 1984, S. Petzoldt, CBS 391.84.

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

**Boeremia exigua** var. *gilvescens* Aveskamp, Gruyter & Verkley, *var. nov.* MycoBank MB515625.


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

**Fig. 8.** Boeremia gen. nov. A. Ostiole configuration of *B. exigua* var. *exigua* (CBS 431.74). B. Pycnidial wall and conidigenous cells of *B. telephii* (CBS 760.73). C. Aseptate and septate conidia of *B. lycoopersici* (CBS 378.67). Scale bars: A = 20 μm; B = C = 10 μm.
**Culture characteristics:** Colonies on OA 75–80 mm diam after 7 d, margin regular or irregular. Immersed mycelium sparsely visible due to coverage by the aerial mycelium, hyaline or black to greenish olivaceous, with many pycnidia; reverse mouse-grey to olivaceous. Colonies on MEA 70–75 mm diam after 7 d, margin regular or irregular. Immersed mycelium completely covered by a compact aerial mat, which is smoke-grey with some mouse-grey zones; reverse black. Colonies on CHA at least (75–)80 mm diam after 7 d, but often the agar surface is completely covered, margin regular or somewhat crenate. Immersed mycelium completely covered by a compact smoke-grey mat of aerial mycelium, or, in some zones floccose, olivaceous with white tufts; reverse shows a dendritic leaden-black zone around the colony centre, with black zones near the colony border. Application of NaOH did not have any effect.

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


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

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


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


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

**Notes:** Although in the present study this variety clusters outside the *B. exigua* cluster, it is phylogenetic affiliation is ambiguous. In previous studies in which fingerprint markers and actin sequences were applied to delineate this species complex (Abeln et al.)
2002, Aveskamp et al. 2009b) the present taxon clusters within Ph. exigua, and is therefore recombined as B. exigua var. lilacis. Further analysis of this complex is, however, advocated.

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


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


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

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

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

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


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

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


*≡* *Phoma exigua* var. *viburni* (Roum. ex. Sacc.) Boerema apud De Gruyter & P. Scheer, J. Phytopathol. 146: 414. 1998.
Boeremia foveata (Foister) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515653.


Boeremia hedericola (Durieu & Mont.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515634.


Note: Strain CBS 367.91 is sterile.

Boeremia lycopersici (Cooke) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515635.


Boeremia noackiana (Allesch.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515636.


≡ Phoma exigua var. noackiana (Allesch.) Aa, Boerema & Gruyter, Persoonia 34: 170. 2000.

For a complete description see Van der Aa et al. (2000).


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

Boeremia sambuci-nigrae (Sacc.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515637.


Boeremia strasseri (Moesz) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515638.


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

Boeremia telephi (Vestergr.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515639.


Group O:

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

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


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


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

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

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


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


Etymology: The epithet refers to the host plant, Verbascum spp.
For a full description see De Gruyter et al. (1993).
Group R:

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

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


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


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

Conidia ellipsoidal, ovoidoida or leuconoida allantoida, glabra, hyalina, continua, (3)–3.5–4.5(–5) × 1.8–2.5(–3) μm, (0–)1–3(–4) guttulas minutis praedita. Matrix conidiorum alba.

Etymology: epithet derived from the small-sized conidia.

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

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


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


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


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

Group S – Stagonosporopsis:

This large group (BPP = 1.00, RBS = 55 %) comprises mainly species with Stagonosporopsis synanamorphs. In the Boeremaean classification system, these species were embedded in the Phoma section Heterospora (Boerema et al. 1997). As with the other sections, this group also appeared to be artificial. Based on LSU and SSU sequences, the type species of the section Heterospora, Ph. heteromorphospora, clusters outside the Didymellaceae (De Gruyter et al. 2009), as do Ph. samarorum and Ph. dimorphospora.
Three species, *Ph. clematidina*, *Ph. glaucii* and *Ph. aquilegiicola* form a separate clade (Group C) within the *Didymellaceae*, and are treated above. Also *Ph. nigripycnidia* and *Ph. narcissi* are not accommodated here.

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

In addition, three other subclades can be recognised in this clade. One (S3) comprises the species *Ph. schneiderae* and *Ph. subboltshauserii* (both of the section *Heterospora*) as well as *Ph. astragali*. This species is known as a pathogen of *Astragalus* spp., and is characterised by a high percentage of “distorted” conidia, but thus far, no records have been made of a *Stagonosporopsis*-like synanamorph. Whereas records of *Ph. astragali* and *Ph. schneiderae* are mainly limited to the American continent, *Ph.
subbolthshauseri appears to occur worldwide on Fabaceae. However, Boerema et al. (2004) suggested that the original host of this species may have been Phaseolus, which is native to the Americas.

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

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

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

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

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


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

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


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


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

Basionym: Phoma artemisiicola Hollós, Mat. Természettud. Közlem. 35: 40. 1926. (as ”artemisiaecola”)

Stagonosporopsis australi (Cooke & Harkn.,) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515657.


Specimen examined: Unknown origin, from Astragalus sp., 1925, A.W. Archer, CBS
78.25 = MUC 9915.

Stagonosporopsis caricae (Sydow & P. Sydow) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515658.


For description of the teleomorph see Sivanesan (1990). Punithalingam (1979b) provides an extensive description, *Ph. caricae* is a synonym of the anamorph.


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

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


Stagonosporopsis cucurbitacearum (Fr.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515660.


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


Stagonosporopsis dorenboschii (Noordel. & Gruyter) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515661.


Stagonosporopsis heliopsidis (H.C. Greene) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515662.


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


Specimens examined: The Netherlands, from an unknown substrate, Mar. 1942, N. Hubbelling, CBS 104.42; from Phaseolus vulgaris, 1979, G.H. Boerema, CBS 572.85 = PD 70/269.

Stagonosporopsis ligulicola var. inoxydabilis (Boerema) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515664.


P H O M A  A N D  R E L A T E D  P L E O S P O R A L E A N  G E N E R A
Specimens examined: Germany, Berlin, from Chrysanthemum indicum, 1963, R. Schneider, CBS H-11952, culture CBS 562.81 = PDCC 6884; Auckland, from the stem of Lotus tenuis, 1979, P.R. Johnston, CBS 628.97 = PD 79/72.

Stagonosporopsis loticola (Died.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515665.
Specimens examined: New Zealand, Auckland, Mt. Albert, from Lotus pedunculatus, 1981, P.R. Johnston, isotype CBS H-7612, ex-isotype culture CBS 562.81 = PDCC 6884; Auckland, from the stem of Lotus tenuis, 1979, P.R. Johnston, CBS 628.97 = PD 79/72.

Specimens examined: Peru, Puno, from Lupinus mutabilis, 1980, CBS H-9061, culture CBS 375.84 = PD 75/303; from Lupinus albus, Apr. 1998, P. van de Graaf, holotype L 996.039.105, ex-holotype culture CBS 101494 = PD 95/5247.

Stagonosporopsis oculo-hominis (Punith.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515666.

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

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

Stagonosporopsis rudbeckiae (Fairm.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515667.
Specimen examined: The Netherlands, from Rudbeckia bicolor, 1979, CBS 109180 = PD 79/175.

Stagonosporopsis trachelli (Allesch.) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515668.
Basionym: Phoma trachelli Allesch., Fungi exs. 4: 360. 1897.

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

Stagonosporopsis valerianellae (Gindrat, Semecnik & Bolay) Aveskamp, Gruyter & Verkley, comb. nov. MycoBank MB515669.

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


Basionym: Mycosphaerella rabiei Kovatsch., The blight of chick pea: 70. 1936.
**Notes:** The placement of this teleomorph in either the *Didymella* or *Mycosphaerella* has been debated regularly in the past (Müller and Arx 1962, Von Arx 1987, Trapero-Casas & Kaiser 1992, Wilson & Kaiser 1995, De Gruyter 2002, Barve et al. 2003). The most recent emendment was by De Gruyter (2002) who judged in favour of *Mycosphaerella rabiei* Kovatsch. ex Gruyter. However, as the genus *Mycosphaerella* is phylogenetically not linked with the Pleosporales (Schoch et al. 2006, 2009b, Crous et al. 2009c), the placement in *Didymella* appears to be more correct.


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


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

Pycnidia solitaria, subglobosa, elongata vel obpyriformia, glabra, epapillata, brunnea, superficialia vel in agar immersa, (140–)170–250(–295) μm. Pycnidia proved to be sterile. In older cultures pycnidial primordia are formed, which are surrounded by clusters of needle-shaped crystals.

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

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

**Culture characteristics:** Colonies on OA, 45–65 mm diam after 7 d, margin regular. Immersed mycelium hyaline, largely covered by mat of felty to compact whitish grey to lavender grey aerial mycelium; reverse iron-grey, but vinaceous-black where the aerial mycelium is present. Colonies on MEA 40–50 mm diam after 7 d,
margin regular. Immersed mycelium mainly hyaline, incidentally black when clustering into thicker hyphal strands. Aerial mycelium sparse, flat, olivaceous green to white near the colonies margin; reverse greenish olivaceous to olivaceous black. Colonies on CHA 70–85 mm diam after 7 d, or even covering the total agar surface, margin regular. Immersed mycelium as on MEA. Aerial mycelium occurring around the colony centre, white, compact to floccose; reverse leaden black. Application of NaOH did not have any effect.


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


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


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

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

Conidia dimora, intradisc pencidium formata. Conidia typus 1 ellipsoidae vel ovoidae, interdum leniter allantoidae, glabra, hyalina, continua, 4.5–9(–9) × (2–)2.5–3.5 μm, (2–)3–6(–8) guttulose. Conidia typus 2 cylindrica vel ellipsoidae, glabra, hyalina, saepe uniseptata, (9–)9.5–13.5(–14.5) × (2.5–)3.5–4.5 μm, interdum septata el guttulose (2–)3–4(–5) in quoque cellula. Matrix conidiorum salmonea.

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

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

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

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

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


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


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

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

**Etymology:** Refers to the elongated necks of the ostioles.

Conidiomata pycnidial, initially solitary, globose, glabrous, slightly papillate and olivaceous buff, produced on the agar surface, measuring (45–)50–115(–130) μm diam. Later developing to black.
broadly globose to irregular conidiomata with many white hyphal outgrows and with a clear elongated neck around the ostioles, giving it a irregular shape, measuring (170–)200–270(–285) × (115–)125–205(–220) μm. Ostioles 1–3(–4), on a long elongated neck (up to 200 μm long). Often these pycnidia merge to an irregular mass of confluent conidiomata. Pycnidial wall pseudoparenchymatous, composed of isodiametric cells, 5–7 layers, 17–22 μm thick. Conidiogenous cells phialidic, hyaline, simple, smooth, flask-shaped, ca. 4–5 × 3–5 μm. Conidia broadly ellipsoidal to ovoid, thin-walled, smooth, hyaline, aseptate 6–8.5(–10) × (3.5–)4–5(–5.5) μm, with (2–)3–9(–12) polar guttules. Conidial matrix crème-white.

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

Specimens examined: Spain, Canary Isles, from Opuntia sp., 1980, J. de Gruyter, holotype designated here CBS H-20238, ex-holotype culture CBS 124514 = PD 801189; Canary Isles, Gran Canaria, from Opuntia sp., June 1982, H.A. van der Aa, CBS 347.82.

Fig. 15. Phoma longicolla (CBS 124514). A–C. Fourteen-day-old colonies on OA (A), MEA (B) and CHA (C). D–F. Pycnidia. G. Section of the pycnidial wall. H. Conidia. Scale bars: E–G = 100 μm; H = 50 μm; I–J = 10 μm.
Notes: This species was isolated twice from Opuntia on the Canary Isles. Around the time of the second isolation (CBS 347.82), also Ph. dimorpha sp. nov. was isolated from the same location and host substrate. This species is described above. A third species that is found in association with Opuntia is Ph. opuntiae, which is, however, rather distinct in morphology and phylogeny.


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


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

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


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


**DISCUSSION**

**What is Phoma?**

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

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

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

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

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

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

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

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

Taxonomic revisions

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

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

Teleomorph relations

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

The finding of multiple teleomorphs with phenotypically indistinguishable associated anamorphs is not uncommon in mycology, yet unwanted, and should be resolved in due course as more data become available. For example, such a situation also applies to major genera such as Aspergillus (Pitt & Samson 2007), Botryosphaeria (Crous et al. 2006), Geotrichum (De Hoog & Smith 2004), Mucosphaerella (Crous et al. 2009a, b) and Penicillium (Pitt 1979).
Boerema et al. (2004) linked Phoma to four teleomorph genera: Didymella, Leptosphaeria, Mycosphaerella and Pleospora. In recent studies it was shown that the association of Phoma with Mycosphaerella was untenable, because the involved telemorphs were apparently morphologically similar but in fact Didymella. The genus Mycosphaerella is phylogenetically distinct and not even associated with the Pleosporales (Schoch et al. 2006, 2009a, b, Crous et al. 2009a, b), whereas their associated Phoma anamorphs proved to be genetically similar to Didymella (De Gruyter et al. 2009). As a consequence, the pawpaw (Carica papaya) pathogen *M. caricae* has been recombined into *D. caricae* in the present study.

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

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

**Can the sections be maintained?**

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

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

**Section Heterospora**

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

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

**Section Macrospora**

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

**Section Paraphoma**

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

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

A third *Paraphoma* species, *Ph. tericola*, is recovered in clade 5 of Fig. 1, which resembles the Cucurbitaceae. This family
also hosts the setae-lacking species *Ph. pratorum*, which was classified in section *Phoma*. Several other koelomycte fungi are accommodated here as well, including *Phialophorophoma litoralis*, *Pleurophoma cava*, a sterile strain that once has been identified as *Coniothyrium* sp. and various *Pyrenochaeta* species. The close morphological relation between the genera *Pyrenochaeta*, *Pleurophoma* and *Phoma* section *Paraphoma* was already noted by Boerema et al. (1996) and Grondona et al. (1997). Like *Phialophorophoma litoralis* and *Pleurophoma cava*, *Pyrenochaeta* is characterised by the formation of elongated, filiform, multiseptate conidiophores, a character that is however not found in the various *Phoma* species embedded in this clade (De Gruyter et al. 2009). A further delineation of the species associated with the genera *Pyrenochaeta* and *Pleurophoma* and the *Phoma* section *Paraphoma* will be provided in a follow-up paper by De Gruyter et al. (2010).

Section *Peyronellae*

The chlamydospore-producing species have been treated before by Aveskamp et al. (2009a), who revealed that also *Phoma* section *Peyronellae* is artificial from an evolutionary point of view. Most species, including the type *Ph. glomerata*, cluster in group K of Fig. 2, along with many other (uni- and multicellular) chlamydospore producing species. To be in accordance with the phylogenetic results, this cluster is elevated to generic level, which is named after the section *Peyronellae*. A second group of species belonging to this section is recovered in clade L, which groups species that generally have swollen cells in older cultures (De Gruyter & Noordeloos 1992), which may be an initial phase of chlamydospore formation.

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

Section *Phyllostictoides*

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

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

Section * Pilosa*

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

Section *Plenodomus*

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

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

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

Section Sclerophomella

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

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

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

DNA Barcoding

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

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

ACKNOWLEDGEMENTS

We thank Mrs Karin Rosendahl-Peters (Plantenziekenkundige Dienst), Dr Amy Rossman (Systematic Botany and Mycology Laboratory), Prof dr dr hc mult. Wolfgang E. Krümbien and Dr Gotbushina (University of Odenburg) for providing cultures. Jeroen Koning (Hubrechts Laboratorium, Utrecht) is thanked for his help in preparing the micromote sections. Dr Cecile Guéidan is kindly thanked for her comments on Phoma paspali. Many thanks also to Mrs Trix Merckx and Mrs Arien van Iperen who helped us with the deposit of strains and herbarium material. Mrs Marjan Vermaas is kindly thanked for her assistance in preparing the photoplates. This research is supported by the Dutch Ministry of Agriculture, Nature and Food Quality through an endowment of the FES programme “Versterking infrastructuur Plantgezondheid”.

REFERENCES

Aa HA van der, Boerema GH, Gruyter J de (2000). Contributions towards a monograph of Phoma (Coelomycetes) – VI-1. Section Phyllostictoides:


INDEX

Arranged according to genus and then epithets. Page numbers of main entries are bolded. A superscript asterisk (*) points to pages with illustrations, a (C) to pages with a cladogram, and a (T) to pages with a table.

Actinonema actaeae, 44
Alternaria, 20
Ampelomyces, 22, 26–27
Ampelomyces artemisiae, 26
Ampelomyces humuli, 26
Ampelomyces quercinus, 22, 26–27
Ampelomyces quisqualis, 6(T), 15(C)
Ampelomyces unciniulae, 26
Aposphaeria, 16
Aposphaeria populina, 6(T), 15(C)–16
Ascochyta, 51–52, 55
Ascochyta bohemica, 46
Ascochyta caricae, 45
Ascochyta caricae-papayae, 45
Ascochyta caulina, 15(C), 17, 22
Ascochyta clematidina, 25
Ascochyta coffeae, 37
Ascochyta fabae, 22
Ascochyta gossypii, 26, 52
Ascochyta hordei, 20, 23
Ascochyta hordei var. hordei, 8(T), 15(C), 18(C), 22
Ascochyta lethalis, 32
Ascochyta liniola, 39
Ascochyta lupini, 46
Ascochyta nepetica, 24
Ascochyta pinodella, 33
Ascochyta pinodes, 22, 30, 33
Ascochyta pisii, 5, 22, 52
Ascochyta rabiei, 52, 55
Ascochyta sp., 6(T), 15(C), 33
Ascochyta tarda, 37
Ascochyta telephii, 40
Ascochyta viburni, 39
Aspergillus, 3, 52
Asteromella, 2
Asteromella tiliae, 6(T), 15(C)–16
Atrahidymella, 3, 4
Belizea, 3
Boeremia, 36–37(*), 52
Boeremia cinicina, 8(T), 20(C), 37
Boeremia diversispora, 8(T), 20(C), 37, 40
Boeremia exigua var. coffeae, 8(T), 20(C), 37
Boeremia exigua var. exigua, 6(T), 8(T), 15(C), 20(C), 37(*)–39
Boeremia exigua var. forsythiae, 8(T), 20(C), 37
Boeremia exigua var. gilvescens, 37–38(*)–39, 48
Boeremia exigua var. heteromorpha, 20(C), 38
Boeremia exigua var. liliaca, 20(C), 38–39
Boeremia exigua var. liniola, 8(T), 20(C), 38–39
Boeremia exigua var. populii, 8(T), 20(C), 39
Boeremia exigua var. pseudollasialis, 8(T), 20(C), 39(*)
Boeremia exigua var. viburnii, 8(T), 20(C), 39
Boeremia foveata, 6(T), 8(T), 15(C), 20(C), 23, 40
Boeremia hedericola, 8(T), 20(C), 40
Boeremia lycopersici, 8(T), 20(C), 37(*), 40
Boeremia noackiana, 8(T), 20(C), 37(*), 40
Boeremia sambuci-nigrae, 8(T), 20(C), 40
Boeremia strasserii, 8(T), 20(C), 40
Boeremia telephii, 8(T), 20(C), 37(*), 40
Botryosphaeria, 52
Chaetosphaeris, 3, 22, 52
Chaetosphaeris erythropthodes, 6(T), 8(T), 15(C), 21(C)–22, 41, 52
Chaetosphaeris hirsutulum, 6(T), 15(C), 17
Cicinobolus, 27
Cicinobolus quercinos, 26
Coniothyrium, 2–5, 16–17, 22, 25
Coniothyrium cerealis, 16
Coniothyrium clematidis-rectae, 25
Coniothyrium concentricum, 6(T), 15(C)
Coniothyrium fuckelii, 6(T), 15(C)–16
Coniothyrium glomeratum, 32
Coniothyrium minutans, 16
Coniothyrium palmarum, 6(T), 15(C), 17
Coniothyrium sp., 6(T), 15(C)–16, 54
Cucurbitaria, 3, 26, 53
Dendryphion, 20
Depazea cannabis, 24
Didymella, 3, 4(T), 22, 25–26, 28, 44–45, 47, 52
Didymella adianticola, 8(T), 18(C), 47
Didymella affectorlophi, 30, 31
Didymella anthophilli, 30–31
Didymella applanata, 8(T), 18(C), 24
Didymella arachidicola, 30, 31
Didymella Bryoniae, 22, 44, 45
Didymella canabris, 8(T), 18(C), 24
Didymella caricae, 8(T), 18(C), 24, 53
Didymella catariae, 24
Didymella exigua, 6(T), 8(T), 15(C), 19(C), 22, 28, 45
Didymella fabae, 6(T), 8(T), 9(T), 15(C), 18(C), 22
Didymella lethalis, 30, 32
Didymella liliocola var. inoxydabilis, 44, 46
Didymella liliocola var. liliocola, 44
Didymella lycopersici, 36, 40
Didymella macropodi, 9(T), 21(C), 46
Didymella pinodes, 22, 30, 33
Didymella pisii, 9(T), 18(C)
Didymella rabiei, 6(T), 9(T), 15(C), 18(C), 46
Didymella urticicola, 9(T), 18(C), 24
Didymella vitalinina, 9(T), 20(C)
Didymella winteriana, 41
Didymella zeae-maydis, 33
Didymosphaeria applanata, 24
Diplodina, 22
Diplodina coloradensis, 9(T), 18(C), 24
Dothiorea, 22
“Dothiorea ulmi”, 9(T), 20(C), 36
Epicoecicum, 22, 30, 33, 35(*), 52
Epicoecicum nigrum, 6(T), 9(T), 15(C), 20(C), 22, 35, 48, 54
Epicoecicum pimpinellinum, 9(T), 20(C), 35(*)
Epicoecicum sorghi, 9(T), 20(C), 35(*)–36, 41
Fenestella, 3
Geotrichum, 52
Hendersonia curtisi, 32
Hendersonia hortensis, 45
Hypocrea, 3
Leptosphaeria, 3, 4(T), 17, 53–55
Leptosphaeria biglobosa, 6(T), 15(C), 17, 55
Leptosphaeria coniothyrium, 16
Leptosphaeria haematis, 54
Leptosphaeria libanotis, 54
Leptosphaeria maculans, 6(T), 15(C), 17, 55
Leptosphaeria purpurea, 54
Leptosphaeria sacchari, 54
Leptosphaeria weimeri, 54
Leptosphaeruina, 3, 4, 22, 25, 53
Leptosphaeruina americana, 9(T), 18(C), 22, 26
Leptosphaeruina arachidicola, 9(T), 18(C), 26
Leptosphaeruina argentinensis, 22
Leptosphaeruina australensis, 22
Leptosphaeruina australis, 6(T), 9(T), 15(C), 18(C), 26
Leptosphaeruina chartarum, 22
Leptosphaeruina crassiasca, 22
Leptosphaeruina trifoli, 9(T), 18(C), 22, 26
Macroventuria, 3, 4, 22, 53
Macroventuria anamochaeta, 26
Macroventuria anomochaeta, 6(T), 9(T), 15(C), 18(C), 22, 26
Macroventuria wentii, 9(T), 18(C), 26
Microphaeropsis, 2, 3, 4, 17, 22, 52
Microphaeropsis olivacea, 6(T), 9(T), 15(C), 18(C), 22, 51–52
Mycosphaerella, 3, 4(T), 26, 44, 47, 52–53
Mycosphaerella arachidicola, 31
Mycosphaerella caricae, 44–45, 53
Mycosphaerella lethals, 32
Mycosphaerella ligulicola, 45
Mycosphaerella pinodes, 33
Mycosphaerella rabiei, 3, 46–47
Mycosphaerella zeae-maydis, 3, 33
Neottiosporina paspali, 6(T), 15(C)–16
Paraconiothyrium, 2, 3, 16
Paraconiothyrium minitans, 6(T), 15(C)–16
Penicillium, 52, 55
Peyronellaea, 30–31, 52–54
Peyronellaea alectorolophi, 9(T), 19(C), 31
Peyronellaea americana, 9(T), 19(C), 31
Peyronellaea anserina, 9(T), 19(C), 31
Peyronellaea arachidicola, 9(T), 19(C), 31
Peyronellaea australis, 9(T), 19(C), 31
Peyronellaea australis, 9(T), 19(C), 31–32
Peyronellaea calorpreferens, 9(T), 19(C), 31–32
Peyronellaea cinerata, 33
Peyronellaea coffeee-arabicae, 9(T), 10(T), 19(C), 32
Peyronellaea curtissii, 10(T), 19(C), 32
Peyronellaea eucalyptica, 10(T), 19(C), 32
Peyronellaea gardeniae, 6(T), 10(T), 15(C), 19(C), 32, 41
Peyronellaea glomerata, 6(T), 10(T), 15(C), 19(C), 31, 32, 41
Peyronellaea lethals, 10(T), 19(C), 32
Peyronellaea musae, 10(T), 19(C), 32
Peyronellaea nigricans, 33
Peyronellaea obtusa, 10(T), 19(C), 33
Peyronellaea pinodella, 6(T), 10(T), 15(C), 19(C), 33
Peyronellaea pinodes, 6(T), 10(T), 15(C), 19(C), 33
Peyronellaea pomorum var. ciricinata, 10(T), 19(C), 31, 33
Peyronellaea pomorum var. cyanea, 10(T), 19(C), 33
Peyronellaea pomorum var. pomorum, 10(T), 19(C), 33
Peyronellaea protuberans, 10(T), 19(C), 33
Peyronellaea sancta, 10(T), 19(C), 33
Peyronellaea subglomerata, 10(T), 19(C), 33
Peyronellaea zeae-maydis, 6(T), 10(T), 15(C), 19(C), 33, 53
Phaeosphaeria, 17
Phaeosphaeria oryzae, 6(T), 15(C)
Phialophora, 4(T)
Phialophorophoma litoralis, 6(T), 15(C)–16, 54
Phoma, 2–4, 16–17, 22, 26–30, 41, 51–53, 55
Phoma acetosellae, 10(T), 19(C), 28
Phoma actaeae, 44
Phoma adianticola, 47
Phoma ajacis, 44
Phoma alectorolophi, 30, 31
Phoma aliens, 10(T), 19(C), 47
Phoma americana, 31
Phoma andigena, 43–44
Phoma andina var. crystalliniformis, 43, 45
Phoma anigozanthi, 10(T), 18(C), 26
Phoma anserina, 30, 31, 54
Phoma apicola, 6(T), 15(C), 17, 54
Phoma aquilegiicola, 10(T), 18(C), 25–26, 43, 53
Phoma arachidicola, 30–31
Phoma arachidis-hypogaeae, 10(T), 18(C), 26
Phoma argillacea, 24
Phoma artemisicola, 43–44
Phoma astragali, 43, 45
Phoma aubrietiae, 10(T), 18(C), 47
Phoma aurea, 30–31, 54
Phoma bellidis, 10(T), 19(C), 27–28
Phoma betae, 17, 20, 54
Phoma boeremae, 11(T), 19(C), 29
Phoma brasiliensis, 11(T), 20(C), 33–34(*)
Phoma bulgarica, 11(T), 18(C), 47(*)
Phoma calidophila, 11(T), 19(C), 42, 48
Phoma calorpreferens, 23, 30–32, 42
Phoma cannabiss, 24
Phoma capitulum, 6(T), 15(C)–16, 54
Phoma caricae, 45
Phoma caricae-papayae, 43–45
Phoma chrysanthemicola, 11(T), 19(C), 48
Phoma chrysanthenicola, 6(T), 15(C), 16–17, 30, 53–54
Phoma clematidina, 11(T), 18(C), 25, 43, 52–53
Phoma clematidis-rectae, 11(T), 18(C), 25, 51, 53
Phoma coffeae, 37
Phoma coffeae-arabicae, 32, 37
Phoma coiffeioca, 37
Phoma coiffeiphila, 37
Phoma commelinicola, 11(T), 21(C), 41
Phoma complanata, 6(T), 11(T), 15(C), 18(C), 48, 55
Phoma costarricensis, 11(T), 21(C), 37, 42
Phoma crinicola, 36, 37, 54
Phoma crystallifera, 11(T), 20(C), 48
Phoma crystalliniformis, 43, 45
Phoma cucurbitacearum, 22, 43–45, 54
Phoma cyanea, 33
Phoma dactylidis, 11(T), 19(C), 48–49(*)
Phoma dennisiis, 45–46
Phoma dennisiis var. oculo-hominis, 46
Phoma deserticola, 16
Phoma destructiva var. destructiva, 11(T), 21(C), 48, 53
Phoma destructiva var. diversispora, 11(T), 21(C), 48, 53
Phoma dictamnicola, 11(T), 21(C), 41
Phoma digitalis, 11(T), 19(C), 27–28
Phoma exigua var. Phoma loticola, Phoma labilis, Phoma insulana, Phoma heteromorpha, Phoma heteroderae, Phoma herbicola, Phoma herbarum f. lilacis, Phoma foveata, Phoma fimeti, Phoma exigua var. heteromorpha, Phoma exigua var. inoxydabilis, Phoma exigua var. lilacis, Phoma exigua var. noackiana, Phoma exigua var. populi, Phoma exigua var. sambuci-nigrae, Phoma exigua var. viburni, Phoma fallens, 6(T), 15(C), 17, 54, Phoma fimeti, 6(T), 15(C)–17, 54, Phoma flavescens, 6(T), 15(C), 17, 54, Phoma flavigena, 7(T), 15(C), 17, 54, Phoma foveata, 36, 40, Phoma fumosa, 52, Phoma fungicola, 6(T), 11(T), 15(C), 18(C), Phoma gardeniae, 22, 30, 53, Phoma glaucii, 11(T), 18(C), 25, 43, 53, Phoma glaucispora, 7(T), 15(C), 17, 20, 54, Phoma glomerata, 26, 30, 52, Phoma gossypicola, 11(T), 18(C), 26–27, 52, Phoma haematocylla, 7(T), 15(C), 17, 54, Phoma hedericola, 36, 40, 54, Phoma helenium, 43, 45, Phoma henningsii, 11(T), 20(C), 33, 49, Phoma herbarum, 3, 11(T), 15(C), 18(C), 20, 23, 27, 41, 49, 52, Phoma herbarum f. lilacis, 38, Phoma herbarum f. sambuci-nigrae, 40, Phoma herbicola, 11(T), 18(C), 49, Phoma heteroderae, 23, 30–32, Phoma heteromorpha, 38, Phoma heteromorphospora, 7(T), 15(C), 17, 22, 42, 53, Phoma huanacayensis, 11(T), 20(C), 49, Phoma humicola, 11(T), 18(C), 23, Phoma incompta, 7(T), 15(C), 17, Phoma infossa, 26, Phoma infossa, 11(T), 18(C), 27, 30, Phoma insulana, 11(T), 21(C), 40, Phoma jolyana, 32, Phoma jolyana var. circinata, 33, Phoma labilis, 12(T), 21(C), 42, Phoma liglicola, 54, Phoma liglicola var. inoxydabilis, 43–44, 46, Phoma liglicola var. liglicola, 43–45, Phoma lingam, 17, Phoma lini, 7(T), 15(C)–16, 54, Phoma longicolla, 12(T), 19(C), 30, 49–50(*), Phoma loticola, 44, 46, Phoma lycopersici, 36, 40, Phoma macrostoma var. incolorata, 12(T), 19(C), 28, Phoma macrostoma var. macrostoma, 7(T), 12(T), 15(C), 19(C), 28, Phoma matteuciiocola, 12(T), 18(C), 23, Phoma medicaginis, 30, Phoma medicaginis var. macrospora, 12(T), 18(C), 51, Phoma medicaginis var. medicaginis, 7(T), 12(T), 15(C), 18(C), 51, Phoma medicaginis var. pinodella, 30, 33, Phoma menthae, 40, Phoma microchlamydospora, 12(T), 19(C), 30, 51, Phoma minor, 12(T), 21(C), 42–43(*), Phoma minutispora, 7(T), 15(C)–16, 54, Phoma multipora, 7(T), 15(C), 17, 54, Phoma multirostrata, 12(T), 21(C), 40, 42, Phoma narcissi, 30, 32, 43–44, Phoma nebulosa, 12(T), 18(C), 51, Phoma neugniana, 12(T), 19(C), 51, Phoma nepetica, 24, Phoma nigricans, 30, 31, 54, Phoma nigrificans, 46, Phoma nigritypnia, 12(T), 18(C), 43, 51, Phoma novae-verbasicola, 12(T), 21(C), 41, Phoma obtusa, 30, 31, 33, Phoma oculi-hominis, 46, Phoma omnivirens, 12(T), 18(C), 30, 51, Phoma opuntiae, 7(T), 15(C), 17, 30, 51, 54, Phoma paspali, 7(T), 12(T), 15(C), 18(C), 20, 23, 48, Phoma pedeae, 12(T), 19(C), 27–28(*), Phoma pereupycyna, 12(T), 21(C), 37, 40–41, Phoma pimprina, 35, 54, Phoma pinodella, 30, 33, Phoma piperas, 12(T), 21(C), 42, Phoma plurivora, 12(T), 20(C), 33, 35, Phoma polemonii, 12(T), 18(C), 24–25, Phoma pomorum, 2, 23, Phoma pomorum var. calorpreferens, 31, Phoma pomorum var. cinnabara, 33, Phoma pomorum var. cyanae, 33, Phoma pomorum var. pomorum, 33, Phoma poolensis, 12(T), 21(C), 41, Phoma poolensis var. verbasica, 41, Phoma pratrorum, 7(T), 15(C), 16, 48, 54, Phoma protuberans, 30–31, 33, Phoma putaminum, 12(T), 18(C), 51, Phoma quercina, 26–27, Phoma rabiei, 3, 16, 42, 55, Phoma radicina, 7(T), 15(C)–16, 53, Phoma rhei, 12(T), 19(C), 48, 51, Phoma rubbeckiae, 43, 46, Phoma samarorum, 7(T), 15(C), 16–17, 22, 42, 44, 45, Phoma sambuci-nigrae, 36, 40, Phoma sancta, 33, Phoma saxe, 12(T), 13(T), 18(C), 23–24(*), Phoma schachtii, 17, 30, Phoma schneiderae, 43, 46, Phoma section Heterospora, 2–4(T)–5, 17, 22, 25, 31, 42–43, 53, Phoma section Macrospora, 2–4(T), 22, 41, 53, Phoma section Paraphoma, 2–4(T)–5, 16, 22, 51, 53–54, Phoma section Peyronella, 2, 4(T), 6, 17, 22, 30, 35, 42, 53–54, Phoma section Phoma, 2–4(T)–5, 16, 20, 22, 36, 41–42, 44, 53–54, Phoma section Phyllostictoides, 2, 4(T), 22, 28, 31, 36, 42–43,
Phomopsis, 2–4(T), 17, 51–52, 54
Phomopsis section Pilosa, 2–4(T), 17, 52–52, 54–55
Phomopsis section Sclerophomella, 2–4(T)–5, 17, 22, 31, 41, 55
Phoma selaginellicola, 13(T), 18(C), 51
Phoma senecionis, 13(T), 19(C), 27–28
Phoma sojicola, 33
Phoma subboltshauserii, 43–45
Phoma subgleromata, 33
Phoma subhberbarum, 13(T), 19(C), 27
Phoma sylvatica, 13(T), 21(C), 41
Phoma tarda, 36–37
Phoma telephii, 36, 40
Phoma terricola, 7(T), 15(C)–16, 53
Phoma tropica, 13(T), 21(C), 42
Phomopsis, 2
Phomopsis quercina, 26
Phlylosticta, 2, 27
Phlylosticta acetiellae, 28
Phlylosticta adianticola, 47
Phlylosticta ajacis, 44
Phlylosticta arachidis-hypogaeae, 26
Phlylosticta argillacea, 24
Phlylosticta commelinicola, 41
Phlylosticta crinicola, 37
Phlylosticta crinica, 37
Phlylosticta cronicola, 37
Phlylosticta dorenboschii, 40
Phlylosticta heliopsidis, 45
Phlylosticta insulana, 40
Phlylosticta maydis, 33
Phlylosticta narcissi, 32
Phlylosticta noackiana, 40
Phlylosticta piperis, 42
Phlylosticta sorghina, 36
Phlylosticta verbasciella, 41
Phlylosticta verbascicola, 41
Plectophomella, 36
Plenodomus, 51
Plenodomus morganjonesii, 51
Plenospora, 3–4(T), 17, 20, 26, 41, 53–54
Plenospora americana, 26
Plenospora betae, 7(T), 15(C), 17
Plenospora herbarum, 7(T), 15(C), 17, 54
Plenophoma, 2, 16, 54
Plenophoma cava, 7(T), 15(C)–16, 54
Polyopeus purpureus var. incolorata, 28
Preussia, 3, 16
Pseudobillardia phragmitis, 7(T), 15(C)–16
Pyrenochaeta, 2, 16, 54
Pyrenochaeta acicola, 7(T), 15(C)–16
Pyrenochaeta gardeniae, 32
Pyrenochaeta lycopersici, 7(T), 15(C)
Pyrenochaeta nobilis, 7(T), 15(C)
Pyrenochaeta romeri, 7(T), 15(C)–16
Sclerophomella aubrietiae, 47
Sclerotium, 4
Sphaerella, 26
Sphaerella cannabis, 24
Sphaerella millepunctata, 26
Sphaeria aliena, 47
Sphaeria bryoniae, 45
Sphaeria catariae, 24
Sphaeria complanata, 48
Sphaeria cucurbitaceaeum, 45
Sphaeria nebulosa, 51
Sphaeria pinodes, 33
Sphaeronaema multistatatum, 41
Sphaeronaema insignis, 46
Sphaerulina trifolii, 26
Sporormiella minima, 7(T), 15(C)–16
Stagonospora, 2
Stagonospora neglecta var. colorata, 7(T), 15(C)
Stagonosporopsis, 4(T), 25, 42–44(*)52–55
Stagonosporopsis actaeae, 13(T), 21(C), 44(*)
Stagonosporopsis ajacis, 13(T), 21(C), 44
Stagonosporopsis andigena, 7(T), 13(T), 15(C), 21(C), 44
Stagonosporopsis artemisicola, 13(T), 21(C), 44
Stagonosporopsis astragalii, 13(T), 21(C), 45
Stagonosporopsis bohemica, 46
Stagonosporopsis caricaceae, 13(T), 21(C), 45
Stagonosporopsis crysalliniformis, 13(T), 21(C), 45
Stagonosporopsis cucurbitaceaeum, 7(T), 13(T), 15(C), 21(C), 44(*)–45
Stagonosporopsis curtisi, 32, 44
Stagonosporopsis dennisi, 7(T), 13(T), 15(C), 21(C), 45–46
Stagonosporopsis dorenboschii, 13(T), 21(C), 45
Stagonosporopsis fraxini, 44
Stagonosporopsis heliopsidis, 13(T), 21(C), 45
Stagonosporopsis hortensis, 13(T), 21(C), 45
Stagonosporopsis hugbollicola var. inoxydabilis, 13(T), 21(C), 45
Stagonosporopsis hugbollicola var. hugbollicola, 13(T), 21(C), 46
Stagonosporopsis loticola, 13(T), 21(C), 46
Stagonosporopsis lupini, 13(T), 14(T), 21(C), 44(*)–46
Stagonosporopsis oculo-hominis, 14(T), 21(C), 46
Stagonosporopsis ruderbeckiae, 14(T), 21(C), 46
Stagonosporopsis trachelii, 14(T), 21(C), 46
Stagnothrypella, 3
Stenocarpella macrosperma, 7(T), 15(C)–17
Trichoderma, 3
Trichophyton, 3
Venturia, 53
Westerdykella, 3
Westerdykella dispersa, 16
Zythia rabei, 46