

Resolving the Phoma enigma

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Abstract: The *Didymellaceae* was established in 2009 to accommodate *Ascochyta*, *Didymella* and *Phoma*, as well as several related phoma-like genera. The family contains numerous plant pathogenic, saprobic and endophytic species associated with a wide range of hosts. *Ascochyta* and *Phoma* are morphologically difficult to distinguish, and species from both genera have in the past been linked to *Didymella* sexual morphs. The aim of the present study was to clarify the generic delimitation in *Didymellaceae* by combing multi-locus phylogenetic analyses based on ITS, LSU, *rpb2* and *tub2*, and morphological observations. The resulting phylogenetic tree revealed 17 well-supported monophyletic clades in *Didymellaceae*, leading to the introduction of nine genera, three species, two *nomina nova* and 84 combinations. Furthermore, 11 epitypes and seven neotypes were designated to help stabilise the taxonomy and use of names. As a result of these data, *Ascochyta*, *Didymella* and *Phoma* were delineated as three distinct genera, and the generic circumscriptions of *Ascochyta*, *Didymella*, *Epicoccum* and *Phoma* emended. Furthermore, the genus *Microsphaeropsis*, which is morphologically distinct from the members of *Didymellaceae*, grouped basal to the *Didymellaceae*, for which a new family *Microsphaeropsidaceae* was introduced.

Key words: Ascochyta, Didymella, Multi-locus phylogeny, Phoma, Taxonomy.

Taxonomic novelties: New family: Microsphaeropsidaceae Q. Chen, L. Cai & Crous; New genera: Allophoma Q. Chen & L. Cai, Calophoma Q. Chen & L. Cai, Heterophoma Q. Chen & L. Cai, Neoascochyta Q. Chen & L. Cai, Neodidymelliopsis Q. Chen & L. Cai, Nothophoma Q. Chen & L. Cai, Paraboeremia Q. Chen & L. Cai, Phomatodes Q. Chen & L. Cai, Xenodidymella Q. Chen & L. Cai; New names: Ascochyta medicaginicola var. medicaginicola Q. Chen & L. Cai, Didymella senecionicola Q. Chen & L. Cai; New species: Allophoma nicaraguensis Q. Chen & L. Cai, Phoma neerlandica Q. Chen & L. Cai, Stagonosporopsis helianthi Q. Chen & L. Cai, New combinations: Allophoma labilis (Sacc.) Q. Chen & L. Cai, All. minor (Aveskamp et al.) Q. Chen & L. Cai, All. piperis (Tassi) Q. Chen & L. Cai, All. tropica (R. Schneid. & Boerema) Q. Chen & L. Cai, All. zantedeschiae (Dippen.) Q. Chen & L. Cai, Ascochyta herbicola (Wehm.) Q. Chen & L. Cai, As. medicaginicola var. macrospora (Boerema et al.) Q. Chen & L. Cai, As. nigripycnidia (Boerema et al.) Q. Chen & L. Cai, As. phacae (Corbaz) Q. Chen & L. Cai, As. versabilis (Boerema et al.) Q. Chen & L. Cai, Boeremia lilacis (Sacc.) Q. Chen & L. Cai, Calophoma aquilegiicola (M. Petrov) Q. Chen & L. Cai, Ca. clematidina (Thum.) Q. Chen & L. Cai, Ca. clematidis-rectae (Petr.) Q. Chen & L. Cai, Ca. complanata (Tode) Q. Chen & L. Cai, Ca. glaucii (Brunaud) Q. Chen & L. Cai, Ca. vodakii (E. Müll.) Q. Chen & L. Cai, Didymella acetosellae (A.L. Sm. & Ramsb.) Q. Chen & L. Cai, D. aliena (Fr.) Q. Chen & L. Cai, D. americana (Morgan-Jones & J.F. White) Q. Chen & L. Cai, D. anserina (Marchal) Q. Chen & L. Cai, D. aurea (Gruyter et al.) Q. Chen & L. Cai, D. bellidis (Neerg.) Q. Chen & L. Cai, D. boeremae (Gruyter) Q. Chen & L. Cai, D. calidophila (Aveskamp et al.) Q. Chen & L. Cai, D. chenopodii (P. Karst. & Har.) Q. Chen & L. Cai, D. coffeae-arabicae (Aveskamp et al.) Q. Chen & L. Cai, D. curtisii (Berk.) Q. Chen & L. Cai, D. dactylidis (Aveskamp et al.) Q. Chen & L. Cai, D. dimorpha (Aveskamp et al.) Q. Chen & L. Cai, D. eucalyptica (Sacc.) Q. Chen & L. Cai, D. gardeniae (S. Chandra & Tandon) Q. Chen & L. Cai, D. glomerata (Corda) Q. Chen & L. Cai, D. heteroderae (Boerema et al.) Q. Chen & L. Cai, D. longicolla (Aveskamp et al.) Q. Chen & L. Cai, D. mascrostoma (Mont.) Q. Chen & L. Cai, D. maydis (Arny & R.R. Nelson) Q. Chen & L. Cai, D. microchlamydospora (Aveskamp & Verkley) Q. Chen & L. Cai, D. molleriana (G. Winter) Q. Chen & L. Cai, D. musae (P. Joly) Q. Chen & L. Cai, D. negriana (Thüm.) Q. Chen & L. Cai, D. nigricans (P.R. Johnst. & Boerema) Q. Chen & L. Cai, D. pedeiae (Aveskamp et al.) Q. Chen & L. Cai, D. pinodella (L.K. Jones) Q. Chen & L. Cai, D. pomorum (Thüm.) Q. Chen & L. Cai, D. protuberans (Lév.) Q. Chen & L. Cai, D. rhei (Ellis & Everh.) Q. Chen & L. Cai, D. rumicicola (Boerema & Loer.) Q. Chen & L. Cai, D. sancta (Aveskamp et al.) Q. Chen & L. Cai, D. subglomerata (Boerema et al.) Q. Chen & L. Cai, D. subherbarum (Gruyter et al.) Q. Chen & L. Cai, D. viburnicola (Oudem.) Q. Chen & L. Cai, Epicoccum brasiliense (Aveskamp et al.) Q. Chen & L. Cai, E. draconis (Berk. ex Cooke) Q. Chen & L. Cai, E. henningsii (Sacc.) Q. Chen & L. Cai, E. huancayense (Turkenst.) Q. Chen & L. Cai, E. plurivorum (P.R. Johnst.) Q. Chen & L. Cai, Heterophoma adonidis (Moesz) Q. Chen & L. Cai, H. nobilis (Kabát & Bubák) Q. Chen & L. Cai, H. novae-verbascicola (Aveskamp et al.) Q. Chen & L. Cai, H. poolensis (Taubenh.) Q. Chen & L. Cai, H. sylvatica (Sacc.) Q. Chen & L. Cai, Neoascochyta desmazieri (Cavara) Q. Chen & L. Cai, Neoa. europaea (Punith) Q. Chen & L. Cai, Neoa. exitialis (Morini) Q. Chen & L. Cai, Neoa. graminicola (Punith.) Q. Chen & L. Cai, Neoa. paspali (P.R. Johnst.) Q. Chen & L. Cai, Neodidymelliopsis cannabis (Aa & Boerema) Q. Chen & L. Cai, Neod. polemonii (Cooke) Q. Chen & L. Cai, Neod. xanthina (Sacc.) Q. Chen & L. Cai, Nothophoma anigozanthi (Tassi) Q. Chen & L. Cai, No. arachidis-hypogaeae (V.G. Rao) Q. Chen & L. Cai, No. gossypiicola (Gruyter) Q. Chen & L. Cai, No. infossa (Ellis & Everh.) Q. Chen & L. Cai, No. quercina (Syd.) Q. Chen & L. Cai, Paraboeremia adianticola (Aa & Boerema) Q. Chen & L. Cai, Pa. putaminum (Speg.) Q. Chen & L. Cai, Pa. selaginellae (Sacc.) Q. Chen & L. Cai, Phomatodes aubrietiae (Moesz) Q. Chen & L. Cai, Phomat. nebulosa (Pers.) Q. Chen & L. Cai, Xenodidymella applanata (Niessl) Q. Chen & L. Cai, X. asphodeli (E. Müll.) Q. Chen & L. Cai, X. catariae (Cooke & Ellis) Q. Chen & L. Cai, X. humicola (J.C. Gilman & E.V. Abbott) Q. Chen & L. Cai.

Available online 26 November 2015; http://dx.doi.org/10.1016/j.simyco.2015.10.003. Hard copy: September 2015.

INTRODUCTION

Although the first *Phoma* spp. were already described in 1821 (Sutton 1980), the genus was only officially introduced 60 years

later by Saccardo (1880), the concept of which was emended by Boerema & Bollen (1975). *Phoma* has been shown to be highly polyphyletic with phoma-like species scattered in at least six families within the *Pleosporales* (Aveskamp *et al.* 2010).

Peer review under responsibility of CBS-KNAW Fungal Biodiversity Centre.

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Although Boerema et al. (2004) subdivided the genus Phoma into nine sections (*i.e. Phoma, Heterospora, Paraphoma, Peyronellaea, Phyllostictoides, Sclerophomella, Plenodomus, Macrospora* and *Pilosa*) based on morphological characters (Boerema 1997), these classifications have been shown to be artificial and failed to reflect the natural evolutionary history of this group of fungi (Aveskamp et al. 2008, 2010). Presently the monophyletic lineage anchored by its type species *Phoma herbarum*, is regarded as *Phoma s. str.*, which belongs to the *Didymellaceae* (Aveskamp et al. 2010).

Results of a phylogenetic study including the type species of all nine *Phoma* sections and allied coelomycetous genera demonstrated that all nine sections grouped in the *Pleosporales* (de Gruyter *et al.* 2009). The type species of the sections *Macrospora, Peyronellaea, Phoma, Phyllostictoides* and *Sclerophomella* resided in *Didymellaceae* (de Gruyter *et al.* 2009, 2012). However, the four other sections, namely *Heterospora, Paraphoma, Pilosa* and *Plenodomus* clustered in several distinct clades outside *Didymellaceae*, and were thus excluded from *Phoma* (de Gruyter *et al.* 2009, Aveskamp *et al.* 2010).

Approximately 70 % of the species recognised by Boerema et al. (2004) could be accommodated in Didvmellaceae. The phylogenetic relationships of Phoma species in Didymellaceae, mainly from sections Macrospora, Peyronellaea, Phoma, Phyllostictoides and Sclerophomella were further assessed, resulting in many species being reclassified in existing genera (e.g. Didymella, Stagonosporopsis), or transferred to Boeremia, Epicoccum and Peyronellaea (Aveskamp et al. 2010). These results also revealed most morphological sections to be polyphyletic, the one exception being section Plenodomus (Aveskamp et al. 2010, de Gruyter et al. 2010, 2012). Species originally classified in sections Heterospora, Paraphoma, Pilosa and Plenodomus were subsequently revised by de Gruyter et al. (2010, 2012). Members of Phoma sect. Paraphoma were transferred to a range of genera including Coniothyrium (Coniothyriaceae), Paraphoma, Setophoma (Phaeosphaeriaceae), Pyrenochaeta and Pyrenochaetopsis (Cucurbitariaceae) (de Gruyter et al. 2010, 2012). Furthermore, Phoma sect. Heterospora was elevated to generic rank in Leptosphaeriaceae (de Gruyter et al. 2012). Species of Phoma sect. Plenodomus were reclassified into Chaetosphaeronema (Phaeosphaeriaceae) (de Gruvter et al. 2010). Leptosphaeria. Paraleptosphaeria, Plenodomus and Subplenodomus (Leptosphaeriaceae) (de Gruyter et al. 2012). Finally, species of Phoma sect. Pilosa were determined to belong to Pleosporaceae (Aveskamp et al. 2010, de Gruyter et al. 2012).

The genus Ascochyta was established by Libert in 1830, and typified by As. pisi (Boerema & Bollen 1975). Ascochyta and Phoma have long been considered closely related since members from both genera are often highly similar in morphology, physiology, pathogenicity and nucleotide sequences (Aveskamp et al. 2010). Research efforts attempting to distinguish these genera have been carried out since Saccardoan times, using their substrate and morphological characters, such as presence or absence of conidial septa (Aveskamp et al. 2010). In Phoma, septate conidia are rare in vitro, although common in vivo (Aveskamp et al. 2008), whereas isolates of Ascochyta produce septate conidia both in vivo and in vitro (de Gruyter et al. 2009). Boerema & Bollen (1975) differentiated Phoma from Ascochyta based on differences in conidiogenesis and conidial septation. They emphasised that in Phoma conidia are produced from phialides with distinct collarettes (Boerema & Bollen 1975), and that conidial euseptation is a secondary process which occurs independently from conidiogenesis, namely after conidial secession (Boerema & Bollen 1975, Aveskamp *et al.* 2010). In contrast, in *Ascochyta* conidia arise from the accumulation of annellations or from a gradually increasing collar of periclinal annellations, and conidial septation is an essential part of conidium development, which can be regarded as holoblastic (Boerema & Bollen 1975, Aveskamp *et al.* 2010). Later Punithalingam (1979a) redefined *Ascochyta*, and reported that holoblastic conidiogenesis was temporary, whereas phialidic conidiogenesis remained functional at the completion of conidial development. He also concluded that conidial development and septation should not be used as taxonomic criteria for distinguishing species in these two genera.

In spite of these arguments, the taxonomy of these two genera remains confused. This is largely demonstrated by the high number of synonyms in this complex (Aveskamp *et al.* 2008). Furthermore, in recent studies the type species of the genus *Ascochyta*, *As. pisi*, also nested in the *Didymellaceae* (de Gruyter *et al.* 2009), close to the type species of *Phoma* (Peever *et al.* 2007, de Gruyter *et al.* 2009, Aveskamp *et al.* 2010). Because merging the genera *Ascochyta* and *Phoma* would prove highly unpopular among phytopathologists, both generic names are still in use, and their links to sexual genera in the *Didymellaceae* (Aveskamp *et al.* 2010).

Didymella was first used at the generic level by Saccardo in 1880, with the description of Didymella exigua (Holm 1975, Corlett 1981), which was later accepted as the type or lectotype species of the genus (von Höhnel 1918, Corbaz 1957, Müller & von Arx 1962, Holm 1975, von Arx & Müller 1975). Didymella was originally accommodated in the Mycosphaerellaceae, and then placed in the Pleosporaceae, Phaeosphaeriaceae, Venturiaceae, or considered as incertae sedis in the Pleosporales (de Gruyter et al. 2009). In the study of de Gruyter et al. (2009), a new family Didymellaceae was introduced for the "Didymella clade", which included most members of Phoma and related asexual genera. As a genus with phytopathological importance, Didymella is also in urgent need of taxonomic revision (Aveskamp et al. 2010), as it appears to be polyphyletic. The four sexual genera that have been linked to Phoma include Didymella, Leptosphaeria, Mycosphaerella and Pleospora (Boerema et al. 2004), while Ascochyta has sexual connections in both Didymella and Mycosphaerella (Corlett 1981, Peever et al. 2007). In recent studies, however, it has been shown that the genus Didymella is the only genus that is correctly linked to Phoma s. str. (Woudenberg et al. 2009, Aveskamp et al. 2010) and Ascochyta (Chilvers et al. 2009, de Gruyter et al. 2009). Nevertheless, Didymella is still a poorly understood genus, with numerous species that remain phylogenetically unresolved. As both Ascochyta and Phoma have been regarded as polyphyletic, a proper study of the genera traditionally accommodating their sexual morphs is urgently needed (Aveskamp et al. 2010).

The genus *Phoma* is ubiquitous and species-rich, with species occurring on a diverse range of substrates, from soil to air, plants to animals, and even humans (Aveskamp *et al.* 2008, 2010). *Phoma* is notorious because includes many important plant pathogen species, some of which are of quarantine concern (Aveskamp *et al.* 2008, 2010, Chen *et al.* 2015). After the studies by Aveskamp *et al.* (2010) and de Gruyter *et al.* (2009, 2012), significant progress has been made to clarify generic boundaries in *Didymellaceae*. However, nearly 70 *Phoma* species embedded in the *Didymellaceae* could not be assigned to definite genera due to a lack of phylogenetic support (Aveskamp et al. 2010). In previous molecular phylogenetic studies, partial small subunit nrDNA (18S, SSU) and partial large subunit nrDNA (28S, LSU) nucleotide sequences were used to resolve the relationships above family level (de Gruyter et al. 2009, 2010, 2012), with many species excluded from Phoma and Didymellaceae. As the LSU and SSU sequence data did not provide sufficient phylogenetic information to distinguish closely related genera nor species, Aveskamp et al. (2009a) sequenced the internal transcribed spacer regions 1 & 2 and intervening 5.8S nrDNA (ITS), and partial gene regions of β-tubulin (tub2) and gamma-actin (actA) to clarify the phylogeny of dictyochlamydospore-producing Phoma taxa. LSU and ITS combined with tub2 were used to infer a phylogeny for genera and species in Didymellaceae (Aveskamp et al. 2010). Although improved resolutions were obtained, most of the internal nodes in the trees remained unresolved, and it was concluded that more DNA loci should be employed to fully resolve closely related taxa in this family. In a subsequent study the RNA polymerase II second largest subunit (rpb2) gene was successfully applied in a combination with ITS, LSU and tub2 to distinguish closely related species in Phoma (Chen et al. 2015).

Given the complexities of *Ascochyta*, *Didymella* and *Phoma*, the objectives of this study were: 1) to determine the phylogenetic relationships of these genera using multi-locus sequence data, *viz*. LSU, ITS, *rpb2* and *tub2*; 2) to delineate the phylogenetic lineages within *Didymellaceae*, and revise its taxonomy by adopting a polyphasic approach; 3) and to designate epitypes to stabilise the application of names within the family.

MATERIALS AND METHODS

Isolates and type specimens

Isolates used in this study included the majority used in Aveskamp et al. (2010). Furthermore, additional isolates previously identified as Ascochyta, Didymella and Phoma based solely on morphological characters, were also selected. In total, 287 strains were obtained from the culture collection of the CBS-KNAW Fungal Biodiversity Centre, Utrecht, the Netherlands (CBS), and the Dutch National Plant Protection Organization, Wageningen, the Netherlands (PD) (Table 1). Freeze-dried isolates were revived overnight in 2 mL malt/peptone (50 % / 50 %) liquid medium and subsequently transferred to oatmeal agar (OA), 2 % malt extract agar (MEA) and potato dextrose agar (PDA) (recipes according to Crous et al. 2009), and incubated at room temperature. Some of the cultures were incubated under near-ultraviolet (UV) light (12 h light, 12 h dark) or on pine needle agar (PNA) (Smith et al. 1996, Su et al. 2012) to promote sporulation if necessary. Loan requests of type specimens were sent to 34 fungaria, viz. ABD, B, BHG, BP, BPI, BR, BRNM, DAR, E, FI, G, H, ILL, K, KIEL, L(U), LE, PAD, PAV, PC, PDD, PR, PRC, PRM, ROPV, S, SIENA, UPS, UV, VALPL, W, WU, Z and ZT. Additional specimens were loaned from BR, BPI, IMI, K, L, M, PDD, SIENA and ZT.

Morphology

Morphological studies of living cultures were conducted following the methods described by Boerema *et al.* (2004) for the cultures grown on MEA, OA and PDA. Colony diameters were measured

after 7 d, and colony morphologies determined after 14 d of incubation. Colony colours on the surface and reverse of inoculated Petri dishes were assessed according to the colour charts of Rayner (1970). Micromorphological descriptions and measurements for 30 replicates of relevant features were carried out from mature conidiomata and conidia mounted in water (Aveskamp et al. 2010, Chen et al. 2015). For conidiomatal pycnidia, pycnidial walls and conidiogenous cells, measurements were taken from 5-10 samples. Observations were conducted with a Leica M125 dissecting microscope and with a Zeiss Axio Imager A2 compound microscope under differential interference contrast (DIC) illumination. Sections of pycnidia were prepared using a Leica CM1950 freezing microtome, to study the anatomy of pycnidial walls and the morphology of conidiogenous cells (Aveskamp et al. 2010, Chen et al. 2015). The NaOH spot test was carried out on MEA cultures to detect the production of metabolite E (Boerema et al. 2004). For the fungarium specimens studied, pycnidia and ascomata were rehydrated in 10 % lactic acid or 5 % KOH for examination. Observations and sections of these materials were conducted using the same methods as described for cultures above.

DNA isolation, PCR amplification and sequencing

Genomic DNA was extracted following the protocol of Cubero et al. (1999), from fungal mycelium growing on MEA. Some of the DNAs were provided by the authors of Aveskamp et al. (2010; Utrecht, the Netherlands), which were extracted using the UltraClean Microbial DNA Isolation Kit (Mo Bio Laboratories, Inc., Carlsbad, CA, USA). The LSU region was amplified with the primer pair LR0R (Rehner & Samuels 1994) and LR7 (Vilgalys & Hester 1990), the ITS region with V9G (de Hoog & Gerrits van den Ende 1998) and ITS4 (White et al. 1990), the tub2 region with the primers Btub2Fd and Btub4Rd (Woudenberg et al. 2009), and the rpb2 region with RPB2-5F2 (Sung et al. 2007) and fRPB2-7cR (Liu et al. 1999), respectively. The PCR amplifications were performed in a total volume of 25 µL containing 2.5 µL 10× EasyTag Buffer (TransGen Biotech, Beijing, China), 50 µM dNTPs, 0.1 µM of each primer, 0.75 U Tag DNA polymerase and 1-10 ng genomic DNA. PCR conditions for LSU. ITS and tub2 were set as follows: an initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation, annealing and extension, and a final extension step at 72 °C for 10 min. For the LSU amplification, the 35 cycles consisted of 45 s at 95 °C, 45 s at 48 °C and 2 min at 72 °C; for the ITS 30 s at 95 °C, 30 s at 48 °C and 80 s at 72 °C; and for the tub2 region 30 s at 95 °C, 30 s at 52 °C and 80 s at 72 °C. The PCR program for rpb2 amplification consisted of 5 cycles of 45 s at 94 °C, 45 s at 60 °C and 2 min at 72 °C, then 5 cycles with a 58 °C annealing temperature and 30 cycles with a 54 °C annealing temperature (Woudenberg et al. 2013). Sequencing was conducted by the Omega Genetics Company (Beijing, China) using the PCR primers and the additional internal sequence primer LR5 (Vilgalys & Hester 1990) for LSU.

Phylogenetic analyses

Sequences from each primer combination were used to obtain consensus sequences with MEGA v. 6.0 (Tamura *et al.* 2013). Reference sequences from Aveskamp *et al.* (2010) were

Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	ssion numb	ers ³
						LSU	ITS	rpb2	tub2
Allophoma labilis	Phoma labilis	CBS 124.93; PD 87/269		Solanum lycopersicum	The Netherlands	GU238091	GU237765	KT389552	GU237619
All. minor	Phoma minor	CBS 325.82	Т	Syzygium aromaticum	Indonesia	GU238107	GU237831	KT389553	GU237632
All. nicaraguensis		CBS 506.91; PD 91/876; IMI 215229	Т	Coffea arabica	Nicaragua	GU238058	GU237876	KT389551	GU23759
All. piperis	Phoma piperis	CBS 268.93; CBS 108.93; PD 88/720	Т	Peperomia pereskiifolia	The Netherlands	GU238129	GU237816	KT389554	GU23764
		CBS 108.93; PD 90/2011		Peperomia sp.	The Netherlands	GU238130	GU237921	KT389555	GU23764
All. tropica	Phoma tropica	CBS 436.75; DSM 63365	Т	Saintpaulia ionantha	Germany	GU238149	GU237864	KT389556	GU23766
All. zantedeschiae	Phoma zantedeschiae	CBS 131.93; PD 69/140		Calla sp.	The Netherlands	GU238159	FJ427084	KT389557	FJ427188
	Didymella rabiei	CBS 229.32		Cicer arietinum	Romania	KT389690	KT389473	KT389558	KT389767
Alternaia japonica	Alternaia japonica	CBS 118390		Brassica chinensis	USA	KC584281	KC584201	KC584405	_
Ascochyta fabae	Ascochyta fabae	CBS 524.77		Phaseolus vulgaris	Belgium	GU237963	GU237880	_	GU237526
		CBS 649.71		Vicia faba	The Netherlands	GU237964	GU237902	_	GU23752
		PD 83/492		Phaseolus vulgaris	The Netherlands	GU237965	GU237917	_	GU237528
As. herbicola	Phoma herbicola	CBS 629.97; PD 76/1017	R	Water	USA	GU238083	GU237898	KP330421	GU237614
As. lentis	Ascochyta lentis	CBS 370.84; PD 81/783		Lens culinaris	_	KT389691	KT389474	_	KT389768
As. medicaginicola var. macrospora	Phoma medicaginis var. macrospora	CBS 112.53	Т	Medicago sativa	USA	GU238101	GU237749	_	GU237628
		CBS 404.65; IMI 116999	R	Medicago sativa	Canada	GU238102	GU237859	KP330423	GU237629
As. medicaginicola var. medicaginicola	Phoma medicaginis var. medicaginis	CBS 316.90		Medicago sativa	Czech Republic	GU238103	GU237828	_	GU237630
As. nigripycnidia	Phoma nigripycnidia	CBS 116.96; PD 95/7930	Т	Vicia cracca	Russia	GU238118	GU237756	_	GU23763
As. phacae	Didymella phacae	CBS 184.55	Т	Phaca alpina	Switzerland	KT389692	KT389475	_	KT389769
As. pisi	Ascochyta pisi	CBS 122750; ATCC 201619		Pisum sativum	USA	KT389694	KT389477	_	KT389771
		CBS 122751; ATCC 201620		Pisum sativum	Canada	KP330444	KP330432	EU874867	KP330388
		CBS 122785; PD 78/517	Т	Pisum sativum	The Netherlands	GU237969	GU237763	_	GU237532
		CBS 126.54		Pisum sativum	The Netherlands	EU754137	GU237772	DQ677967	GU23753 ⁻
	As. juglandis	CBS 108.49		Juglans regia	The Netherlands	KT389693	KT389476	_	KT389770
As. rabiei	As. rabiei	CBS 206.30		_	_	KT389695	KT389478	KT389559	KT389772
		CBS 237.37	Т	Cicer arietinum	Bulgaria	KT389696	KT389479	_	KT389773
		CBS 534.65		Cicer arietinum	India	GU237970	GU237886	KP330405	GU237533
Ascochyta sp. 1	As. fabae	CBS 372.84; PD 80/1246		Pisum sativum	Australia	KT389697	KT389480	_	KT389774
		CBS 373.84; PD 80/1247		Pisum sativum	Australia	KT389698	KT389481	KT389560	KT389775

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Table 1. (Continued).									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	ssion numb	ers ³
						LSU	ITS	rpb2	tub2
Ascochyta sp. 2	Didymella astragalina	CBS 113797		Lathyrus vernus	Sweden	KT389699	KT389482	_	KT389776
As. syringae	Ascochyta syringae	CBS 545.72		Syringa vulgaris	The Netherlands	KT389700	KT389483	_	KT389777
As. versabilis	Phoma versabilis	CBS 876.97; PD 82/1008	R	Silene sp.	The Netherlands	GU238152	GU237909	KT389561	GU237664
As. viciae	Ascochyta viciae	CBS 451.68		Vicia sepium	The Netherlands	KT389701	KT389484	KT389562	KT389778
As. viciae-pannonicae	As. viciae-pannonicae	CBS 254.92		Vicia pannonica	Czech Republic	KT389702	KT389485	_	KT389779
Bipolaris maydis	Bipolaris maydis	CBS 134.39; DSM 1149		Zea mays	_	AY544645	DQ491489	DQ247790	_
Boeremia crinicola	Boeremia crinicola	CBS 109.79; PD 77/747	R	Crinum powellii	The Netherlands	GU237927	GU237737	KT389563	GU237489
Boeremia diversispora	B. diversispora	CBS 102.80; IMI 331907; PD 79/61		Phaseolus vulgaris	Kenya	GU237930	GU237725	KT389565	GU237492
		CBS 101194; PD 79/687; IMI 373349		Phaseolus vulgaris	The Netherlands	GU237929	GU237716	KT389564	GU237491
B. exigua	Ascochyta cheiranthi	CBS 118.38		Cheiranthus cheiri	Denmark	KT389706	KT389489	KT389582	KT389783
	As. ducometii	CBS 119.38		Nicotiana tabacum	_	KT389707	KT389490	KT389583	KT389784
	As. abelmoschi	CBS 107.21		Abelmoschus esculentus	_	KT389708	KT389491	_	KT389785
B. exigua var. coffeae	Boeremia exigua var. coffeae	CBS 119730		Coffea arabica	Brazil	GU237942	GU237759	KT389567	GU237504
		CBS 109183; PD 2000/10506; IMI 300060	R	Coffea arabica	Cameroon	GU237943	GU237748	KT389566	GU237505
B. exigua var. exigua	B. exigua var. exigua	CBS 431.74; PD 74/2447	R	Solanum tuberosum	The Netherlands	EU754183	FJ427001	KT389569	FJ427112
B. exigua var. forsythiae	B. exigua var. forsythiae	CBS 101197; PD 95/721		Forsythia sp.	The Netherlands	GU237931	GU237718	KT389570	GU237493
		CBS 101213; PD 92/959	R	Forsythia sp.	The Netherlands	GU237932	GU237723	KT389571	GU237494
B. exigua var. gilvescens	B. exigua var. exigua	CBS 101150; PD 79/118		Cichorium intybus	The Netherlands	EU754182	GU237715	KT389568	GU237495
B. exigua var. heteromorpha	B. exigua var. heteromorpha	CBS 443.94	Т	Nerium oleander	Italy	GU237935	GU237866	KT389573	GU237497
		CBS 101196; PD 79/176		Nerium oleander	France	GU237934	GU237717	KT389572	GU237496
B. exigua var. linicola	B. exigua var. linicola	CBS 114.28		Linum usitatissimum	The Netherlands	GU237937	GU237752	_	GU237499
		CBS 116.76; ATCC 32332; IMI 197074; PD 75/544	R	Linum usitatissimum	The Netherlands	GU237938	GU237754	KT389574	GU237500
	Phoma nemophilae	CBS 248.38		Nemophila insignis	The Netherlands	KT389703	KT389486	KT389575	KT389780
B. exigua var. populi	Boeremia exigua var. populi	CBS 100167; PD 93/217	Т	Populus (×) euramericana	The Netherlands	GU237939	GU237707	_	GU237501
								(continued	on next page)

Table 1. (Continued).									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	ssion numb	ers ³
						LSU	ITS	rpb2	tub2
B. exigua var. pseudolilacis	B. exigua var. pseudolilacis	CBS 101207; PD 94/614	Т	Syringa vulgaris	The Netherlands	GU237941	GU237721	_	GU237503
	Ascochyta lamiorum	CBS 462.67		Lamium maculatum	The Netherlands	KT389705	KT389488	_	KT389782
	As. lathyri	CBS 423.67		Lathyrus sp.	The Netherlands	KT389704	KT389487	KT389576	KT389781
B. exigua var. viburni	Boeremia exigua var. viburni	CBS 100354; PD 83/448	R	Viburnum opulus	The Netherlands	GU237944	GU237711	KT389577	GU237506
B. foveata	B. foveata	CBS 109176; PD 94/1394	R	Solanum tuberosum	Bulgaria	GU237946	GU237742	KT389578	GU237508
B. hedericola	B. hedericola	CBS 367.91; PD 87/229	R	Hedera helix	The Netherlands	GU237949	GU237842	KT389579	GU237511
B. lilacis	B. exigua var. lilacis	CBS 569.79; PD 72/741; IMI 331909	R	Syringa vulgaris	The Netherlands	GU237936	GU237892	_	GU237498
	Ascochyta philadelphi	CBS 588.67		Philadelphus sp.	The Netherlands	KT389709	KT389492	—	KT389786
B. lycopersici	Boeremia lycopersici	CBS 378.67; PD 67/276	R	Solanum lycopersicum	The Netherlands	GU237950	GU237848	KT389580	GU237512
B. noackiana	B. noackiana	CBS 101203; PD 79/1114		Phaseolus vulgaris	Colombia	GU237953	GU237720	KT389581	GU237515
		CBS 100353; PD 87/718	R	Phaseolus vulgaris	Guatemala	GU237952	GU237710	—	GU237514
B. sambuci-nigrae	B. sambuci-nigrae	CBS 629.68; CECT 20048; IMI 331913; PD 67/753	Т	Sambucus nigra	The Netherlands	GU237955	GU237897	_	GU237517
B. strasseri	B. strasseri	CBS 126.93; PD 73/642		Mentha sp.	The Netherlands	GU237956	GU237773	KT389584	GU237518
B. telephii	B. telephii	CBS 760.73; PD 71/1616	R	Sedum telephium	The Netherlands	GU237959	GU237905	—	GU237521
		CBS 109175; PD 79/524	R	Sedum telephium	The Netherlands	GU237958	GU237741	KT389585	GU237520
Calophoma aquilegiicola	Ascochyta aquilegiae	CBS 107.31		<i>Aquilegia</i> sp.	—	KT389710	KT389493	—	KT389787
	Phoma aquilegiicola	CBS 107.96; PD 73/598	R	Aconitum pyramidale	The Netherlands	GU238041	GU237735	KT389586	GU237581
	Phoma aquilegiicola	CBS 108.96; PD 79/611	R	<i>Aquilegia</i> sp.	The Netherlands	GU238042	GU237736	—	GU237582
	Phoma aquilegiicola	CBS 109.96; PD 83/832		Aquilegia sp.	The Netherlands	KT389711	KT389494	_	KT389788
	Phoma aquilegiicola	CBS 116402		Thalictrum dipterocarpum	New Zealand	KT389712	KT389495	_	KT389789
Ca. clematidina	Phoma clematidina	CBS 102.66		Clematis sp.	UK	FJ515630	FJ426988	KT389587	FJ427099
		CBS 108.79; PD 78/522	Т	Clematis sp.	The Netherlands	FJ515632	FJ426989	KT389588	FJ427100
Ca. clematidis-rectae	Phoma clematidis-rectae	CBS 507.63; PD 07/03486747; MUCL 9574		Clematis sp.	The Netherlands	FJ515647	FJ515606	KT389589	FJ515624
Ca. complanata	Phoma complanata	CBS 268.92 = PD 75/3		Angelica sylvestris	The Netherlands	EU754180	FJ515608	GU371778	FJ515626
		CBS 100311		Heracleum sphondylium	The Netherlands	EU754181	GU237709	KT389590	GU237594
Ca. glaucii	Phoma glaucii	CBS 112.96; PD 79/765		Dicentra sp.	The Netherlands	GU238077	GU237750	_	GU237610
		CBS 114.96; PD 94/888		Chelidonium majus	The Netherlands	FJ515649	FJ515609	—	FJ515627
Calophoma sp. 1	Didymella vincetoxici	CBS 186.55		Vincetoxicum officinale	Switzerland	KT389713	KT389496	_	KT389790

Table 1. (Continued).									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	ssion numb	ers ³
						LSU	ITS	rpb2	tub2
Ca. vodakii	D. vodakii	CBS 173.53	Т	Hepatica triloba	Switzerland	KT389714	KT389497	_	KT389791
Coniothyrium cartei	Coniothyrium cartei	CBS 105.91		Quercus robur	Germany	GQ387594	JF740181	KT389591	KF252700
Co. glycines	C. glycines	CBS 124141		Glycine max	Zimbabwe	GQ387598	JF740185	_	KF252702
Co. palmarum	C. palmarum	CBS 400.71		Chamaerops humilis	Italy	EU754153	AY720708	KT389592	KT389792
Co. telephii	C. telephii	CBS 188.71		Air	Finland	GQ387599	JF740188	KT389593	KT389793
Cucurbitaria berberidis	Cucurbitaria berberidis	CBS 363.93		Berberis vulgaris	The Netherlands	GQ387606	JF740191	_	KT389794
Didymella acetosellae	Phoma acetosellae	CBS 179.97		Rumex hydrolapathum	The Netherlands	GU238034	GU237793	KP330415	GU237575
D. aliena	Phoma aliena	CBS 379.93; PD 82/945		<i>Berberis</i> sp.	The Netherlands	GU238037	GU237851	KP330416	GU237578
D. americana	Peyronellaea americana	CBS 185.85; PD 80/1191	R	Zea mays	USA	GU237990	FJ426972	KT389594	FJ427088
		CBS 568.97; ATCC 44494; PD 94/1544		Glycine max	USA	GU237991	FJ426974	_	FJ427090
D. anserina	Phoma radicis-callunae	CBS 253.80		_	Germany	KT389715	KT389498	KT389595	KT389795
		CBS 285.29		Calluna sp.	UK	KT389716	KT389499	_	KT389796
	Peyronellaea anserina	CBS 360.84	R	Potato flour	The Netherlands	GU237993	GU237839	KT389596	GU237551
	Phoma radicis-callunae	CBS 397.65		Plastic	Germany	KT389717	KT389500	KT389597	KT389797
D. arachidicola	Peyronellaea arachidicola	CBS 333.75; ATCC 28333; IMI 386092; PREM 44889	Т	Arachis hypogaea	South Africa	GU237996	GU237833	KT389598	GU237554
D. aurea	Pe. aurea	CBS 269.93; PD 78/1087	Т	Medicago polymorpha	New Zealand	GU237999	GU237818	KT389599	GU237557
D. bellidis	Phoma bellidis	CBS 714.85; PD 74/265	R	Bellis perennis	The Netherlands	GU238046	GU237904	KP330417	GU237586
		PD 94/886		Bellis sp.	The Netherlands	GU238047	GU237923	_	GU237587
D. boeremae	Phoma boeremae	CBS 109942; PD 84/402	Т	Medicago littoralis cv. Harbinger	Australia	GU238048	FJ426982	KT389600	FJ427097
D. calidophila	Phoma calidophila	CBS 448.83	Т	Soil	Egypt	GU238052	FJ427059	_	FJ427168
		PD 84/109		Cucumis sativus	The Netherlands	GU238053	FJ427060	_	FJ427169
D. chenopodii	Phoma chenopodiicola	CBS 128.93; PD 79/140	R	Chenopodium quinoa cv. Sajana	Peru	GU238055	GU237775	KT389602	GU237591
D. coffeae-arabicae	Peyronellaea coffeae-arabicae	CBS 123380; PD 84/1013	Т	Coffea arabica	Ethiopia	GU238005	FJ426993	KT389603	FJ427104
D. curtisii	Pe. curtisii	CBS 251.92; PD 86/1145	R	Nerine sp.	The Netherlands	GU238013	FJ427038	_	FJ427148
		PD 92/1460		Sprekelia sp.	The Netherlands	GU238012	FJ427041	KT389604	FJ427151
D. dactylidis	Phoma dactylidis	CBS 124513; PD 73/1414	Т	Dactylis glomerata	USA	GU238061	GU237766	_	GU237599
D. dimorpha	Phoma dimorpha	CBS 346.82	Т	<i>Opuntiae</i> sp	Spain	GU238068	GU237835	_	GU237606
D. eucalyptica	Peyronellaea eucalyptica	CBS 377.91; PD 79/210	R	Eucalyptus sp.	Australia	GU238007	GU237846	KT389605	GU237562
D. exigua	Didymella exigua	CBS 183.55	Т	Rumex arifolius	France	EU754155	GU237794	EU874850	GU237525
								(continued)	on next page)

Table 1. (Continued).									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	ssion numb	ers ³
						LSU	ITS	rpb2	tub2
D. gardeniae	Peyronellaea gardeniae	CBS 626.68; IMI 108771	Т	Gardenia jasminoides	India	GQ387595	FJ427003	KT389606	FJ427114
D. glomerata	Pe. glomerata	CBS 133.72		Fresco in church	Romania	KT389718	FJ427004	_	FJ427115
		CBS 528.66; PD 63/590	R	Chrysanthemum sp.	The Netherlands	EU754184	FJ427013	GU371781	FJ427124
D. heteroderae	Pe. heteroderae	CBS 109.92; PD 73/1405	Т	Undefined food material	The Netherlands	GU238002	FJ426983	KT389601	FJ427098
D. lethalis	Pe. lethalis	CBS 103.25		_	_	GU238010	GU237729	KT389607	GU237564
D. longicolla	Phoma longicolla	CBS 124514; PD 80/1189	Т	<i>Opuntia</i> sp.	Spain	GU238095	GU237767	_	GU237622
D. mascrostoma	Phoma mascrostoma var. mascrostoma	CBS 482.95		Larix decidua	Germany	GU238099	GU237869	KT389609	GU237626
		CBS 529.66; PD 66/521	R	Malus sylvestris	The Netherlands	GU238098	GU237885	_	GU237625
	Phoma mascrostoma var. incolorata	CBS 223.69	R	Acer pseudoplatanus	Switzerland	GU238096	GU237801	KT389608	GU237623
	Phoma libertiana	CBS 247.38		Pinus nigra var. astriaca	_	KT389719	KT389501	_	KT389798
D. maydis	Peyronellaea maydis	CBS 588.69	Т	Zea mays	USA	EU754192	FJ427086	GU371782	FJ427190
D. microchlamydospora	Phoma microchlamydospora	CBS 105.95	Т	<i>Eucalyptus</i> sp.	UK	GU238104	FJ427028	KP330424	FJ427138
D. molleriana	Phoma digitalis	CBS 229.79; LEV 7660	R	Digitalis purpurea	New Zealand	GU238067	GU237802	KP330418	GU237605
		CBS 109179; PD 90/835-1		<i>Digitalis</i> sp.	The Netherlands	GU238066	GU237744	_	GU237604
D. musae	Peyronellaea musae	CBS 463.69	R	Mangifera indica	India	GU238011	FJ427026	_	FJ427136
D. negriana	Phoma negriana	CBS 358.71	R	Vitis vinifera	Germany	GU238116	GU237838	KT389610	GU237635
D. nigricans	Peyronellaea australis	CBS 444.81; PDDCC 6546	Т	Actinidia chinensis	New Zealand	GU238000	GU237867	_	GU237558
		PD 77/919		Actinidea chinensis	New Zealand	GU238001	GU237915	KT389611	GU237559
D. pedeiae	Phoma pedeiae	CBS 124517; PD 92/612A	Т	Schefflera elegantissima	The Netherlands	GU238127	GU237770	KT389612	GU237642
D. pinodella	Peyronellaea pinodella	CBS 318.90; PD 81/729		Pisum sativum	The Netherlands	GU238016	FJ427051	_	FJ427161
		CBS 531.66		Trifolium pretense	USA	GU238017	FJ427052	KT389613	FJ427162
D. pinodes	Pe. pinodes	CBS 525.77	Т	Pisum sativum	Belgium	GU238023	GU237883	KT389614	GU237572
D. pomorum	Pe. pomorum var. circinata	CBS 285.76; ATCC 26241; IMI 176742; VKM F-1843		Heracleum dissectum	Russia	GU238025	FJ427053	KT389615	FJ427163
	Pe. pomorum var. cyanea	CBS 388.80		Triticum sp.	South Africa	GU238027	FJ427055	KT389617	FJ427165
	Pe. pomorum var. pomorum	CBS 539.66; ATCC 16791; IMI 122266; PD 64/914	R	Polygonum tataricum	The Netherlands	GU238028	FJ427056	KT389618	FJ427166
	Phoma triticina	CBS 354.52		Triticum spelta	Switzerland	KT389720	KT389502	KT389616	KT389799
D. protuberans	Peyronellaea alectorolophi	CBS 132.96; PD 93/853		Rhinanthus major	The Netherlands	GU237989	GU237778	_	GU237550
	Pe. obtusa	CBS 377.93; PD 80/976		Daucus carota	The Netherlands	GU238014	GU237847	KT389619	GU237565
		CBS 391.93; PD 80/87		Spinacia oleracea	The Netherlands	GU238015	GU237858	KT389621	GU237566

Table 1. (Continued).									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	ssion numb	ers ³
						LSU	ITS	rpb2	tub2
	Pe. protuberans	CBS 381.96; PD 71/706	Т	Lycium halifolium	The Netherlands	GU238029	GU237853	KT389620	GU237574
D. rhei	Phoma rhei	CBS 109177; LEV 15165; PD 2000/9941	R	Rheum rhaponticum	New Zealand	GU238139	GU237743	KP330428	GU237653
D. rumicicola	Phoma rumicicola	CBS 683.79; LEV 15094	Т	Rumex obtusifolius	New Zealand	KT389721	KT389503	KT389622	KT389800
D. sancta	Peyronellaea sancta	CBS 281.83	Т	Ailanthus altissima	South Africa	GU238030	FJ427063	KT389623	FJ427170
D. senecionicola	Phoma senecionis	CBS 160.78; LEV 11451	R	Senecio jacobaea	New Zealand	GU238143	GU237787	—	GU237657
<i>Didymella</i> sp. 1	Didymella adianticola	CBS 379.96		<i>Pteris</i> sp.	The Netherlands	KT389722	KT389504	KT389624	KT389801
Didymella sp. 2	Ascochyta pyrethri	CBS 115.58; DSM 62044		Chrysanthemum roseum	Germany	KT389723	KT389505	KT389625	KT389802
D. subglomerata	Peyronellaea subglomerata	CBS 110.92; PD 76/1010	R	<i>Triticum</i> sp.	USA	GU238032	FJ427080	KT389626	FJ427186
D. subherbarum	Phoma subherbarum	CBS 249.92; PD 78/1088		Solanum sp.	Peru	GU238144	GU237808	—	GU237658
		CBS 250.92; DAOM 171914; PD 92/371	Т	Zea mays	Canada	GU238145	GU237809	—	GU237659
D. viburnicola	Phoma viburnicola	CBS 523.73; PD 69/800	R	Viburnum cassioides	The Netherlands	GU238155	GU237879	KP330430	GU237667
Epicoccum brasiliense	Phoma brasiliensis	CBS 120105	Т	Amaranthus sp.	Brazil	GU238049	GU237760	KT389627	GU237588
E. draconis	Phoma draconis	CBS 186.83; PD 82/47	R	Dracaena sp.	Rwanda	GU238070	GU237795	KT389628	GU237607
E. henningsii	Phoma henningsii	CBS 104.80; PD 74/1017	R	Acacia mearnsii	Kenya	GU238081	GU237731	KT389629	GU237612
E. huancayense	Phoma huancayensis	CBS 105.80; PD 75/908	Т	Solanum sp.	Peru	GU238084	GU237732	KT389630	GU237615
E. nigrum	Epicoccum nigrum	CBS 125.82; IMI 331914; CECT 20044		Human toenail	The Netherlands	GU237974	FJ426995	KT389631	FJ427106
		CBS 173.73; ATCC 24428; IMI 164070	Т	Dactylis glomerata	USA	GU237975	FJ426996	KT389632	FJ427107
E. pimprinum	E. pimprinum	CBS 246.60; ATCC 22237; ATCC 16652; IMI 81601	Т	Soil	India	GU237976	FJ427049	_	FJ427159
		PD 77/1028		Soil	India	GU237977	FJ427050	KT389633	FJ427160
E. plurivorum	Phoma plurivora	CBS 558.81; PDDCC 6873	Т	Setaria sp.	New Zealand	GU238132	GU237888	KT389634	GU237647
E. sorghinum	Epicoccum sorghinum	CBS 179.80; PD 76/1018		Sorghum vulgare	Puerto Rico	GU237978	FJ427067	KT389635	FJ427173
		CBS 627.68; PD 66/926		Citrus sp.	France	GU237979	FJ427072	KT389636	FJ427178
Heterophoma adonidis	Didymella adonidis	CBS 114309; UPSC 2982		Adonis vernalis	Sweden	KT389724	KT389506	KT389637	KT389803
H. dictamnicola	Phoma dictamnicola	CBS 507.91; PD 74/148		Dictamnus albus	The Netherlands	GU238065	GU237877	KT389638	GU237603
H. novae-verbascicola	Phoma novae-verbascicola	CBS 127.93; PD 92/347		Verbascum densiflorum	The Netherlands	GU238120	GU237774	_	GU237639
H. poolensis	Phoma poolensis	CBS 113.20; PD 92/774		_	_	GU238119	GU237751	_	GU237638
		CBS 116.93; PD 71/884		Antirrhinum majus	The Netherlands	GU238134	GU237755	_	GU237649
H. sylvatica	Phoma sylvatica	CBS 874.97; PD 93/764		Melampyrum pratense	The Netherlands	GU238148	GU237907	_	GU237662
								(continued	on next page)

Table 1. (Continued).									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	ssion numb	ers ³
						LSU	ITS	rpb2	tub2
Leptosphaeria conoidea	Leptosphaeria conoidea	CBS 616.75; ATCC 32813; IMI 199777; PD 74/56		Lunaria annua	The Netherlands	JF740279	JF740201	KT389639	KT389804
Leptosphaeria doliolum	Leptosphaeria doliolum	CBS 505.75	Т	Urtica dioica	The Netherlands	GQ387576	JF740205	KT389640	JF740144
Leptosphaerulina americana	Leptosphaerulina americana	CBS 213.55		Trifolium pratense	USA	GU237981	GU237799	KT389641	GU237539
L. arachidicola	L. arachidicola	CBS 275.59; ATCC 13446		Arachis hypogaea	Taiwan, China	GU237983	GU237820	_	GU237543
L. australis	L. australis	CBS 317.83		Eugenia aromatica	Indonesia	EU754166	GU237829	GU371790	GU237540
L. trifolii	L. trifolii	CBS 235.58		Trifolium sp.	The Netherlands	GU237982	GU237806	_	GU237542
Macroventuria anomochaeta	Macroventuria anomochaeta	CBS 502.72		Medicago sativa	South Africa	GU237985	GU237873	_	GU237545
		CBS 525.71	Т	Decayed canvas	South Africa	GU237984	GU237881	GU456346	GU237544
Ma. wentii	Ma. wentii	CBS 526.71	Т	Plant litter	USA	GU237986	GU237884	KT389642	GU237546
Microsphaeropsis olivacea	Microsphaeropsis olivacea	CBS 233.77		Pirus Iaricio	France	GU237988	GU237803	KT389643	GU237549
		CBS 432.71		Sarothamnus sp.	The Netherlands	GU237987	GU237863	_	GU237548
Mi. proteae	Mi. proteae	CBS 111319; CPC 1425		Protea nitida	South Africa	JN712563	JN712497	_	JN712650
Neoascochyta desmazieri	Ascochyta desmazieri	CBS 247.79		Gramineae	Austria	KT389725	KT389507	_	KT389805
	As. desmazieri	CBS 297.69	Т	Lolium perenne	Germany	KT389726	KT389508	KT389644	KT389806
	As. agrostidis	CBS 758.97		Нау	Norway	KT389727	KT389509	_	KT389807
Neoa. europaea	As. hordei var. europaea	CBS 819.84		Hordeum vulgare	Germany	KT389728	KT389510	KT389645	KT389808
		CBS 820.84	Т	Hordeum vulgare	Germany	KT389729	KT389511	KT389646	KT389809
Neoa. exitialis	Didymella arcuata	CBS 118.40		_	_	KT389732	KT389514	KT389647	KT389812
	D. exitialis	CBS 389.86		Triticum aestivum	Switzerland	KT389733	KT389515	KT389648	KT389813
	Ascochyta avenae	CBS 811.84		Secale cereale	Germany	KT389734	KT389516	—	KT389814
	As. avenae	CBS 812.84		Hordeum vulgare	Germany	KT389735	KT389517	—	KT389815
	As. skagwayensis	CBS 110124		Triticum sp.	The Netherlands	KT389730	KT389512	_	KT389810
	As. allii	CBS 113693; UPSC 1929		Allium sp.	Sweden	KT389731	KT389513	—	KT389811
Neoa. graminicola	As. sorghi	CBS 301.69		Lolium multiflorum	Germany	KT389737	KT389519	KT389650	KT389817
	Didymella exitialis	CBS 447.82		Triticum aestivum	Germany	KT389738	KT389520	—	KT389818
	Ascochyta graminea	CBS 586.79		Hordeum vulgare	Belgium	KT389739	KT389521	—	KT389819
	As. hordei var. americana	CBS 815.84		Hordeum vulgare	Germany	KT389740	KT389522	_	KT389820
	As. hordei var. americana	CBS 816.84		Hordeum vulgare	Germany	KT389741	KT389523	KT389651	KT389821
	Didymella graminicola	CBS 102789	R	Lolium perenne	New Zealand	KT389736	KT389518	KT389649	KT389816

Table 1. (Continued).									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	ssion numb	ers ³
						LSU	ITS	rpb2	tub2
Neoa. paspali	Phoma paspali	CBS 560.81; PD 92/1569	Т	Paspalum dilatatum	New Zealand	GU238124	FJ427048	KP330426	FJ427158
Neoascochyta sp. 1	Ascochyta hordei	CBS 112524		Triticum aestivum	Argentina	KT389742	KT389524	_	KT389822
Neoascochyta sp. 2	Didymella graminicola	CBS 516.81		Oryza sativa	Italy	KT389743	KT389525	KT389653	KT389823
Neoascochyta sp. 3	Ascochyta festucae	CBS 689.97		Hay	Norway	KT389744	KT389526	KT389654	KT389824
Neoascochyta sp. 4	As. hordei var. hordei	CBS 544.74		Triticum aestivum	South Africa	EU754134	GU237887	KT389652	GU237488
Neoascochyta sp. 5	As. brachypodii	CBS 876.72		Straw	South Africa	KT389745	KT389527	_	KT389825
Neodidymelliopsis cannabis	Didymella urticicola	CBS 121.75; ATCC 32164; IMI 194767; PD 73/584	т	Urtica dioica	The Netherlands	GU237972	GU237761	_	GU237535
	D. cannabis	CBS 234.37		Cannabis sativa	—	GU237961	GU237804	KP330403	GU237523
	D. eupyrena	CBS 591.67		Urtica dioica	The Netherlands	KT389746	KT389528	_	KT389826
	D. cannabis	CBS 629.76		Packing material	The Netherlands	KT389747	KT389529	_	KT389827
Neod. polemonii	Ascochyta polemonii	CBS 375.67		Polemonium caeruleum	The Netherlands	KT389748	KT389530	_	KT389828
	Phoma polemonii	CBS 109181; PD 83/757	Т	Polemonium caeruleum	The Netherlands	GU238133	GU237746	KP330427	GU237648
Neodidymelliopsis sp. 1	Ascochyta achlydis	CBS 256.77		Achlys triphylla	Canada	KT389749	KT389531	_	KT389829
Neodidymelliopsis sp. 2	As. scotinospora	CBS 382.96		Soil in desert	Israel	KT389750	KT389532	—	KT389830
Neod. xanthina	As. aquilegiae	CBS 168.70		Delphinium sp.	The Netherlands	KT389751	KT389533	—	KT389831
	Phoma xanthina	CBS 383.68	Т	Delphinium sp.	The Netherlands	GU238157	GU237855	KP330431	GU237668
Nothophoma anigozanthi	Phoma anigozanthi	CBS 381.91; PD 79/1110	Т	Anigozanthus maugleisii	The Netherlands	GU238039	GU237852	KT389655	GU237580
No. arachidis-hypogaeae	Phoma arachidis-hypogaeae	CBS 125.93; PD 77/1029	R	Arachis hypogaea	India	GU238043	GU237771	KT389656	GU237583
No. gossypiicola	Phoma gossypiicola	CBS 377.67		Gossypium sp.	USA	GU238079	GU237845	KT389658	GU237611
No. infossa	Phoma infossa	CBS 123395	Т	Fraxinus pennsylvanica	Argentina	GU238089	FJ427025	KT389659	FJ427135
No. quercina	Phoma fungicola	CBS 633.92; ATCC 36786; VKM MF-325		<i>Microsphaera alphitoides</i> from <i>Quercus</i> sp.	Ukraine	EU754127	GU237900	KT389657	GU237609
Ophiosphaerella herpotricha	Ophiosphaerella herpotricha	CBS 620.86		Bromus erectus	Switzerland	DQ678062	KF498728	DQ677958	—
Paraboeremia adianticola	Didymella adianticola	CBS 187.83; PD 82/128		Polystichum adiantiforme	USA	GU238035	GU237796	KP330401	GU237576
		CBS 260.92; PD 86/1103		Pteris ensiformis	—	KT389752	KT389534	_	KT389832
Pa. putaminum	Phoma putaminum	CBS 130.69; CECT 20054; IMI 331916	R	Malus sylvestris	Denmark	GU238138	GU237777	—	GU237652
		CBS 372.91; PD 75/960	R	<i>Ulmus</i> sp.	The Netherlands	GU238137	GU237843	_	GU237651
Pa. selaginellae	Phoma selaginellicola	CBS 122.93; PD 77/1049	Т	Selaginella sp.	The Netherlands	GU238142	GU237762	_	GU237656
Paraleptosphaeria nitschkei	Paraleptosphaeria nitschkei	CBS 306.51	Т	Cirsium spinosissimum	Switzerland	JF740308	JF740239	KT389660	KT389833

(continued on next page)

Table 1. (Continued).									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	sion numb	ers ³
						LSU	ITS	rpb2	tub2
Phaeosphaeria ammophilae	Phaeosphaeria ammophilae	CBS 114595		Ammophila arenaria	Sweden	GU301859	KF766146	GU371724	—
Phaeosphaeriopsis triseptata	Phaeosphaeriopsis triseptata	MFLUCC 13-0347		Ruscus aculeatus	Italy	KJ522480	KJ522476	KJ522486	_
Phoma neerlandica		CBS 134.96; PD 84/676	Т	Delphinium sp.	The Netherlands	KT389753	KT389535	KT389661	KT389834
Phoma herbarum	Phoma cruris-hominis	CBS 377.92; IMI 213845		Human leg	The Netherlands	KT389756	KT389536	KT389663	KT389837
	Phoma herbarum	CBS 502.91; PD 82/276		Nerium sp.	The Netherlands	GU238082	GU237874	KP330419	GU237613
	Phoma herbarum	CBS 615.75; PD 73/665; IMI 199779	R	<i>Rosa multiflora</i> cv. Cathayensis	The Netherlands	EU754186	FJ427022	KP330420	FJ427133
	Atradidymella muscivora	CBS 127589; UAMH 10909		Polytrichum juniperinum	USA	KT389757	KT389539	KT389664	KT389838
	Phoma acuum	CBS 274.37		Picea excelsa	UK	KT389754	KT389537	KT389662	KT389835
	Leptosphaeria millefolii	CBS 304.51		Achillea millefolium	Switzerland	KT389755	KT389538	_	KT389836
Phomatodes aubrietiae	Phoma aubrietiae	CBS 383.67; PD 65/223	R	<i>Aubrietia hybrida</i> cv. Superbissima	The Netherlands	GU238044	GU237854	—	GU237584
		CBS 627.97; PD 70/714	Т	Aubrietia sp.	The Netherlands	GU238045	GU237895	KT389665	GU237585
Phomat. nebulosa	Phoma nebulosa	CBS 117.93; PD 83/90		Mercurialis perennis	The Netherlands	GU238114	GU237757	KP330425	GU237633
		CBS 100191		Thlaspi arvense	Poland	KP330446	KP330434	KT389666	KP330390
		CBS 740.96		Armoracia rusticana	The Netherlands	KT389758	KT389540	KT389667	KT389839
Plenodomus biglobosus	Plenodomus biglobosus	CBS 532.66; PD 65/911		Brassica sp.	The Netherlands	KT389759	KT389541	KT389668	KT389840
Plen. lingam	Plen. lingam	CBS 275.63		Brassica sp.	UK	JF740306	JF740234	KT389669	KT389841
Pleospora betae	Pleospora betae	CBS 523.66		Beta vulgaris	The Netherlands	EU754179	FJ426981	KT389670	KT389842
Pleo. herbarum	Pleo. herbarum	CBS 191.86	Т	Medicago sativa	India	GU238160	KC584239	KC584471	—
Pleo. typhicola	Pleo. typhicola	CBS 132.69		Typha angustifolia	The Netherlands	JF740325	JF740105	KC584505	KT389843
Pyrenochaeta cava	Pyrenochaeta cava	CBS 257.68; CECT 20043; IMI 331911		Soil from wheat-field	Germany	EU754199	JF740260	_	KT389844
Pyrenochaeta nobilis	Pyrenochaeta nobilis	CBS 407.76	Т	Laurus nobilis	Italy	EU754206	NR_103598	DQ677991	KT389845
Pyrenochaetopsis pratorum	Pyrenochaetopsis pratorum	CBS 445.81	Т	Lolium perenne	New Zealand	GU238136	NR_111623	KT389671	KT389846
Pyrenophora phaeocomes	Pyrenophora phaeocomes	DAOM 222769		Calamagrostis villosa	Switzerland	JN940093	JN943649	DQ497614	_
Setomelanomma holmii	Setomelanomma holmii	CBS 110217		Picea pungens	USA	GQ387633	KT389542	GU371800	_
Sporomiella minima	Sporomiella minima	CBS 524.50		Dung of goat	Panama	DQ678056	KT389543	DQ677950	_
Stagonosporopsis actaeae	Stagonosporopsis actaeae	CBS 106.96; PD 94/1318	Т	Actaea spicata	The Netherlands	GU238166	GU237734	KT389672	GU237671

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Table 1. (Continued)									
Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	Ge	nBank acces	sion numb	ers ³
						LSU	ITS	rpb2	tub2
	Didymella hellebori	CBS 114303; UPSC 2962		Actaea spicata	Sweden	KT389760	KT389544	_	KT389847
S. ajacis	S. ajacis	CBS 177.93; PD 90/115	Т	Delphinium sp.	Kenya	GU238168	GU237791	KT389673	GU237673
S. andigena	S. andigena	CBS 101.80; PD 75/909; IMI 386090	R	Solanum sp.	Peru	GU238169	GU237714	—	GU237674
		CBS 269.80; PD 75/914		Solanum sp.	Peru	GU238170	GU237817	_	GU237675
S. artemisiicola	S. artemisiicola	CBS 102636; PD 73/1409	R	Artemisia dracunculus	France	GU238171	GU237728	KT389674	GU237676
S. astragali	S. astragali	CBS 178.25; MUCL 9915	R	Astragalus sp.	—	GU238172	GU237792	_	GU237677
S. caricae	S. caricae	CBS 248.90		Carica papaya	Chile	GU238175	GU237807	_	GU237680
		CBS 282.76		<i>Brassica</i> sp.	Indonesia	GU238177	GU237821	_	GU237682
S. chrysanthemi	S. chrysanthemi	CBS 500.63; MUCL 8090	R	Chrysanthemum indicum	Germany	GU238190	GU237871	_	GU237695
		CBS 137.96; PD 84/75	R	Chrysanthemum indicum	The Netherlands	GU238191	GU237783	_	GU237696
S. crystalliniformis	S. crystalliniformis	CBS 713.85; ATCC 76027; PD 83/826	Т	Solanum lycopersicum	Colombia	GU238178	GU237903	KT389675	GU237683
S. cucurbitacearum	S. cucurbitacearum	CBS 133.96;PD 79/127		Cucumis sp.	New Zealand	GU238181	GU237780	KT389676	GU237686
S. dennisii	S. dennisii	CBS 631.68; PD 68/147	Т	Solidago floribunda	The Netherlands	GU238182	GU237899	KT389677	GU237687
S. dorenboschii	S. dorenboschii	CBS 426.90; IMI 386093; PD 86/551	Т	Physostegia virginiana	The Netherlands	GU238185	GU237862	KT389678	GU237690
S. helianthi		CBS 200.87	Т	Helianthus annuus	Italy	KT389761	KT389545	KT389683	KT389848
S. heliopsidis	S. heliopsidis	CBS 109182; PD 74/231	R	Heliopsis patula	The Netherlands	GU238186	GU237747	KT389679	GU237691
S. hortensis	S. hortensis	CBS 104.42	R	_	The Netherlands	GU238198	GU237730	KT389680	GU237703
		CBS 572.85; PD 79/269	R	Phaseolus vulgaris	The Netherlands	GU238199	GU237893	KT389681	GU237704
S. inoxydabilis	S. inoxydabilis	CBS 425.90; PD 81/520	Т	Chrysanthemum parthenii	The Netherlands	GU238188	GU237861	KT389682	GU237693
S. loticola	S. loticola	CBS 562.81; PDDCC 6884	Т	Lotus pedunculatus	New Zealand	GU238192	GU237890	KT389684	GU237697
S. lupini	S. lupini	CBS 101494; PD 98/5247	Т	Lupinus albus	UK	GU238194	GU237724	KT389685	GU237699
S. oculo-hominis	S. oculo-hominis	CBS 634.92; IMI 193307	Т	Human corneal ulcer	USA	GU238196	GU237901	KT389686	GU237701
S. rudbeckiae	S. rudbeckiae	CBS 109180; PD 79/175	R	Rudbeckia bicolor	The Netherlands	GU238197	GU237745	_	GU237702
S. tanaceti	S. tanaceti	CBS 131484	Т	Tanacetum cinerariifolium	Australia	JQ897461	NR_111724	_	JQ897496
S. trachelii	S. trachelii	CBS 379.91; PD 77/675	R	Campanula isophylla	The Netherlands	GU238173	GU237850	KT389687	GU237678
		CBS 384.68	R	Campanula isophylla	Sweden	GU238174	GU237856	_	GU237679
S. valerianellae	S. valerianellae	CBS 273.92; PD 82/43		Valerianella locusta	The Netherlands	GU238200	GU237819	_	GU237705
		CBS 329.67; PD 66/302	Т	Valerianella locusta var. oleracea	The Netherlands	GU238201	GU237832	_	GU237706
								(continued	on next page)

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Resolving Phoma enigma

Table 1. (Continued).

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Species	Old name	Strain number ¹	Status ²	Host, substrate	Country	GenBank accession		ssion numb	ers ³
						LSU	ITS	rpb2	tub2
Subplenodomus violicola	Subplenodomus violicola	CBS 306.68		Viola tricolor	The Netherlands	GU238156	FJ427083	_	KT389849
Xenodidymella applanata	Didymella applanata	CBS 195.36	Т	Rubus idaeus	The Netherlands	KT389764	KT389548	_	KT389852
		CBS 205.63		Rubus idaeus	The Netherlands	GU237998	GU237798	KP330402	GU237556
		CBS 115577		Rubus idaeus	Sweden	KT389762	KT389546	KT389688	KT389850
		CBS 115578		Rubus arcticus nothossp. stellarcticus	Sweden	KT389763	KT389547	_	KT389851
X. asphodeli	D. asphodeli	CBS 375.62	Т	Asphodelus albus	France	KT389765	KT389549	KT389689	_
		CBS 499.72		Asphodelus ramosus	Italy	KT389766	KT389550	_	KT389853
X. catariae X. humicola	D. catariae Phoma humicola	CBS 102635; PD 77/1131 CBS 220.85; PD 71/1030	R	Nepeta catenaria Franseria sp.	The Netherlands USA	GU237962 GU238086	GU237727 GU237800	KP330404 KP330422	GU237524 GU237617

¹ ATCC: American Type Culture Collection, Virginia, USA; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CECT: Colección Española de Cultivos Tipo, Valencia University, Spain; CPC: Culture collection of Pedro Crous, housed at CBS; DAOM: Canadian Collection of Fungal Cultures, Ottawa, Canada; DSM: Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, UK; LEV: Plant Health and Diagnostic Station, Auckland, New Zealand; MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MUCL: Mycotheque de l'Universite catholique de Louvain, Louvain-Ia-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; UAMH: University of Alberta Microfungus Collection and Herbarium, Canada; UPSC: Uppsala University Culture Collection, Sweden; VKM: All-Russian Collection of Microorganisms, Pushchino, Russia.

² T: ex-type strain; R: representative strain.

³ ITS: internal transcribed spacer regions 1 & 2 including 5.8S nrDNA gene; LSU: 28S large subunit of the nrRNA gene; *rpb2*: RNA polymerase II second largest subunit; *tub2*: ß-tubulin.

downloaded from GenBank, and are listed in Table 1. Alignments of all consensus sequences, as well as the reference sequences were generated with MAFFT v. 7 (http://mafft.cbrc.jp/alignment/ server/index.html; Katoh & Standley 2013), and were improved manually when necessary. Ambiguous regions were excluded from the analyses and gaps were treated as missing data. A 70 % neighbour-joining (NJ) reciprocal bootstrap method with maximum-likelihood distance was applied to check the congruence of the individual loci in the multi-locus dataset (Mason-Gamer & Kellogg 1996). Phylogenetic analyses of both individual and combined aligned data consisted of Bayesian and maximum-likelihood analyses.

MrModeltest v. 2.3 (Nylander 2004) was used to determine the best nucleotide substitution model settings for each locus. The Bayesian analyses of the combined four-locus dataset and individual locus data were performed with MrBayes v. 3.2.1 (Ronquist et al. 2012) based on the results of the MrModeltest. The Markov Chain Monte Carlo sampling (MCMC) analysis of four chains started in parallel from a random tree topology. The number of generations was set at 10 million and the run was stopped automatically when the average standard deviation of split frequencies fall below 0.01. Trees were saved each 1 000 generations. Burn-in was set at 25 % after which the likelihood values were stationary and the remaining trees were used to calculate posterior probabilities. Maximum-likelihood analyses including 1000 bootstrap replicates were conducted using RAxML v. 7.2.6 (Stamatakis & Alachiotis 2010). A general time reversible model (GTR) was applied with a gamma-distributed rate variation. Novel sequences generated in this study were deposited in GenBank (Table 1), the final matrices used for phylogenetic analyses in TreeBASE (www.treebase.org; accession number: S18162), and novel taxonomic descriptions and nomenclature in MycoBank (www.MycoBank.org; Crous et al. 2004).

RESULTS

Phylogenetic analyses

The final concatenated alignment contained 286 ingroup taxa with a total of 2 620 characters including gaps (966 characters for LSU, 648 for ITS, 395 for *tub2* and 599 for *rpb2*) of which 883 were unique site patterns (45 for LSU, 270 for ITS, 216 for *tub2* and 352 for *rpb2*), and *Sporormiella minima* (CBS 524.50) served as the outgroup taxon. The first 57 and the last 342 characters including gaps of the original LSU alignment was excluded from the analyses as these regions are unalignable. The general time reversible model with inverse gamma rates (GTR + I + G) was determined to be the best for all four loci by MrModeltest. The LSU, ITS, *tub2* and *rpb2* sequence datasets did not show any conflicts in the tree topologies for the 70 % reciprocal bootstrap trees, which allowed to combine the four loci for the multi-locus analysis.

The single locus phylogenies of LSU and ITS display low resolution at both generic and species level. The LSU phylogeny was only able to distinguish *Boeremia*, *Calophoma*, *Leptosphaerulina*, *Macroventuria*, *Neoascochyta* and *Neodidymelliopsis* clades, but failed for the other 11 genera. The ITS phylogeny was only able to distinguish 9 of 17 generic clades and failed for *Allophoma*, *Ascochyta*, *Didymella*, *Epicoccum*,

Heterophoma, Macroventuria, Nothophoma and Xenodidymella. The *rpb2* phylogeny was able to distinguish all 17 generic clades and with good resolution of species among these genera. The *tub2* phylogeny was able to distinguish 13 of 17 generic clades and failed for *Allophoma*, *Ascochyta*, *Calophoma* and *Stagonosporopsis*.

For the multi-locus analyses, a total of 12858 trees were sampled after the burn-in with a stop value of 0.01. The topology of the BI tree confirmed that of ML tree for the distinctions of 17 well supported monophyletic clades, and therefore only the ML consensus tree with Bayesian posterior probabilities (BPP) and RAxML bootstrap support (MLBS) values are indicated in Fig. 1. Clustering basal in the four-locus tree (Fig. 1) were the outgroup taxon Sporormiella minima (CBS 524.50) and five monophyletic groups representing the five other families in *Pleosporales* close to Didymellaceae, namely Coniothyriaceae (BPP = 0.93; MLBS = 75 %) comprising four species, Coniothyrium carteri, Co. glycines, Co. palmarum and Co. telephii; Leptosphaeriaceae (BPP = 1; MLBS = 69 %) containing six species, Leptosphaeria conoidea, Leptosphaeria doliolum, Paraleptosphaeria nitschkei, Plenodomus biglobosus, Plen. lingam and Subplenodomus violicola; Cucurbitariaceae (BPP = 1; MLBS = 50 %) comprising four species, Cucurbitaria berberidis, Pyrenochaeta cava, Pyrenochaeta nobilis and Pyrenochaetopsis pratorum; Pleosporaceae (BPP = 1; MLBS = 83 %) comprising six species, Alternaria japonica, Bipolaris maydis, three Pleospora species, viz. Pleospora betae, Pleo. herbarum and Pleo. typhicola, and Pyrenophora phaeocomes; and Phaeosphaeriaceae (BPP = 1; MLBS = 100 %) comprising four species, Ophiosphaerella herpotricha, Phaeosphaeria ammophilae, Phaeosphaeriopsis triseptata and Setomelanomma holmii.

The remaining ingroup could be divided into a basal *Microsphaeropsis* clade (BPP = 0.99; MLBS = 94 %, three isolates including the type species of *Microsphaeropsis*, *Mi. olivacea*) and the main *Didymellaceae* clade (BPP = 0.98; MLBS = 67 %). In the *Didymellaceae* clade, 17 well-supported monophyletic lineages were resolved, of which eight represent existing genera, and the remaining nine are described as new genera.

At the most terminal position, a well-supported clade, Clade 1 (BPP = 1; MLBS = 91 %, 29 isolates) accommodated all the species of the genus Stagonosporopsis, which was in congruence with the results of Aveskamp et al. (2010). Clade 2 (BPP = 1; MLBS = 100 %, eight isolates) comprised five "Phoma" species and a novel species, which formed a novel genus Allophoma, i.e. All. nicaraguensis, All. labilis (syn. Phoma labili), All. minor (syn. Phoma minor), All. piperis (syn. Phoma piperis), All. tropica (syn. Phoma tropica), and All. zantedeschiae (syn. Phoma zantedeschiae). Clade 3 (BPP = 1; MLBS = 97 %, six isolates) comprised five species accommodated in a novel genus Heterophoma, i.e. H. adonidis (syn. Didymella adonidis), H. nobilis (syn. Ascochyta nobilis), H. novae-verbascicola (syn. Phoma novae-verbascicola), H. poolensis (syn. Phoma poolensis), and H. sylvatica (syn. Phoma sylvatica). In congruence with the study of Aveskamp et al. (2010), the Boeremia species grouped in a well-defined cluster. Clade 4 (BPP = 1; MLBS = 100 %, 33 isolates), including B. exigua varieties and 10 other Boeremia species. Clade 5 (BPP = 0.98; MLBS = 99 %, 11 isolates) included three species of the genus Epicoccum, E. nigrum, E. pimprinum and E. sorghinum, and another five species of Phoma which were recombined into this genus, E. brasiliense (syn. Phoma brasiliensis), E. draconis (syn. Phoma draconis), E. henningsii (syn. Phoma henningsii), E. huancayense (syn. Phoma huancayensis) and E. plurivorum



Fig. 1. Phylogenetic tree inferred from a Maximum likelihood analysis based on a concatenated alignment of LSU, ITS, *rpb2* and *tub2* sequences of 287 strains representing *Didymellaceae* and allied families. The RAxML bootstrap support values (MLBS) and Bayesian posterior probabilities (BPP) are given at the nodes (BPP/MLBS). Some branches were shortened to fit them to the page – these are indicated by two diagonal lines with the number of times a branch was shortened indicated next to the lines. Extype strains are marked by an asterisk (*). The tree was rooted to *Sporormiella minima* (CBS 524.50).



Fig. 1. (Continued).



Fig. 1. (Continued).



Fig. 1. (Continued).





(syn. Phoma plurivora). Clade 6 (BPP = 1; MLBS = 95 %, 62 isolates) accommodated the type genus of the family Didymellaceae, Didymella, with the type species D. exigua (CBS 183.55). The subclade 6a accommodated 20 taxa belonging to the recently resurrected genus Peyronellaea, which were recombined into the genus Didymella. The subclade 6b comprised a cluster containing D. bellidis (syn. Phoma bellidis), D. chenopodii (syn. Phoma chenopodiicola), D. molleriana (syn. Phoma digitalis), D. senecionicola (syn. Phoma senecionis) and an isolate received as "Ascochyta pyrethri" (CBS 115.58). Between these two subclades there were several small groups comprised of D. acetosellae (syn. Phoma acetosellae), D. aliena (syn. Phoma aliena), D. boeremae (syn. Phoma boeremae), D. calidophila (syn. Phoma calidophila), D. dactylidis (syn. Phoma dactylidis), D. dimorpha (syn. Phoma dimorpha), the aforementioned D. exigua, D. longicolla (syn. Phoma longicolla), D. mascrostoma (syn. Phoma mascrostoma var. mascrostoma), D. microchlamydospora (syn. Phoma microchlamydospora), D. pedeiae (syn. Phoma pedeiae), D. rhei (syn. Phoma rhei), D. rumicicola (syn. Phoma rumicicola), D. subherbarum (syn. Phoma subherbarum), D. viburnicola (syn. Phoma viburnicola), an isolate received as "Phoma libertiana" (CBS 247.38) and an isolate representing a single lineage (CBS 379.96). Clade 7 (BPP = 1; MLBS = 100 %) comprised five isolates representing three species, which belong to a newly introduced genus Paraboeremia, namely Pa. adianticola (syn. D. adianticola), Pa. putaminum (syn. Phoma putaminum), and Pa. selaginellae (syn. Phoma selaginellicola). Clade 8 (BPP = 1; MLBS = 100 %) contained three isolates of Macroventuria including the generic type, Ma. anomochaeta. Clade 9 (BPP = 1; MLBS = 92 %, 25 isolates) accommodated the genus Ascochyta with its type species, As. pisi, and other Ascochyta species, As. fabae, As. herbicola (syn. Phoma herbicola), As. lentis, As. medicaginicola var. macrospora (syn. Phoma medicaginis var. macrospora), As. medicaginicola var. medicaginicola (syn. Phoma medicaginis var. medicaginis), As. nigripycnidia (syn. Phoma nigripycnidia), As. rabiei, As. syringae, As. versabilis (syn. Phoma versabilis), As. viciae, As. viciae-pannonicae, As. phacae and three isolates representing two insufficiently known species (CBS 372.84, CBS 373.84, CBS 113797). Two species that produced phoma-like conidia were embedded in clade 10 (BPP = 1; MLBS = 100 %, five isolates), which is proposed here as a new genus, Phomatodes, including Phomat. aubrietiae (syn. Phoma aubrietiae) and Phomat. nebulosa (syn. Phoma nebulosa). The majority of the isolates that clustered in clade 11 (BPP = 1; MLBS = 96 %, 14 isolates) were identified as "Phoma" sp., and a new generic name Calophoma is introduced below for this clade, which comprised five accepted species, Ca. aquilegiicola (syn. Phoma aquilegiicola), Ca. clematidina (syn. Phoma clematidina), Ca. clematidis-rectae (syn. Phoma clematidis-rectae), Ca. complanata (syn. Phoma complanata), Ca. glaucii (syn. Phoma glaucii), Ca. vodakii (syn. D. vodakii) and an insufficiently known species (CBS 186.55). Clade 12 (BPP = 1; MLBS = 100 %, seven isolates) accommodated the genus Phoma, including the generic type, Phoma herbarum and its sexual morph (based on Atradidymella muscivora strain UAMH 10909), and a new species Phoma neerlandica. Clade 13 (BPP = 1; MLBS = 100 %) comprised four isolates of Leptosphaerulina, including its type species, L. australis. Clade 14 (BPP = 1; MLBS = 90 %, 23 isolates) comprised a "Phoma" isolate and 22 isolates formerly identified as "Ascochyta", and a "Didymella" species, most of which were subjected to molecular analysis for the first time. A new generic name Neoascochyta is proposed below for these

taxa. These included Neoa. desmazieri (syn. Ascochyta desmazieri), Neoa. exitialis (syn. Didymella exitialis), Neoa. graminicola (syn. Didymella graminicola), Neoa. europaea (syn. As. hordei var. europaea), Neoa. paspali (syn. Phoma paspali) and five insufficiently known isolates (CBS 516.81, CBS 544.74, CBS 689.97, CBS 876.72 and CBS 112524). Clade 15 (BPP = 1; MLBS = 97 %, eight isolates) accommodated a newly established sexual genus, Xenodidymella, including X. applanata (syn. Didymella applanata), X. asphodeli (syn. D. asphodeli), X. catariae (svn, D. catariae) and X. humicola (svn, Phoma humicola), Clade 16 (BPP = 1; MLBS = 100 %) contained 10 isolates initially classified in the genera Ascochyta and Didymella, as well as Phoma, and for this well-supported cluster the new generic name Neodidymelliopsis is proposed below, including six species, Neod. cannabis (syn. D. cannabis), Neod. polemonii (syn. Phoma polemonii), Neod. xanthina (syn. Phoma xanthina) and two insufficiently known isolates (CBS 256.77, CBS 382.96). Clade 17 (BPP = 1; MLBS = 85 %, five isolates) contained five species that were accommodated in a new genus proposed below, Nothophoma, namely No. anigozanthi (syn. Phoma anigozanthi), No. arachidis-hypogaeae (syn. Phoma arachidis-hypogaeae), No. guercina (syn. Phoma fungicola), No. gossypiicola (syn. Phoma gossypiicola) and No. infossa (syn. Phoma infossa).

Taxonomy

Phylogenetic analyses based on the combined LSU, ITS, tub2 and rpb2 sequences resolved a total of 24 clades, in which 17 clades including 162 taxa belonged to the Didymellaceae. With morphological examination of the type specimens and isolates, nine new genera, three new species, 84 new combinations, two new names and 11 epitypifications and seven neotypifications are proposed below. All recognised clades are treated, and the novelties, as well as epitypifications and neotypifications are described and illustrated below. The main morphological characters of accepted genera in Didymellaceae were provided in Table 2. The identity of several species and / or isolates could not be resolved, mostly because the type materials were unavailable for study. Their identities remain uncertain and will be resolved in future studies. The genus Microsphaeropsis grouped basal to the Didymellaceae, for which a new family Microsphaeropsidaceae was introduced.

Treatment of monophyletic lineages

Clade 1: Stagonosporopsis

Stagonosporopsis Died. emend. Aveskamp *et al.*, Stud. Mycol. 65: 44. 2010.

Conidiomata pycnidial, globose to subglobose, superficial on or immersed into the agar, solitary or confluent, ostiolate or poroid. *Pycnidial wall* pseudoparenchymatous, 2–6-layered, with an outer wall composed of 1–3 layers of brown olivaceous cells. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform or doliiform. *Conidia* often dimorphic: majority aseptate, hyaline, ellipsoidal to subglobose, thin- and smooth-walled. Conidia of the second type smaller in size, can be produced both *in vivo* and *in vitro* in the same pycnidia, unicellular or with up to 3 septa. *Ascomata* pseudothecial, if present, occurring only *in vivo*, globose to subglobose, sometimes with a somewhat conical neck. *Asci* cylindrical or subclavate, 8-

Table 2. Overview of the main characters of genera in the Didymellaceae.											
Genera	As	exual morph		Sexual m	orph						
	Conidia	Septa	Chlamydospores	Ascospores	Septa						
Allophoma	ovoid, oblong, ellipsoidal to cylindrical, or slightly allantoid	aseptate	-	-	-						
Ascochyta	ovoid, oblong, subcylindrical, ellipsoidal, cymbiform, allantoid	0-1(-3)	unicellular or multicellular	ovoid to ellipsoidal, slightly biconic	1 or 3						
Boeremia	variable in shape	0-1(-2)	-	ellipsoidal	1						
Calophoma	subglobose, subcylindrical, ellipsoidal, somewhat obclavate-fusiform	0–1	unicellular or multicellular	-	-						
Didymella	ellipsoidal to subglobose, cylindrical, oblong, ovoid, sometimes allantoid	aseptate	unicellular or multicellular	ellipsoidal to cymbiform	1 or multiseptate						
Epicoccum	ovoid, ellipsoidal to oblong, (sub-)cylindrical; epicoccoid conidia: multicellular-phragmosporous, subglobose-pyriform	aseptate; septa being obscured by the dark verrucose wall	unicellular or multicellular	-	-						
Heterophoma	ellipsoidal, oblong, cylindrical, reniform, or slightly allantoid	0-1(-2)	unicellular	-	-						
Leptosphaerulina	-	-	-	muriform, oblong, ellipsoidal to obovoid, subfusoid	1(-6)						
Macroventuria	-	_	-	ellipsoidal	1						
Neoascochyta	fusoid to cylindrical, obclavate-ovoid to ellipsoidal	0–1	-	cylindrical to ovoid, ellipsoidal	1						
Neodidymelliopsis	ovoid to ellipsoidal, cylindrical, allantoid	0–1	unicellular or multicellular	subovoid to oblong, ellipsoidal	1(-3)						
Nothophoma	ovoid, oblong to ellipsoidal	aseptate	-	-	-						
Paraboeremia	ellipsoidal	aseptate	-	subcylindrical	1						
Phoma	oblong to cylindrical, ellipsoidal, sometimes fusiform	aseptate	-	fusiform	1						
Phomatodes	cylindrical to allantoid	aseptate	-	-	-						
Stagonosporopsis	ellipsoidal to subglobose	0-3	-	ellipsoidal, fusiform or obovoid	1						
Xenodidymella	ellipsoidal to allantoid, subcylindrical, oblong, pyriform	0–1	unicellular	obovoid to oblong, clavate, ellipsoidal	1						

spored, biseriate. *Ascospores* ellipsoidal, fusiform or obovoid, 1-septate, guttulate (from Aveskamp *et al.* 2010).

Type species: Stagonosporopsis hortensis (Sacc. & Malbr.) Petr., Ann. Mycol. 19: 21. 1921.

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

Basionym: Actinonema actaeae Allesch., Ber. Bayer. Bot. Ges. 5: 7. 1897.

= Phoma actaeae Boerema et al., Persoonia 16: 347. 1997.

Specimens examined: Sweden, Uppland, Dalby par., Jerusalem, from Actaea spicata, 16 Jun. 1989, K. & L. Holm, CBS 114303 = UPSC 2962. The Netherlands, Limburg, Schaersbergerbos, from a leaf spot of Actaea spicata, 22 Sep. 1994 (holotype of Phoma actaeae L 992.167-501, culture ex-holotype CBS 106.96 = PD 94/1318).

Notes: Isolate CBS 114303, received as "*Didymella hellebori*", was also isolated from the same host as the holotype of *Stagonosporopsis actaeae*, and is genetically identical to CBS 106.96 in all sequenced loci. It appears that CBS 114303 represents the sexual morph for *S. actaeae*.

Stagonosporopsis ajacis (Thüm.) Aveskamp *et al.*, Stud. Mycol. 65: 44. 2010.

Basionym: Phyllosticta ajacis Thüm., Boll. Soc. Adriat. Sci. Nat. Trieste 6: 329. 1880.

= Phoma ajacis Aa & Boerema, Persoonia 15: 383. 1993.

Specimen examined: Kenya, from *Delphinium* sp., 1990, Hopman (neotype of *Phoma ajacis* L 993.034.225, culture ex-neotype CBS 177.93 = PD 90/ 115).

Stagonosporopsis andigena (Turkenst.) Aveskamp et al., Stud. Mycol. 65: 44. 2010.

Basionym: Phoma andigena Turkenst., Persoonia 16: 131. 1995.

Specimens examined: **Peru**, Dep. Junin, Huancayo, near Valle del Mantaro, from a leaf of *Solanum* sp., deposited in CBS Jan. 1980, G.H. Boerema, CBS 101.80 = PD 75/909 = IMI 386090; Dep. Junin, Huancayo, near Valle del Mantaro, from a leaf of *Solanum* sp., 1975, L.J. Turkensteen, CBS 269.80 = PD 75/914.

Stagonosporopsis artemisiicola (Hollós) Aveskamp *et al.*, Stud. Mycol. 65: 44. 2010.

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

Specimen examined: France, from a stem base of Artemisia dracunculus, deposited in CBS Mar. 2000, CBS 102636 = PD 73/1409.

Stagonosporopsis astragali (Cooke & Harkn.) Aveskamp *et al.*, Stud. Mycol. 65: 45. 2010.

Basionym: Phoma astragali Cooke & Harkn., Grevillea 13: 111. 1885.

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

Stagonosporopsis caricae (Syd. & P. Syd.) Aveskamp et al., Stud. Mycol. 65: 45. 2010.

Basionym: Mycosphaerella caricae Syd. & P. Syd., Ann. Mycol. 11: 403. 1913.

- = *Ascochyta caricae-papayae* Tarr., The fungi and plant diseases of Sudan: 53. 1955.
 - ≡ *Phoma caricae-papayae* (Tarr.) Punith., Trans Brit. Mycol. Soc. 75: 340. 1980.
- = Phoma caricae Punith., C.M.I. Descript. Pathog. Fungi Bact. 634: 1. 1979.

Specimens examined: Chile, from fruit of Carica papaya, deposited in CBS Jun. 1990, CBS 248.90. Indonesia, Java, Segunung, from *Brassica* sp., Feb. 1976, H. Vermeulen, CBS 282.76.

Stagonosporopsis chrysanthemi (F. Stevens) Crous *et al.*, Australas. Pl. Pathol. 41: 681. 2012.

Basionym: Ascochyta chrysanthemi F. Stevens, Bot. Gaz. 44: 246. 1907.

Mycosphaerella ligulicola K.F. Baker *et al.*, Phytopathology 39: 799. 1949.
Didymella ligulicola (K.F. Baker *et al.*) Arx, Beitr. Kryptogamenfl. Schweiz. 11: 364. 1962.

≡ Didymella ligulicola var. ligulicola (K.F. Baker et al.) Arx, Stud. Mycol. 32: 9. 1990.

≡ Stagonosporopsis ligulicola var. ligulicola (K.F. Baker et al.) Aveskamp et al., Stud. Mycol. 65: 46. 2010.

= Phoma ligulicola var. ligulicola Boerema, Stud. Mycol. 32: 9. 1990.

Specimens examined: **Germany**, Berlin, from *Chrysanthemum indicum*, deposited in CBS Dec. 1963, R. Schneider, CBS H-11952, culture CBS 500.63 = MUCL 8090. **The Netherlands**, near Lisse, from a leaf of *Chrysanthemum indicum*, deposited in CBS Feb. 1996, CBS 137.96 = PD 84/75.

Stagonosporopsis crystalliniformis (Loer. et al.) Aveskamp et al., Stud. Mycol. 65: 45. 2010.

Basionym: Phoma andina var. crystalliniformis Loer. et al., Fitopatología 21: 100. 1986.

≡ *Phoma crystalliniformis* (Loer. *et al.*) Noordel. & Gruyter, Mycol. Res. 97: 1344. 1993.

Specimens examined: **Colombia**, Antioquia, Rionegro, from a stem base of *Lycopersicon esculentum*, 1983, R. Navarro (**holotype** CBS H-3926, culture exholotype CBS 713.85 = ATCC 76027 = PD 83/826).

Stagonosporopsis cucurbitacearum (Fr.) Aveskamp et al., Stud. Mycol. 65: 45. 2010.

Basionym: Sphaeria cucurbitacearum Fr., Syst. Mycol. 2: 502. 1823.

≡ Phoma cucurbitacearum (Fr.) Sacc., Syll. Fung. 3: 148. 1884.

= Sphaeria bryoniae Fuckel, Jahrb. Nassauischen Vereins Naturk. 23-24: 112. 1870.

≡ *Didymella bryoniae* (Fuckel) Rehm, Ber. Naturhist. Vereins Augsburg 26: 27. 1881.

Specimen examined: New Zealand, from Cucumis sp., deposited in CBS May 1996, CBS 133.96 = PD 79/127.

Stagonosporopsis dennisii Boerema et al., Persoonia 16: 350. 1997. Fig. 2.

= Phoma dennisii Boerema, Trans. Brit. Mycol. Soc. 67: 307. 1976.

Description from ex-epitype culture (CBS 631.68): Conidiomata pycnidial, confluent, subglobose, glabrous, superficial on or immersed into the agar, $(110-)170-400 \times (110-)130-275(-300) \mu m$. Ostioles 1–2, slightly papillate or non-papillate. Pycnidial wall pseudoparenchymatous, composed of oblong to isodiametric cells, 2–3 layers, 11–14 μm thick. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, 5–8.5 × 3.5–7(–9.5) μm . Conidia ellipsoidal to cylindrical, thin-walled, smooth, aseptate, 3.5–5.5 × 1.5–3.5 μm , egutullate or sometimes with 1–3 small gutules. Conidial matrix cream to buff.

Culture characteristics: Colonies on OA, 65–70 mm diam after 7 d, margin regular, in some sectors covered by floccose aerial mycelia, white to greenish olivaceous; reverse olivaceous, buff in some sectors. Colonies on MEA 65–70 mm diam after 7 d, margin regular, aerial mycelium sparse, white to pale olivaceous; reverse white, pale olivaceous near the centre. Colonies on PDA, 70–75 mm diam after 7 d, margin regular, floccose aerial mycelium covering the whole colony, white to pale grey; reverse hazel with some sectors in brown olivaceous. NaOH spot test: a slight reddish discolouration on MEA.

Specimens examined: **The Netherlands**, Arnhem, from a stem of *Solidago floribunda*, deposited in CBS Sep. 1968 (epitype designated here HMAS 246703, MBT202490, culture ex-epitype CBS 631.68 = PD 68/147); Wageningen, from dead stems of *Solidago virgaurea*, Oct. 1976, M.M.J. Dorenbosch (holotype L 996, 047-028).

Notes: This fungus was originally described from dead stems of *Solidago virgaurea*, with conidia $2.5-8.5 \times 1-3.5 \mu m$ (Boerema 1976). The epitype from *Solidago floribunda* agrees well in morphology with the type material as conidia are aseptate, measuring $3.5-5.5 \times 1.5-3.5 \mu m$.

Stagonosporopsis dorenboschii (Noordel. & Gruyter) Aveskamp *et al.*, Stud. Mycol. 65: 45. 2010.

Basionym: Phoma dorenboschii Noordel. & Gruyter, Persoonia 15: 83. 1992.

Specimen examined: **The Netherlands**, Rijnsburg, from *Physostegia virginiana*, deposited in CBS Oct. 1990, M.E. Noordeloos (**holotype** L 988.202-121, **isotype** CBS H-7604, culture ex-holotype CBS 426. 90 = IMI 386093 = PD 86/551).

Stagonosporopsis heliopsidis (H.C. Greene) Aveskamp et al., Stud. Mycol. 65: 45. 2010.

Basionym: Phyllosticta heliopsidis H.C. Greene, Trans. Wisconsin Acad. Sci. 50: 158. 1961.

≡ Phoma heliopsidis (H.C. Greene) Aa & Boerema, Persoonia 18: 40. 2002.

Specimen examined: The Netherlands, from Heliopsis patula, deposited in CBS Jan. 2001, H. de Gruyter, CBS 109182 = PD 74/231.

Stagonosporopsis hortensis (Sacc. & Malbr.) Petr., Ann. Mycol. 19: 21. 1921.

Basionym: Hendersonia hortensis Sacc. & Malbr., Michelia 2: 629. 1882.

= Phoma subboltshauseri Boerema et al., Persoonia 16: 360. 1997.

= Ascochyta boltshauseri Sacc. Z. Pflanzenkrankh. 1: 136. 1891.



Fig. 2. Stagonosporopsis dennisii (CBS 631.68). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidium. H. Section of pycnidial wall. I. Conidiogenous cells. J. Conidia. Scale bars: G = 100 μm; H–J = 10 μm.

≡ Stagonosporopsis boltshauseri (Sacc.) Died., Ann Mycol. 10: 141. 1912.

Specimen examined: **The Netherlands**, from an unknown substrate, deposited in CBS Mar. 1942, N. Hubbeling, CBS 104.42; from *Phaseolus vulgaris*, deposited in CBS Sep. 1985, G.H. Boerema, culture CBS 572.85 = PD 79/269.

Note: As no generic type was designated by Diedicke (1912) when he established the genus *Stagonosporopsis*, *S. hortensis* was chosen as the type for this genus (Boerema & Verhoeven 1979, Vaghefi *et al.* 2012).

Stagonosporopsis inoxydabilis (Boerema) Crous *et al.*, Australas. Pl. Pathol. 41: 682. 2012.

Basionym: Didymella ligulicola var. *inoxydabilis* Boerema, Stud. Mycol. 32: 9. 1990.

≡ Stagonosporopsis ligulicola var. inoxydabilis (Boerema) Aveskamp et al., Stud. Mycol. 65: 45. 2010.

= Phoma ligulicola var. *inoxydabilis* Boerema, Stud. Mycol. 32: 10. 1990. Description and illustration (Vaghefi *et al.* 2012).

Specimen examined: The Netherlands, from Chrysanthemum parthenii, deposited in CBS Oct. 1990, (holotype CBS H-7611, culture ex-holotype CBS 425.90 = PD 81/520).

Stagonosporopsis helianthi Q. Chen & L. Cai, **sp. nov.** MycoBank MB814078. Fig. 3.

Etymology: Name after the host genus from which it was collected, *Helianthus*.



Fig. 3. Stagonosporopsis helianthi (CBS 200.87). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidia. I. Section of pycnidial wall. J. Conidiogenous cells. K. Conidia. Scale bars: G = 200 µm; H = 100 µm; I–K = 10 µm.

Description from ex-holotype culture (CBS 200.87): Conidiomata pycnidial, solitary or aggregated, subglobose, glabrous or covered with hyphal outgrows, mostly produced on the agar surface, sometimes immersed, $350-550 \times 330-550 \mu$ m. Ostiole single, slightly papillate or non-papillate. Pycnidial wall pseudo-parenchymatous, 2–4 layered, 13–25 µm thick, composed of isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, 6–10.5 × 6.5–10 µm. Conidia broadly ellipsoidal, hyaline, smooth- and thin-walled, aseptate, $2-4 \times 2-3 \mu$ m, with 0–3 guttules. Conidial matrix whitish cream.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular, aerial mycelia sparse, abundant pycnidia semi-immersed in concentric rings, pale grey to olivaceous; reverse concolourous. Colonies on MEA 30–35 mm diam after

7 d, margin regular, aerial mycelium sparse, wooly, white, pale olivaceous near the centre; reverse concolourous. Colonies on PDA, 45–50 mm diam after 7 d, margin regular, floccose, pycnidia produced in concentric rings, grey, white near the colony margin and somewhat olivaceous near the centre; reverse dark grey in concentric rings, white near the margin and buff near the centre. NaOH spot test: a slight greenish discolouration on MEA, reddish near the margin.

Specimen examined: Italy, Perugia, from Helianthus annuus, deposited in CBS Mar. 1987 (holotype HMAS 246704, culture ex-holotype CBS 200.87).

Notes: Isolate CBS 200.87 was received as "Didymella lophospora", which was isolated from Helianthus annuus, and is different from the original host of *D. lophospora* (Pteridium aquilinum). The type material of *D. lophospora* was not obtained from the fungaria consulted (see Materials and Methods). Although we did not observe the sexual morph of CBS 200.87, we consider this isolate to represent a different species from *D. lophospora*, because they are from different host families, and there is no record of an asexual morph of *D. lophospora* to compare with our isolate CBS 200.87. Therefore we introduce a new species, *Stagonosporopsis helianthi* based on CBS 200.87. *Stagonosporopsis helianthi* was resolved in a sister clade to *S. heliopsidis* (CBS 109182), and is significantly different from *S. heliopsidis* in morphology: pycnidia (*ca.* 350–550 µm diam in *S. helianthi* vs. 70–300 µm diam in *S. heliopsidis*), conidiogenous cells (6–10.5 × 6.5–10 µm in *S. helianthi* vs. $4-8 \times 4-8$ µm in *S. heliopsidis*), and conidia (2–4 × 2–3 µm in *S. helianthi* vs. 6–8 × 1.5–3 µm in *S. heliopsidis*).

Stagonosporopsis loticola (Died.) Aveskamp *et al.*, Stud. Mycol. 65: 46. 2010.

Basionym: Phoma loticola Died., Kryptog.-FI. Mark Brandenburg. 9: 152. 1912.

= Phoma lotivora P.R. Johnst., New Zealand J. Bot. 19: 178. 1981

Specimen examined: New Zealand, Auckland, Mt. Albert, from *Lotus pedun-culatus*, May 1980, P.R. Johnston (isotype CBS H-7612, culture ex-isotype CBS 562.81 = PDDCC 6884).

Stagonosporopsis lupini (Boerema & R. Schneid.) Boerema *et al.*, Persoonia 17: 283. 1999.

Basionym: Ascochyta lupini Boerema & R. Schneid., Verslagen Meded. Plantenziektenk. Dienst Wageningen 162: 28. 1984.

= Phoma schneiderae Boerema et al., Persoonia 17: 282. 1999.

Specimen examined: UK, Cambridgeshire, Mepal, from *Lupinus albus*, Apr. 1998 (holotype of *Phoma schneiderae* L 998.099.105, culture ex-holotype CBS 101494 = PD 98/5247).

Stagonosporopsis oculo-hominis (Punith.) Aveskamp et al., Stud. Mycol. 65: 46. 2010.

Basionym: Phoma oculi-hominis Punith., Trans. Brit. Mycol. Soc. 67: 142. 1976. (as "oculo-hominis")

≡ Phoma dennisii var. oculo-hominis (Punith.) Boerema et al., Persoonia 16: 351. 1997.

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

Stagonosporopsis rudbeckiae (Fairm.) Aveskamp *et al.*, Stud. Mycol. 65: 46. 2010.

Basionym: Phoma rudbeckiae Fairm., Proc. Rochester Acad. Sci. 1: 51. 1890.

Specimen examined: The Netherlands, from Rudbeckia bicolor, deposited in CBS Jan. 2001, H. de Gruyter, CBS 109180 = PD 79/175.

Stagonosporopsis tanaceti Vaghefi *et al.*, Australas. Pl. Pathol. 41: 682. 2012.

Specimen examined: Australia, Northern Tasmania, Scottsdale, from *Tanacetum cinerariifolium*, S.J. Pethybridge (holotype CBS H-20947, culture ex-holotype CBS 131484).

Stagonosporopsis trachelii (Allesch.) Aveskamp *et al.*, Stud. Mycol. 65: 46. 2010.

Basionym: Phoma trachelii Allesch., Hedwigia 34: 259. 1895.
= Ascochyta bohemica Kabát & Bubák, Hedwigia 44: 352. 1905.
= Stagonosporopsis bohemica (Kabát & Bubák) Boerema et al., Personia 16: 361. 1997.

Description and illustrations (Vaghefi et al. 2012).

Specimens examined: Sweden, Svalöv, from Campanula isophylla, deposited in CBS May 1968, W. Södergren, CBS H-8972, culture CBS 384.68. The Netherlands, from a leaf of Campanula isophylla, deposited in CBS Jun. 1991, CBS 379.91 = PD 77/675.

Stagonosporopsis valerianellae (Gindrat et al.) Aveskamp et al., Stud. Mycol. 65: 46. 2010.

Basionym: Phoma valerianellae Gindrat *et al.*, Rev. Hort. Suisse. 40: 350. 1967.

Specimens examined: **The Netherlands**, Wageningen, from Valerianella locusta var. oleracea, deposited in CBS Jul. 1967, G.H. Boerema (**holotype** L 965.300.24, **isotype** CBS H-7631, culture ex-isotype CBS 329.67 = PD 66/302); from Valerianella locusta, deposited in CBS Jun. 1992, J. de Gruyter, CBS 273.92 = PD 82/43.

Clade 2: Allophoma

Allophoma Q. Chen & L. Cai, gen. nov. MycoBank MB814058.

Etymology: Allo = allos in Greek, different; phoma-like conidia.

Conidiomata pycnidial, globose to flask-shaped, superficial on or immersed into the agar, solitary or confluent, ostiolate. *Pycnidial wall* pseudoparenchymatous, 2–5-layered. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to doliiform, sometimes flask-shaped or isodiametric. *Conidia* variable in shape and size, hyaline, thin-walled, smooth, aseptate, *i.e.* ovoid, oblong, ellipsoidal to cylindrical, or slightly allantoid, mostly guttulate.

Type species: Allophoma tropica (R. Schneid. & Boerema) Q. Chen & L. Cai.

Allophoma labilis (Sacc.) Q. Chen & L. Cai, comb. nov. MycoBank MB814068.

Basionym: Phoma labilis Sacc., Michelia 2: 341. 1881. Description (de Gruyter *et al.* 1993).

Specimen examined: The Netherlands, Barendrecht, from a stem of Lycopersicon esculentum, deposited in CBS Jan 1993, J. de Gruyter, CBS 124.93 = PD 87/269.

Allophoma minor (Aveskamp *et al.*) Q. Chen & L. Cai, comb. nov. MycoBank MB814069.

Basionym: Phoma minor Aveskamp et al., Stud. Mycol. 65: 42. 2010.

Description and illustration (Aveskamp et al. 2010).

Specimen examined: Indonesia, Sumatra, from Syzygium aromaticum, Apr. 1982, R. Kasim (holotype CBS H-20236, culture ex-holotype CBS 325.82).

Allophoma nicaraguensis Q. Chen & L. Cai, **sp. nov.** MycoBank MB814067. Fig. 4.

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



Fig. 4. Allophoma nicaraguensis (CBS 506.91). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidium. H. Section of pycnidial wall. I. Conidiogenous cells. J. Conidia. Scale bars: G = 20 µm; H, J = 10 µm; I = 5 µm.

Description from ex-holotype culture (CBS 506.91): Conidiomata pycnidial, solitary, globose to flask-shaped, glabrous, semiimmersed or immersed, $30-150(-180) \times 28-120(-165) \mu m$. Ostiole single, slightly papillate or non-papillate. Pycnidial wall pseudoparenchymatous, 3-5-layered, $8-12 \mu m$ thick, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, $3-4.5 \times 3.5-4.5(-5.5) \mu m$. Conidia ellipsoidal to oblong, thin-walled, smooth, aseptate, $2.5-4 \times 1.5-2.5 \mu m$, egutullate or sometimes with 1(-3) small guttules. Conidial matrix whitish.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular, floccose, greenish olivaceous, white near the margins; reverse white, olivaceous near the centre. Colonies on MEA 45–50 mm diam after 7 d, margin regular, aerial mycelium sparse, white to pale olivaceous; reverse white, pale olivaceous near the centre. Colonies on PDA, 45–50 mm diam after 7 d, margin regular, floccose, white to pale olivaceous; reverse white to pale brown, olivaceous near the centre. NaOH test negative.

Specimen examined: Nicaragua, from a twig of *Coffea arabica*, deposited in CBS Sep. 1991, J. de Gruyter (holotype HMAS 246701, culture ex-holotype CBS 506.91 = PD 91/876 = IMI 215229).

Notes: Since isolate CBS 506.91 was collected from *Coffea arabica*, the same host as *Phoma costaricensis*, this isolate was initially identified as "*P. costaricensis*". However, its conidia $(2.5-4 \times 1.5-2.5 \ \mu\text{m})$ were found to differ from the original description of *P. costaricensis* $[5-6(-7) \times 2-3 \ \mu\text{m};$ Echandi 1957]. We therefore introduced a new species, *All. nicaraguensis*, to accommodate this isolate. *Allophoma nicaraguensis*

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showed a close phylogenetic relationship with *All. tropica* (syn. *Phoma tropica*). However, the pycnidia of *All. tropica* ($100-300 \mu m$) are larger than *All. nicaraguensis* ($50-150 \mu m$), and with more conspicuous ostioles (1-5), as compared to a single ostiole in *All. nicaraguensis* (Boerema *et al.* 2004).

Allophoma piperis (Tassi) Q. Chen & L. Cai, comb. nov. MycoBank MB814070. Fig. 5.

Basionym: Phyllosticta piperis Tassi, Bull. Labor. Ort. Bot. Siena 3: 28. 1900.

≡ Phoma piperis (Tassi) Aa & Boerema, Persoonia 15: 398. 1993.

Description from holotype (N 354): Leaf spots elliptical to circular, brown to black. Conidiomata pycnidial, on leaves of Peperomia pereskifolia, solitary, subglobose, $115-245 \times 85-230 \mu m$. Ostiole single, slightly papillate. Pycnidial wall pseudoparenchymatous, composed of isodiametric cells. Conidiogenous cells phialidic, hyaline, simple, smooth, doliiform. Conidia ellipsoidal to ovoid, thin-walled, smooth, aseptate, $3.5-5.5 \times 1.5-2.5 \mu m$, with 1-2 large guttules.

Description from ex-epitype culture (CBS 268.93): Conidiomata pycnidial, solitary, globose to subglobose, glabrous or with some hyphal outgrowths, on the agar surface, $110-240 \times 100-200 \mu m$. Ostiole single, slightly papillate. Pycnidial wall pseudoparenchymatous, composed of oblong to isodiametric cells, 3-5 layers, $7.5-12.5 \mu m$ thick. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, $2.5-3.5 \times 2-3 \mu m$. Conidia oblong to ellipsoidal, thin-walled, smooth, aseptate, $2.5-4 \times 1.5-2.5 \mu m$, with 2 polar guttules. Conidial exudates not recorded.



Fig. 5. Allophoma piperis (CBS 268.93). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidium. I. Section of pycnidium. J. Conidiogenous cells. K. Section of pycnidial wall. L. Conidia. Scale bars: G = 100 μm; H–I = 20 μm; J = 5 μm; K–L = 10 μm.

Culture characteristics: Colonies on OA, 40–45 mm diam after 7 d, margin regular, covered by floccose aerial mycelia, dull green, pale grey olivaceous near the colony margin; reverse olivaceous. Colonies on MEA 35–40 mm diam after 7 d, margin regular, aerial mycelium sparse, white, pale green near the centre; reverse concolourous. Colonies on PDA, 40–45 mm diam after 7 d, margin regular, covered by densely grey felty aerial mycelium, pycnidia in a concentric ring; reverse dull green to olivaceous. NaOH test negative.

Specimens examined: Italy, from leaves of *Piper longum*, Mar. 1899 (holotype N 354 in SIENA). The Netherlands, Tiel, from a leaf of *Peperomia pereskiifolia*, deposited in CBS Apr 1993, J. de Gruyter (epitype designated here HMAS 246702, MBT202493, culture ex-epitype CBS 268.93 = PD 88/720); Ressen, from *Peperomia pereskiifolia*, deposited in CBS Jan. 1993, J. de Gruyter, CBS 108.93 = PD 90/2011.

Notes: The holotype of *Phoma piperis* was described from *Piper longum* collected in Italy, with conidia measuring $3.5-5.5 \times 1.5-2.5 \mu m$. De Gruyter *et al.* (1993) reported a similar conidial size of $3-5 \times 1.5 \mu m$ based on an authentic strain CBS 268.93, which was from the Netherlands and from *Peperomia pereskiifolia*, another host genus in *Piperaceae*. The collection HMAS 246702 (living culture CBS 268.93) is from the same host family, and the conidia we observed ($2.5-4 \times 1.5-2.5 \mu m$) generally agree with the type material and that of de Gruyter *et al.* (1993). We thus designated HMAS 246702 as epitype. *Allophoma piperis* was reported as a pathogen that caused leaf spots of *Piper* spp., especially *Piper* longus, and sometimes also infected Peperomia spp. (de Gruyter et al. 1993).

Allophoma tropica (R. Schneid. & Boerema) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814071.

Basionym: Phoma tropica R. Schneid. & Boerema, Phytopathol. Z. 83: 361. 1975.

Description (de Gruyter & Noordeloos 1992).

Specimen examined: Germany, Horrheim, from Saintpaulia ionantha, deposited in CBS Aug. 1975, R. Schneider (isotype CBS H-7629, culture ex-isotype CBS 436.75 = DSM 63365).

Allophoma zantedeschiae (Dippen.) Q. Chen & L. Cai, comb. nov. MycoBank MB814072.

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

= *Phyllosticta richardiae* F.T. Brooks, Ann. Appl. Biol.: 18. 1932. Description (Boerema 1993).

Specimens examined: Romania, from Cicer arietinum, deposited in CBS Apr. 1932, T. Savulescu, CBS 229.32. The Netherlands, from a bulb of Zantedeschiae sp., deposited in CBS Jan 1993, J, de Gruyter, CBS 131.93 = PD 69/140.

Notes: The isolate CBS 229.32 was received as "*Didymella rabiei*". It is however genetically distinct from other strains of *D. rabiei* (CBS 206.30, CBS 237.37 and CBS 534.65), but identical to the authentic strain of *Phoma zantedeschiae* (CBS 131.93) based on four sequenced loci.

Clade 3: Heterophoma

Heterophoma Q. Chen & L. Cai, gen. nov. MycoBank MB814059.

Etymology: Heter = $\epsilon_{\tau\epsilon\rho\sigma\varsigma}$ in Greek, other; morphologically similar to but phylogenetically different from *Phoma*.

Conidiomata pycnidial, globose to subglobose, superficial on or immersed into the agar, solitary or confluent, ostiolate. *Pycnidial wall* pseudoparenchymatous, 5-12-layered. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to doliiform. *Conidia* variable in shape and size, hyaline, thin-walled, smooth, 0-1(-2) septate, *i.e.* ellipsoidal, oblong, cylindrical, reniform, or slightly allantoid, mostly guttulate. *Chlamydospores* unicellular, globose, intercalary in chains, olivaceous.

Type species: Heterophoma sylvatica (Sacc.) Q. Chen & L. Cai.

Heterophoma adonidis (Moesz) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814073. Fig. 6.

Basionym: Didymella adonidis Moesz, Bot. Közlem. 8: 219. 1909.

Description from culture (CBS 114309): Conidiomata pycnidial, solitary or aggregated, (sub-)globose, glabrous or with some hyphal outgrows, superficial and immersed, later developing to black subglobose or irregular conidiomata and with a short wide elongated neck around the ostiole, $(85-)100-400(-450) \times (80-)100-245 \ \mu m$. Ostiole single, slightly papillate or non-papillate. Pycnidial wall pseudoparenchymatous, 6–8 layered, 27–35 $\ \mu m$ thick, composed of isodiametric cells, outer wall 2–3–layered, pigmented. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, 4.5–8.5 \times 4.5–8(–9) $\ \mu m$. Conidia oblong to cylindrical, hyaline, thin-walled, smooth, often uniseptate, 10.5–16.5 \times 3–4 $\ \mu m$, always somewhat constricted at the septum, with 5–15 guttules per cell. Conidial matrix yellowish.

Culture characteristics: Colonies on OA, 35–40 mm diam after 7 d, margin regular, floccose, white, pale olivaceous near the centre, flat near the margin; reverse buff. Colonies on MEA 40–45 mm diam after 7 d, margin regular, aerial mycelium sparse, white to pale olivaceous; reverse white, pale olivaceous near the centre. Colonies on PDA, 40–45 mm diam after 7 d, margin regular, floccose, white or somewhat buff; reverse pale saffron. NaOH spot test: a luteous discolouration on MEA, later changing to three colour layers, via dull green, dark brown to reddish, from the centre to outer ring.

Specimen examined: Sweden, Öland, Mörbylilla, on Adonis vernalis, Jun. 1989, K. & L. Holm, CBS 114309 = UPSC 2982.

Notes: The holotype of *Didymella adonidis* was on *Adonis vernalis* from Hungary, and could not be located from BP or MICH for examination. The culture CBS 114309, isolated from same host from Sweden, was deposited in CBS under the name "*Didymella adonidis*". The original description of *D. adonidis* only had details of a sexual morph, with asci clavate, $50-66 \times 12-13 \mu m$ and uniseptate ascospores, oblong-ellipsoidal, $19-26.5 \times 3-5 \mu m$. CBS 114309 was however, strictly asexual in culture.

Heterophoma nobilis (Kabát & Bubák) Q. Chen & L. Cai, comb. nov. MycoBank MB814074.

Basionym: Ascochyta nobilis Kabát & Bubák, Oesterr. Bot. Z. 54: 3. 1904.

≡ Phoma dictamnicola Boerema *et al.*, Persoonia 15: 90. 1992. Description (de Gruyter & Noordeloos 1992).

Specimen examined: The Netherlands, Arnhem, from a stem of Dictamnus albus, deposited in CBS Sep. 1991, J. de Gruyter, CBS 507.91 = PD 74/148.

Notes: Heterophoma nobilis is the only species that produces chlamydospores in this genus, and its conidia are more variable in size and shape *in vivo* than those *in vitro*. This species was originally described in the genus *Ascochyta* based on its large, septate conidia, and later replaced by a new name *Phoma dictamnicola* by de Gruyter & Noordeloos (1992).

Heterophoma novae-verbascicola (Aveskamp *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814075.

Basionym: Phoma novae-verbascicola Aveskamp et al., Stud. Mycol. 65: 41. 2010. Description (de Gruyter et al. 1993).

Specimens examined: **The Netherlands**, Zeist, Abburg nursery, from Verbascum sp. (**holotype** L 9893.00.134); Haarlem, from dead stem material of Verbascum densiflorum, deposited in CBS Jan 1993, J, de Gruyter, CBS 127.93 = PD 92/347.

Heterophoma poolensis (Taubenh.) Q. Chen & L. Cai, comb. nov. MycoBank MB814076.

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

Description (de Gruyter et al. 1993).

Specimens examined: **The Netherlands**, Bennekom, from a stem of *Antirrhinum majus*, deposited in CBS Jan 1993, J. de Gruyter, CBS 116.93 = PD 71/884. **Unknown origin**, from unknown substrate, deposited in CBS Aug. 1920, E.M. Smiley, CBS 113.20 = PD 92/774.

Note: According to the records in the USDA database, this is the only species in *Phoma s. lat.* that is reported to be associated with *Antirrhinum* sp. (Farr & Rossman 2015).

Heterophoma sylvatica (Sacc.) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814077. Fig. 7. *Basionym: Phoma sylvatica* Sacc., Michelia 2: 337. 1881.

Description from ex-neotype culture (CBS 874.97): Conidiomata pycnidial, solitary or confluent, globose to subglobose, with some hyphal outgrows, superficial on and immersed into the agar, 110–330 µm diam. Ostiole mainly single, occasionally two ostiolate, non-papillate or slightly papillate. Pycnidial wall 5-9(-20)-layered, outer layers pigmented. Conidiogenous cells phialidic, hyaline, smooth, bottle-shaped, $3-6 \times 3-6$ µm. Conidia cylindrical, sometimes slightly allantoid, smooth- and thin-walled, aseptate, $3.5-6 \times 1-2$ µm, with 2 small polar guttules. Conidial exudates not recorded.

Culture characteristics: Colonies on OA, 65–75 mm diam after 7 d, margin regular to slightly irregular, floccose, pale olivaceous grey, black pycnidia visible; reverse concolourous. Colonies on MEA 60–65 mm diam after 7 d, margin regular to slightly irregular, woolly, dull green to (pale) olivaceous grey; reverse greenish olivaceous to dull green, partly with vinaceous buff tinges,



Fig. 6. Heterophoma adonidis (CBS 114309). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H–I. Pycnidia. J. Conidiogenous cells. K. Section of pycnidia. L. Section of pycnidial wall. M. Conidia. Scale bars: G = 200 µm; H = 100 µm; K = 50 µm; I = 20 µm; J, L, M = 10 µm.

olivaceous black near the centre. Colonies on MEA, 55–60 mm diam after 7 d, margin irregular, with compact, woolly to floccose, pale olivaceous grey to olivaceous, staining the agar in sienna to scarlet due to the production of a diffusible pigment; reverse olivaceous to sepia. NaOH spot test: a greenish discolouration on MEA, later changing to red (from Boerema & de Gruyter 1998).

Specimen examined: **The Netherlands**, Wageningen, from a stem of *Mel-ampyrum pratense*, deposited in CBS Jun. 1997 (**neotype designated here** HMAS 246700, MBT202494, culture ex-neotype CBS 874.97 = PD 93/764).

Notes: The holotype of *Phoma sylvatica* was not located in any of the fungaria consulted, and is considered lost. Here we designate CBS 874.97 as neotype, as conidial size of the neotype $(3.5-6 \times 1-2 \ \mu\text{m})$ agrees well with the original description of *Phoma sylvatica* (4 × 1 μm). Although *H. sylvatica* is morphologically similar to *H. novae-verbascicola*, *H. sylvatica* was frequently reported on *Melampyrum* spp. (Boerema & de Gruyter 1998), while *H. novae-verbascicola* occurs on *Verbascum* spp.

(Aveskamp *et al.* 2010). In the phylogenetic tree, they are clearly distinct from each other, forming two sister clades.

Clade 4: Boeremia

Boeremia Aveskamp et al., Stud. Mycol. 65: 36. 2010.

Conidiomata pycnidial, variable in shape and size, mostly globose to subglobose, superficial on or immersed into the agar, solitary or confluent. Ostioles 1-2(-3), non-pappillate or pappillate, lined internally with a hyaline cells when mature. *Pycnidial wall* pseudoparenchymatous, 2-8-layered, outer wall 1-3-layered, brown pigmented. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform. Conidia variable in shape, hyaline, smooth- and thin-walled, mainly aseptate, but regularly 1(-2)-septate larger conidia may be found. Ascomata pseudothecial, only recorded in one species *in vivo*, sub-globose. Asci cylindrical or subclavate, always 8-spored,



Fig. 7. Heterophoma sylvatica (CBS 874.97). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H–I. Section of pycnidia. J. Section of pycnidial wall. K. Conidiogenous cells. L. Conidia. Scale bars: G = 200 μm; H = 100 μm; I = 50 μm; J, L = 10 μm; K = 5 μm.

biseriate. Ascospores ellipsoidal, 1-septate (from Aveskamp et al. 2010).

Type species: Boeremia exigua (Desm.) Aveskamp *et al.*, Stud. Mycol. 65: 36. 2010.

Boeremia crinicola (Siemasko) Aveskamp *et al.*, Stud. Mycol. 65: 37. 2010.

Basionym: Phyllosticta crinicola Siemasko, Acta Soc. Bot. Poloniae 1: 22. 1923.

≡ Phoma crinicola (Siemasko) Boerema, Verslagen Meded. Plantenziektenk. Dienst Wageningen 153: 18. 1979.

Specimen examined: **The Netherlands**, Haarlem, from a bulb of *Crinum powellii*, Mar. 1976, G.H. Boerema, CBS H-16198, culture CBS 109.79 = PD 77/747.

Boeremia diversispora (Bubák) Aveskamp *et al.*, Stud. Mycol. 65: 37. 2010.

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

≡ Phoma exigua var. diversispora (Bubák) Boerema, Gewasbescherming 11: 122. 1980.

Specimens examined: **Kenya**, from a pod of *Phaseolus vulgaris*, 1979, G.H. Boerema, CBS H-16308, CBS 102.80 = CECT 20049 = IMI 331907 = PD 79/61. **The Netherlands**, near Tilburg, from *Phaseolus vulgaris*, deposited in CBS Sep. 1998, J. de Gruyter, CBS 101194 = PD 79/687 = IMI 373349.

Boeremia exigua (Desm.) Aveskamp *et al.*, Stud. Mycol. 65: 36. 2010.

Specimen examined: Denmark, from necrotic stems of Cheiranthus cheiri, Apr. 1938, CBS 118.38. Unknown origin, from Nicotiana tabacum, deposited in CBS Jun. 1938, R. Fourmont, CBS 119.38; from Abelmoschus esculentus, deposited in CBS Feb. 1921, L.L. Harter, CBS 107.21.

Notes: CBS 118.38 and CBS 119.38, received as "Ascochyta cheiranthi" and "Ascochyta ducometii", clustered together with

Boeremia exigua var. exigua (CBS 431.74), *B. exigua* var. forsythiae (CBS 101197, CBS 101213), and *B. exigua* var. viburni (CBS 100354) in the phylogenetic tree (Fig. 1). Therefore, these two isolates were reidentified as *B. exigua* here. Ascochyta cheiranthi and As. ducometii might be synonyms of *B. exigua*, but this needs to be confirmed by examining the type specimens.

Isolate CBS 107.21 was received as "Ascochyta abelmoschi" and is from the original host of *A. abelmoschi* (Abelmoschus esculentus). It clustered in a single lineage, which is distinct from other varieties in the *B. exigua* clade (Fig. 1), and might represent a new variety.

Boeremia exigua var. coffeae (Henn.) Aveskamp et al., Stud. Mycol. 65: 37. 2010.

Basionym: Ascochyta coffeae Henn., Hedwigia 41: 307. 1902; non Phoma coffeae Delacr. 1897.

= Ascochyta tarda R.B. Stewart, Mycologia 49: 430. 1957.

≡ Phoma tarda (R.B. Stewart) H. Verm., Coffee Berry Dis. Kenya: 14. 1979.

Specimens examined: **Brazil**, Patrocínio, from leaf of *Coffea arabica*, deposited in CBS by L.H. Pfenning, CBS 119730. **Cameroon**, Bemenda, from *Coffea arabica*, deposited in CBS Jan. 2001, H. de Gruyter, CBS 109183 = PD 2000/10506 = IMI 300060.

Boeremia exigua var. exigua (Desm.) Aveskamp et al., Stud. Mvcol. 65: 37. 2010.

Basionym: Phoma exigua Desm., Ann. Sci. Nat. Bot. III 11: 282. 1849.

Specimens examined: **The Netherlands**, Emmeloord, from a tuber of Solanum tuberosum, deposited in CBS Jul. 1974, G.H. Boerema, CBS 431.74 = PD 74/ 2447; from a graft of *Ulmus*, 1961, H.M. Heybroek, CBS 373.61.

Boeremia exigua var. *forsythiae* (Sacc.) Aveskamp *et al.*, Stud. Mycol. 65: 37. 2010.

Basionym: Phyllosticta forsythiae Sacc., Michelia 1: 93. 1877. ≡ Ascochyta forsythiae (Sacc.) Höhn., Verh. Naturf. Vereins Brünn 47: 36. 1909.

≡ *Phoma exigua* var. *forsythiae* (Sacc.) Aa *et al.*, Persoonia 17: 452. 2000.

Specimens examined: The Netherlands, from Forsythia sp., deposited in CBS Sep. 1998, J. de Gruyter, CBS 101213 = PD 92/959; from Forsythia sp., deposited in CBS Sep. 1998, J. de Gruyter, CBS 101197 = PD 95/721.

Boeremia exigua var. **gilvescens** Aveskamp *et al.*, Stud. Mycol. 65: 37. 2010.

Specimens examined: **The Netherlands**, Baarn, from leaves of *Dactylis purpurea*, 1970, H.A. van der Aa (**holotype** CBS H-16281, culture ex-holotype CBS 761.70); Emmeloord, from *Cichorium intybus*, deposited in CBS Sep. 1998, H. de Gruyter, CBS 101150 = PD 79/118.

Boeremia exigua var. *heteromorpha* (Schulzer & Sacc.) Aveskamp *et al.*, Stud. Mycol. 65: 38. 2010. Fig. 8.

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

≡ *Phoma exigua* var. *heteromorpha* (Schulzer & Sacc.) Noordel. & Boerema, Verslagen Meded. Plantenziektenk. Dienst Wageningen 166: 109. 1989.

Description from ex-neotype culture (CBS 443.94): Conidiomata pycnidial, solitary or aggregated, globose to subglobose,

glabrous or with few hyphal outgrows, superficial and immersed, later developing to irregular conidiomata and with a short broad elongated neck, $120-320 \times 105-285 \mu m$. Ostioles 1-4(-5), on a short elongated neck. Pycnidial wall pseudoparenchymatous 3-8-layered, $16-50 \mu m$ thick, composed of oblong to isodiametric cells, outer wall 2-3-layered, pigmented. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, $3-8 \times 3-5.5 \mu m$. Conidia ovoid, ellipsoidal to cylindrical, thinwalled, smooth, mainly aseptate, occasionally 1-2 septate, $4.5-8(-10.5) \times 2.5-4 \mu m$, with (0-)2-8 minute guttules. Conidial matrix buff.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular, floccose, white, honey to pale olivaceous near the centre; reverse concolourous. Colonies on MEA 40–45 mm diam after 7 d, margin irregular, aerial mycelium sparse, white to pale olivaceous; reverse concolourous. Colonies on PDA, 15–20 mm diam after 7 d, margin regular, floccose, white, brown near the centre; reverse buff to brown, white near the margin. NaOH spot test: a greenish discolouration on MEA, later changing to reddish near the margin.

Specimens examined: **France**, Antibes, from *Nerium oleander*, deposited in CBS Sep. 1998, J. de Gruyter, CBS 101196 = PD 79/176. **Italy**, Perugia, from *Nerium oleander*, deposited in CBS Aug. 1994, A. Zazzerini (**neotype designated here** HMAS 246695, MBT202495, culture ex-neotype CBS 443.94).

Notes: The type specimen of *Phoma heteromorpha* could not be located, and is presumed lost. Conidia of the neotype are mostly aseptate, $4.5-8(-10.5) \times 2.5-4 \mu m$, which agree well with the original description. *Boeremia exigua* var. *heteromorpha* clustered with *B. exigua* var. *populi* in the phylogenetic tree, but *B. exigua* var. *heteromorpha* occurred on *Nerium oleander*, while *B. exigua* var. *populi* on *Populus* and *Salix* spp. respectively (Boerema *et al.* 2004).

Boeremia exigua var. **Iinicola** (Naumov & Vassiljevsky) Aveskamp *et al.*, Stud. Mycol. 65: 39. 2010.

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

≡ Phoma exigua var. linicola (Naumov & Vassiljevsky) P.W.T. Maas, Netherlands J. Pl. Pathol. 71: 118. 1965.

Specimens examined: **The Netherlands**, Flevoland, from a stem of *Linum usitatissimum*, deposited in CBS Feb. 1976, G.H. Boerema, CBS 116.76 = ATCC 32332 = CECT 20022 = CECT 20023 = IMI 197074 = PD 75/544; Wageningen, from seeds of *Nemophila insignis*, deposited in CBS Oct. 1938, P. Neergaard, CBS 248.38; Zierikzee, from *Linum usitatissimum*, deposited in CBS Dec.1928, H.A. Diddens, CBS 114.28.

Notes: Isolate CBS 248.38, deposited as "*Phoma nemophilae*", clustered with authentic cultures of *B. exigua* var. *linicola* (CBS 114.28, CBS 116.76) in the phylogenetic tree. The LSU, ITS, *tub2* and *rpb2* loci sequences proved to be identical among these three strains originating from the Netherlands. It is therefore concluded that the materials studied belong to the same variety, *B. exigua* var. *linicola*.

Boeremia exigua var. **populi** (Gruyter & P. Scheer) Aveskamp *et al.*, Stud. Mycol. 65: 39. 2010. *Basionym: Phoma exigua* var. *populi* Gruyter & P. Scheer, J. Phytopathol. 146: 413. 1998.



Fig. 8. Boeremia exigua var. heteromorpha (CBS 443.94). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H–I. Pycnidia. J. Section of pycnidia. K. Section of pycnidial wall. L. Conidia. Scale bars: G = 200 μm; H–I = 40 μm; J = 50 μm; K–L = 10 μm.

Specimen examined: The Netherlands, Deil, from a twig of *Populus* (×) *eur-americana* cv. Robusta, deposited in CBS Nov. 1997 (holotype L 995.263.325, culture ex-holotype CBS 100167 = PD 93/217).

Boeremia exigua var. **pseudolilacis** Aveskamp *et al.*, Stud. Mycol. 65: 39. 2010.

Specimens examined: **The Netherlands**, Baarn, from leaf spots in *Lamium maculatum*, deposited in CBS Nov. 1967, CBS 462.67; Baarn, from leaf spots of *Lathyrus* sp., deposited in CBS Oct. 1967, H.A. van der Aa, CBS H-9059, culture CBS 423.67; near Boskoop, from *Syringa vulgaris*, deposited in CBS Sep. 1998, J. de Gruyter (**holotype** CBS H-20371, culture ex-holotype CBS 101207 = PD 94/614).

Notes: Isolates CBS 462.67 and CBS 423.67 were initially deposited as "*Ascochyta lamiorum*" and "*Ascochyta lathyri*" respectively. But these two isolates grouped with the ex-type culture of *B. exigua* var. *pseudolilacis* (CBS 101207) in the phylogenetic tree with all four sequenced loci being identical. Therefore, we concluded that CBS 462.67 and CBS 423.67 belong to a same variety *B. exigua* var. *pseudolilacis*.

Boeremia exigua var. viburni (Roum. ex. Sacc.) Aveskamp et al., Stud. Mycol. 65: 39. 2010.

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

≡ *Phoma viburni* (Roum. ex. Sacc.) Boerema & M.J. Griffin, Trans. Brit. Mycol. Soc. 63: 110. 1974.

≡ Phoma exigua var. *viburni* (Roum. ex. Sacc.) Boerema, J. Phytopathol. 146: 414. 1998.

Specimen examined: The Netherlands, Boskoop, from Viburnum opulus, deposited in CBS Jan 1998, CBS 100354 = PD 83/448.

Boeremia foveata (Foister) Aveskamp *et al.*, Stud. Mycol. 65: 40. 2010.

Basionym: Phoma foveata Foister, Trans. & Proc. Bot. Soc. Edinburgh 33: 66. 1940.

Specimen examined: Bulgaria, from a tuber of Solanum tuberosum, deposited in CBS Jan. 2001, H. de Gruyter, CBS 109176 = CECT 2828 = PD 94/ 1394.

Boeremia hedericola (Durieu & Mont.) Aveskamp *et al.*, Stud. Mycol. 65: 40. 2010.

Basionym: Phyllosticta hedericola Durieu & Mont., Flore d'Algérie Cryptog. 1: 611. 1849. (as "hederaecola"; see also Sylloge Pl. crypt.: 279. 1856.)

Specimens examined: The Netherlands, from Hedera helix, deposited in CBS Jun. 1991, J. de Gruyter, CBS 367.91 = PD 87/229.

Boeremia lilacis (Sacc.) Q. Chen & L. Cai, comb. et stat. nov. MycoBank MB814751.

Basionym: Phoma herbarum f. lilacis Sacc., Michelia 2: 93. 1880. ≡ Phoma exigua var. lilacis (Sacc.) Boerema, Phytopathol. Medit. 18: 105. 1980.

≡ *Boeremia exigua* var. *lilacis* (Sacc.) Aveskamp *et al.*, Stud. Mycol. 65: 38. 2010.

Specimen examined: **The Netherlands**, Baarn, from leaf spots of *Philadelphus* sp., Nov. 1967, H.A. van der Aa, CBS H-9070, culture CBS 588.67; Wageningen, from a twig of *Syringa vulgaris*, deposited in CBS Aug. 1979, G.H. Boerema, CBS H-163131, culture CBS 569.79 = PD 72/741 = CECT 20050 = IMI 331909.

Notes: This taxon was elevated to species level based on the multilocus phylogeny of the *Boeremia exigua* varieties (Berner *et al.* 2015). A single isolate deposited as "Ascochyta philadelphi" was re-identified as *B. lilacis* in this study. The name *As. philadelphi* might need to be synonymised, but since the type was not obtained for comparison, this awaits confirmation in future study.

Boeremia lycopersici (Cooke) Aveskamp *et al.*, Stud. Mycol. 65: 40. 2010.

Basionym: Phoma lycopersici Cooke, Grevelia 13: 94. 1885. = Didymella lycopersici Kleb., Z. Pflanzenkrankh. 31: 9. 1921.

Specimen examined: The Netherlands, Heerde, from fruit of Lycopersicon escu-

lentum, deposited in CBS Aug. 1967, G.H. Boerema, CBS 378.67 = PD 67/276.

Boeremia noackiana (Allesch.) Aveskamp *et al.*, Stud. Mycol. 65: 40, 2010. Fig. 9.

Basionym: Phyllosticta noackiana Allesch., Bol. Técn. Inst. Agron. Estado São Paulo 9: 85. 1898.

≡ *Phoma exigua* var. *noackiana* (Allesch.) Aa, Boerema & Gruyter, Persoonia 17: 450. 2000.

Description from ex-epitype culture (CBS 101203): Conidiomata pycnidial, solitary or confluent, globose to subglobose, covered with hyphal outgrowths, semi-immersed or immersed, $130-315(-345) \times 110-265(-310) \mu m$. Ostioles 1–2, slightly papillate or non-papillate. *Pycnidial wall* pseudoparenchymatous 3–5-layered, 6–12 µm thick, composed of oblong to isodiametric cells, outer cell layer brown. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to flask-shaped, 3–5 × 2–3.5 µm. Conidia ellipsoidal to oblong, sometimes allantoid, hyaline, thinwalled, smooth, mainly aseptate, 4.5–8.5 × 2–3 µm, but occasionally 1-septate, 8–13 × 3.5–5 µm, with small guttules. Conidial matrix yellowish.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular, covered by white, wooly aerial mycelia, olivaceous to iron grey, with dendritic leaden-black zones; reverse buff to olivaceous, with some leaden-black zones. Colonies on MEA 25–30 mm diam after 7 d, margin regular, white

aerial mycelium sparse, olivaceous to greenish olivaceous; reverse concolourous. Colonies on PDA, 25–30 mm diam after 7 d, margin regular, felty, pale olivaceous, white near the margin; reverse olivaceous, white near the margin. NaOH spot test: a brown discolouration on MEA.

Specimens examined: **Brazil**, Brasilien, Campinas, from *Phaseolus* sp., Mar. 1897, F. Noack (holotype F52544). **Colombia**, from *Phaseolus vulgaris*, deposited in CBS Sep. 1998, J. de Gruyter (epitype designated here HMAS 246697, MBT202496, culture ex-epitype CBS 101203 = PD 79/1114). **Guatemala**, from *Phaseolus vulgaris*, deposited in CBS Jan. 1998, IPO Wageningen, CBS 100353 = PD 87/718.

Notes: Boeremia noackiana was formerly treated as a variety of *Phoma exigua* (van der Aa *et al.* 2000), but in our analysis it appears to be genetically distinct from the *Phoma exigua* complex, which is in congruence with the results of Aveskamp *et al.* (2010), who elevated it to species level. The type specimen of *Phyllosticta noackiana* is preserved in B, and conidia of this species were described as oblong, $4-6 \times 2 \mu m$ (Saccardo 1902). The morphological characters of HMAS 246697 agree well with those of the representative culture of this species reported by van der Aa *et al.* (2000). Here we designate HMAS 246697 as its epitype because it agrees well with the original description with regard to morphology, host and locality.

Boeremia sambuci-nigrae (Sacc.) Aveskamp *et al.*, Stud. Mycol. 65: 40. 2010.

Basionym: Phoma herbarum f. sambuci-nigrae Sacc., Syll. Fung. 3: 133. 1884.

≡ Phoma exigua var. sambuci-nigrae (Sacc.) Boerema & Höweler, Persoonia 5: 26. 1967.

≡ *Phoma sambuci-nigrae* (Sacc.) E. Monte, Bridge & B. Sutton, Mycopathologia 115: 102. 1991.

Specimen examined: **The Netherlands**, Wageningen, from a leaf of Sambucus nigra, deposited in CBS Sep. 1968 (**lectotype** CBS H-16314, culture ex-lectotype CBS 629.68 = CECT 20048 = IMI 331913 = PD 67/753).

Boeremia strasseri (Moesz) Aveskamp *et al.*, Stud. Mycol. 65: 40. 2010. Fig. 10.

Basionym: Phoma strasseri Moesz, Bot. Közlem. 22: 45. 1924.

Description from ex-neotype culture (CBS 126.93): Conidiomata pycnidial, solitary or confluent, globose to subglobose, glabrous or covered with hyphae, semi-immersed or immersed, (145-) 175–330(–355) × 125–320 µm. Ostioles 1–3, slightly papillate or non-papillate. *Pycnidial wall* pseudoparenchymatous, composed of oblong to isodiametric cells, 5–7 layers, 15–30 µm thick. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to doliiform, 4–7 × (2.5–)3.5–5.5 µm. *Conidia* ellipsoidal to cylindrical, hyaline, thin-walled, smooth, aseptate, 4–7 × 2–3 µm, with 2–4 polar guttules. *Conidial matrix* whitish.

Culture characteristics: Colonies on OA, 60–65 mm diam after 7 d, margin regular, felty, pale grey olivaceous; reverse olivaceous near the margin, towards the centre of colony becoming buff, pale olivaceous to olivaceous. Colonies on MEA 65–70 mm diam after 7 d, margin regular, aerial mycelium sparse, greenish olivaceous; reverse concolourous. Colonies on PDA, 70–75 mm diam after 7 d, margin regular, floccose, white; reverse olivaceous with buff tinge in some sections. NaOH spot test: a brown discolouration on MEA.

[≡] *Phoma hedericola* (Durieu & Mont.) Boerema, Trans. Brit. Mycol. Soc. 67: 295. 1976.



Fig. 9. Boeremia noackiana (CBS 101203). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Colonies sporulating on OA.H. Pycnidium. I. Conidia. Scale bars: G = 200 µm; H = 50 µm; I = 10 µm.

Specimen examined: **The Netherlands**, Arnhem, from a stem of *Mentha* sp., deposited in CBS Jan 1993, J, de Gruyter (**neotype designated here** HMAS 246698, MBT202497, culture ex-neotype CBS 126.93 = PD 73/642).

Notes: This species was initially described as Phoma menthae Strasser. However, this name was illegitimate and thus replaced by a new name, Phoma strasseri (Moesz 1925). The type specimen of this species could not be located, and is considered lost. The holotype was on Mentha silvestris collected from Austria, with conidia measuring 4-5 × 3-3.5 µm (Moesz 1925). Strain CBS 126.93 was also from *Mentha* sp., with conidia measuring $4-7 \times 2-3 \mu m$, which is in general agreement with the original description. Hence the specimen HMAS 246698 (ex CBS 126.93) is designated as neotype.

This species is phylogenetically and morphological similar to *B. crinicola*, but *B. strasseri* is only known from *Amaryllidaceae* (de Gruyter *et al.* 1993), while *B. crinicola* is mainly known from *Mentha* spp. or occasionally from other species also belonging to *Labiatae* (de Gruyter *et al.* 2002).

Boeremia telephii (Vestergr.) Aveskamp *et al.*, Stud. Mycol. 65: 40. 2010.

Basionym: Ascochyta telephii Vestergr., Öfvers. Finska Vetensk.-Soc. Förh. 54: 41, 1897.

≡ Phoma telephii (Vestergr.) Kesteren, Netherlands J. Pl. Pathol. 78: 117. 1972.

Specimens examined: **The Netherlands**, Utrecht, from a stem of Sedum telephium, deposited in CBS Sep. 1973, G.H. Boerema, CBS 760.73 = PD 71/1616; from Sedum spectabile, deposited in CBS Jan. 2001, H. de Gruyter, CBS 109175 = PD 79/524.

Clade 5: Epicoccum

Epicoccum Link, Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 7: 32. 1815, *emend.* Q. Chen & L. Cai.

Conidiomata pycnidial, globose to subglobose, or to irregularly shaped, superficial on or immersed into the agar, solitary or confluent. Ostioles papillate or non-papillate, sometimes on pronounced necks. Pycnidial wall pseudoparenchymatous, 2-9layered, outer wall brown olivaceous. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, globose to flask-shaped. Conidia variable in shape and size, hvaline or in later stages a slight brownish pigmentation may be found, smooth- and thin-walled, *i.e.* ovoid, ellipsoidal to oblong, (sub-)cylindrical, sometimes slightly curved, always aseptate. Synasexual morph: Sporodochia semiimmersed, scattered or aggregated, clavate. Conidia multicellular-phragmosporous, but septa being obscured by the dark verrucose wall, subglobose-pyriform, often with a basal cell, variable in dimensions, arising in gradually growing clusters as solitary, terminal elements of mycelial branches, from a more or less globose pseudoparenchymatous stroma. Chlamydospores variable and irregular, unicellular or multicellular, intercalary or terminal, solitary or in chains, smooth, verrucose or incidentally tuberculate, subhvaline to dark brown, where multicellular globose or irregular shaped, dictyosporous or botryoid (Punithalingam et al. 1972, Boerema et al. 2004, Aveskamp et al. 2010).

Type species: Epicoccum nigrum Link, Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 7: 32. 1815.



Fig. 10. Boeremia strasseri (CBS 126.93). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia producing on OA. H. Section of pycnidial wall. I. Conidia. Scale bars: G = 100 µm; H–I = 10 µm.

Notes: Based on our phylogenetic results, five *Phoma* species were recombined into the genus *Epicoccum*. The generic circumscription of *Epicoccum* is therefore emended to incorporate the morphological features of epicoccoid conidia and these newly added species, such as irregular pycnidial conidiomata and subcylindrical shaped conidia.

Epicoccum brasiliense (Aveskamp *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814079.

Basionym: Phoma brasiliensis Aveskamp *et al.*, Stud. Mycol. 65: 35. 2010.

Description and illustrations (Aveskamp et al. 2010).

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

Epicoccum draconis (Berk. ex Cooke) Q. Chen & L. Cai, comb. nov. MycoBank MB814080.

Basionym: Phyllosticta draconis Berk. ex Cooke, Grevillea 19: 8. 1890.

≡ Phoma draconis (Berk. ex Cooke) Boerema, Jaarb. Plziektenk. Dienst Wageningen 159: 24. 1982.

Description (de Gruyter et al. 1998).

Specimen examined: Rwanda, from a leaf of *Dracaena* sp., deposited in CBS Feb. 1983, G.H. Boerema, CBS H-16207, culture CBS 186.83 = PD 82/47.

Notes: In the original description of *Phyllosticta draconis*, the ellipsoidal conidia are cited as $7 \times 3 \mu m$ (Cooke 1890). However, de Gruyter *et al.* (1998) described a representative culture of *Phoma draconis* (CBS 186.83), whose conidia measure $4-8.5 \times 2-4 \mu m$, which agrees with the holotype. CBS 186.83 clustered in the *Epicoccum* clade in Fig. 1, and thus we treat this taxon as a new combination in the genus *Epicoccum*, *E. draconis*.

Epicoccum henningsii (Sacc.) Q. Chen & L. Cai, comb. nov. MycoBank MB814081.

Basionym: Phoma henningsii Sacc., Syll. Fung. 10: 139. 1892. Description (de Gruyter *et al.* 1993).

Specimen examined: Kenya, Maguga, from the bark of Acacia mearnsii, deposited in CBS Jan 1980, G.H. Boerema, CBS H-16354, culture CBS 104.80 = PD 74/1017.

Notes: "Phoma acacia Henn." was the first name of this species, which was illegitimate and therefore replaced by Phoma henningsii Sacc., with conidia measuring $3.5-5 \times 2 \mu m$ (Saccardo 1892). Herein a new combination in *Epicoccum* is proposed for this species.

Epicoccum huancayense (Turkenst.) Q. Chen & L. Cai, comb. nov. MycoBank MB814082.

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

Description (de Gruyter et al. 1998).

Specimen examined: **Peru**, Dep. Junin, Huancayo, near Vallis Mantaro, from a stem of *Solanum* sp., Feb. 1974, L.J. Turkensteen (**isotype** CBS H-7609, culture ex-isotype CBS 105.80 = PD 75/908).

Epicoccum nigrum Link, Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 7: 32. 1815.

= *Phoma epicoccina* Punith., Tulloch & Leach, Trans. Brit. Mycol. Soc. 59: 341. 1972.

Specimens examined: **The Netherlands**, Geleen, from human toenail, deposited in CBS Dec. 1981, CBS 125.82 = IMI 331914 = CECT 20044. **USA**, Oregon, from seeds of *Dactylis glomerata*, deposited in CBS Jan 1973, M. Tulloch (**holotype** of *Phoma epicoccina* IMI 164070, culture ex-holotype CBS 173.73 = ATCC 24428 = IMI 164070).
Notes: Sequences of the two isolates studied here were identical in LSU, ITS and *tub2* (Aveskamp *et al.* 2010), but have 22 bp differences in *rpb2*, which is responsible for their distance in the phylogenetic tree. Since CBS 173.73 is the ex-type culture, further study is required to confirm if CBS 125.82 represents the same or a different species.

Epicoccum pimprinum (P.N. Mathur *et al.*) Aveskamp *et al.*, Stud. Mycol. 65: 35. 2010.

Basionym: Phoma pimprina P.N. Mathur *et al.*, Sydowia 13: 146. 1959.

Specimens examined: India, Poona, Pimpri, from soil, deposited in CBS Jun. 1960, M.J. Thirumalachar (culture **ex-isotype** CBS 246.60 = ATCC 22237 = ATCC 16652 = IMI 81601); from soil, 1977, PD 77/1028.

Notes: Isolate PD 77/1028 differs from the ex-type culture CBS 246.60 in one bp and 10 bp differences in LSU and *tub2* respectively. Since the sequencing of the *rpb2* locus of CBS 246.60 was unsuccessful, it can not be compared in the present study. If PD 77/1028 represents a different species remains to be confirmed.

Epicoccum plurivorum (P.R. Johnst.) Q. Chen & L. Cai, comb. nov. MycoBank MB814083.

Basionym: Phoma plurivora P.R. Johnst., New Zealand J. Bot. 19: 181. 1981.

Description (de Gruyter et al. 1998).

Specimen examined: New Zealand, Auckland, Mt Albert, from a leaf of Setaria *sp.*, Feb. 1979, P.R. Johnston (holotype PDD 40397, CBS H-7624, culture exisotype CBS 558.81 = PDDCC 6873).

Epicoccum sorghinum (Sacc.) Aveskamp *et al.*, Stud. Mycol. 65: 36. 2010.

Basionym: Phyllosticta sorghina Sacc., Michelia 1: 140. 1878. ≡ Phoma sorghina (Sacc.) Boerema *et al.*, Persoonia 7: 134. 1973.

Specimens examined: France, Antibes, from a twig of *Citrus* sp., deposited in CBS Sep. 1968, CBS 627.68 = PD 66/926. **Puerto Rico**, Mayaguez, from *Sorghum vulgare*, deposited in CBS Apr. 1980, G.H. Boerema, CBS 179.80 = PD 76/1018.

Clade 6: Didymella

Didymella Sacc. ex Sacc., Syll. Fung. 1: 545. 1882. emend. Q. Chen & L. Cai.

= Peyronellaea Goid. ex Togliani, Ann. Sperim. Agrar. II 6: 93. 1952.

Conidiomata pycnidial, subglobose to ellipsoidal, becoming irregular, superficial on or immersed into the agar, solitary or confluent, ostiolate or poroid, sometimes with elongated necks. Micropycnidia occur in some species. *Pycnidial wall* pseudoparenchymatous, 2–8-layered, with a pigmented outer wall. *Conidiogenous cells* phialidic, hyaline, smooth, flask-shaped, ampulliform or doliiform. *Conidia* generally aseptate, variable in shape, smoothand thin-walled, *i.e.* ellipsoidal to subglobose, cylindrical, oblong, ovoid, sometimes allantoid, hyaline, but in older cultures conidia may become pigmented, larger or septated conidia may occur in at least one species, mostly guttulate. *Unicellular chlamydospores* often abundantly formed in and on the agar and in the aerial mycelium, globose, intercalary, brown or (pale) olivaceous pigmented. *Multicellular chlamydospores* mainly alternarioid, terminal

or intercalary, often in chains, brown or (pale) olivaceous . Ascomata pseudothecial, immersed or erumpent, (sub-)globose to flattened, solitary or confluent, ostiolate, 2–5(–8)-layered, composed of pseudoparenchymatous cells. Asci cylindrical to clavate or saccate, 8-spored, bitunicate, arising from a broad hymenium among pseudoparaphyses. Ascospores mostly hyaline or brownish, ellipsoidal to cymbiform, uniseptate, symmetrical or asymmetrical, constricted at the septum, or multiseptate (de Gruyter et al. 2009, Aveskamp et al. 2010, Zhang et al. 2012).

Type species: Didymella exigua (Niessl) Sacc., Michelia 2: 58. 1880.

Notes: The genus *Didymella* was emended to accommodate the genus *Peyronellaea* and several other associated phoma-like species that clustered together with type species of *Didymella*, *i.e. D. exigua*. Most species in this genus produced chlamydo-spores in culture.

Didymella acetosellae (A.L. Sm. & Ramsb.) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814089.

Basionym: Phyllosticta acetosellae A.L. Sm. & Ramsb., Trans. Brit. Mycol. Soc. 4: 173. 1913.

≡ Phoma acetosellae (A.L. Sm. & Ramsb.) Aa & Boerema, Persoonia 18: 16. 2002.

Description (de Gruyter et al. 2002).

Specimen examined: The Netherlands, Baarn, from a stem of Rumex hydrolapathum, Mar. 1996, H.A. van der Aa, CBS 179.97.

Didymella aliena (Fr.) Q. Chen & L. Cai, comb. nov. MycoBank MB814090.

Basionym: Sphaeria aliena Fr., Syst. Mycol. 2: 502. 1823. ≡ Phoma aliena (Fr.) Aa & Boerema, Persoonia 16: 486. 1998. Description (de Gruyter *et al.* 1998).

Specimens examined: France, Vosges, from branches of *Euonymus europeus*, B.D. Mougeot (neotype PAD Roum. F. gallici exs. 765). The Netherlands, from a twig of *Berberis* sp., deposited in CBS Jul. 1993, J. de Gruyter, CBS 379.93 = PD 82/945.

Didymella americana (Morgan-Jones & J.F. White) Q. Chen & L. Cai, comb. nov. MycoBank MB814091.

Basionym: Phoma americana Morgan-Jones & J.F. White, Mycotaxon 16: 406. 1983.

≡ Peyronellaea americana (Morgan-Jones & J.F. White) Aveskamp et al., Stud. Mycol. 65: 31. 2010.

Description (Boerema 1993).

Specimens examined: **USA**, Arkansas, from pod lesions of *Glycine max*, 1981, H.J. Walters, CBS 568.97 = ATCC 44494 = PD 94/1544; Georgia, from *Zea mays*, deposited in CBS Mar. 1985, G.H. Boerema, CBS H-16144, culture CBS 185.85 = PD 80/1191.

Notes: The holotype of *Phoma americana* is from leaves of *Triticum aestivum* collected by A.K. Hagan in the USA. Strains described by Boerema (1993) are morphologically similar to the original description, and our sequence data revealed that this species belongs to the genus *Didymella*.

Didymella anserina (Marchal) Q. Chen & L. Cai, comb. nov. MvcoBank MB814092.

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



Fig. 11. Nothophoma anigozanthi (N 3622). A. Type collection packet. B. Ascomata on host substrate. C. Asci. D. Section of ascomata. E. Ascospores. Scale bar: C-E = 10 µm.

≡ *Peyronellaea anserina* (Marchal) Aveskamp *et al.*, Stud. Mycol. 65: 31. 2010.

= Phoma radicis-callunae R.W. Rayner, Bot. Gaz. 73: 231. 1922.

= *Phoma suecica* J.F.H. Beyma, Antonie van Leeuwenhoek 8: 110. 1942. Description (de Gruyter & Noordeloos 1992).

Specimens examined: Germany, Giessen, Dec. 1979, R. Hadlok, CBS H-16562, culture CBS 253.80; former West-Germany, from plastic, deposited in CBS Dec. 1965, H. Kühlwein, CBS 397.65. **The Netherlands**, Ter Apel, from potato flour, 1983, CBS 360.84. **UK**, from *Calluna* sp., deposited in CBS Nov. 1929, R.W. Rayner (culture **ex-holotype** of "*Phoma radicis-callunae*" CBS 285.29).

Notes: This species was treated as new combination (*Peyronellaea anserina*) by Aveskamp *et al.* (2010), and here we recombine it into *Didymella*, as *D. anserina*. *Phoma radicis-callunae* was initially isolated from *Calluna* as endophyte (Rayner 1922), and reduced to synonymy of *P. anserina* (Boerema *et al.* 2004). Isolate CBS 397.65 was initially identified as *P. suecica*, which is also a synonym of *P. anserina*.

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

Basionym: Mycosphaerella arachidicola Khokhr., Bolezni i vrediteli maslichnykh kul'tur 1: 29. 1934.

≡ Peyronellaea arachidicola (Khokhr.) Aveskamp et al., Stud. Mycol. 65: 31. 2010.

= *Phoma arachidicola* Marasas, Pauer & Boerema, Phytophylactica 6: 200. 1974.

Specimens examined: **South Africa**, Cape Province, Jan Kempdorp, Vaalharts Research Station, from a leaf of *Arachis hypogaea*, deposited in CBS May 1975, W.F.O. Marasas (**isotype** of *Phoma arachidicola* CBS H-7601, culture ex-isotype CBS 333.75 = ATCC 28333 = IMI 386092).

Notes: The sexual morph of *Didymella arachidicola* was originally described as *Mycosphaerella arachidicola* (Khokhriakov 1934), and later transferred to *Didymella* (Tomilin 1979) and *Peyronellaea* (Aveskamp *et al.* 2010). Here we reinstate the *Didymella* name based on its phylogenetic affinity.

Didymella aurea (Gruyter *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814093.

Basionym: Phoma aurea Gruyter et al., Persoonia 15: 394. 1993. ≡ Peyronellaea aurea (Gruyter et al.) Aveskamp et al., Stud. Mycol. 65: 31. 2010.

Description (de Gruyter et al. 1993).

Specimen examined: New Zealand, Auckland, from a stem of *Medicago polymorpha*, deposited in CBS Jan 1993, J. de Gruyter (holotype L 992.177.422, culture ex-holotype CBS 269.93 = PD 78/1087).

Didymella bellidis (Neerg.) Q. Chen & L. Cai, comb. nov. MycoBank MB814094.

Basionym: Phoma bellidis Neerg., Friesia 4: 74. 1950. Description (de Gruyter *et al.* 1993).

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

Notes: The type of *Phoma bellidis* is on *Bellis perennis* collected from Denmark. Conidia from the ex-type strain measure $4.5-6 \times 1.5-3 \mu m$, which is in agreement with that of CBS 714.85 as described by de Gruyter *et al.* (4–6.5 × 2–2.5 μm ; 1993). Hence, we introduce a new combination for this species as *Didymella bellidis*.

Didymella boeremae (Gruyter) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814095.

Basionym: Phoma boeremae Gruyter, Persoonia 18: 91. 2002. Description (de Gruyter *et al.* 2002).

Specimen examined: Australia, Victoria, Burnley Gardens, from seed of *Medicago littoralis* cv. Harbinger, deposited in CBS Jan. 2002, H. de Gruyter (**neotype** L 996.294.536, culture ex-neotype CBS 109942 = PD 84/402).

Didymella calidophila (Aveskamp *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814096.

Basionym: Phoma calidophila Aveskamp *et al.*, Mycologia 101: 368. 2009.



Fig. 12. Nothophoma anigozanthi (CBS 381.91). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H–I. Pycnidia. J. Section of pycnidial wall. K–L. Conidiogenous cells. M. Conidia. Scale bars: G = 200 μm; H = 40 μm; I = 20 μm; J, M = 10 μm; K–L = 5 μm.

Description (Boerema 1993).

Specimens examined: Egypt, from desert soil, deposited in CBS Jun. 1983, M.I.A. Abdel-Kader (neotype CBS H-20168, culture ex-neotype CBS 448.83). The Netherlands, Wageningen, from seeds of Cucumis sativus, RPVZ, PD 84/ 109.

Didymella chenopodii (P. Karst. & Har.) Q. Chen & L. Cai, comb. nov. MycoBank MB814097.

Basionym: Gloeosporium chenopodii P. Karst. & Har., J. Bot., Paris 3: 207. 1889.

≡ Phoma chenopodiicola Gruyter *et al.*, Persoonia 15: 395. 1993. Description (de Gruyter *et al.* 1993).

Specimen examined: Peru, from a stem of Chenopodium quinoa cv. Sajana, deposited in CBS Jan 1993, J, de Gruyter, CBS 128.93 = PD 79/140.

Notes: This species was initially described as Gloeosporium chenopodii, and later replaced by a nomen novum, Phoma

chenopodiicola (de Gruyter *et al.* 1993). Here a new combination is proposed for this species as *Didymella chenopodii*. The type specimen was collected from *Chenopodium album* in France, and is preserved in PC.

Didymella coffeae-arabicae (Aveskamp *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814098.

Basionym: Phoma coffeae-arabicae Aveskamp et al., Mycologia 101: 371. 2009.

≡ Peyronellaea coffeae-arabicae (Aveskamp et al.) Aveskamp et al., Stud. Mycol. 65: 32. 2010.

Description (Aveskamp et al. 2009a).

Specimen examined: Ethiopia, from Coffea arabica, 1984, M.M.J. Dorenbosch (holotype CBS H-20143, culture ex-holotype CBS 123380 = PD 84/1013).

Didymella curtisii (Berk.) Q. Chen & L. Cai, comb. nov. MycoBank MB814099.

Basionym: Hendersonia curtisii Berk., Nuovo Giorn. Bot. Ital. 10: 19. 1878.

- ≡ Stagonosporopsis curtisii (Berk.) Boerema, Verslagen Meded. Plantenziektenk. Dienst Wageningen 157: 20. 1981.
- ≡ *Peyronellaea curtisii* (Berk.) Aveskamp *et al.*, Stud. Mycol. 65: 32. 2010.
- = Phyllosticta narcissi Aderh., Centralbl. Bakteriol., 2 Abth. 6: 632. 1900.

≡ Phoma narcissi (Aderh.) Boerema *et al.*, Persoonia 15: 215. 1993. Description (Boerema 1993).

Specimens examined: **The Netherlands**, from *Nerine* sp., deposited in CBS May 1992, J. de Gruyter, culture CBS 251.92 = PD 86/1145; from *Sprekelia* sp., PD 92/1460.

Notes: This species was recombined into *Peyronellaea* by Aveskamp *et al.* (2010) as *Peyronellaea curtisii*, and herein we treat it as a new combination in *Didymella*. The two isolates have two and five bp differences in ITS and *tub2* respectively, and thus may not be conspecific. Since the type material was not obtained, its taxonomy awaits future study.

Didymella dactylidis (Aveskamp *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814100.

Basionym: Phoma dactylidis Aveskamp et al., Stud. Mycol. 65: 48. 2010.

Description and illustration (Aveskamp et al. 2010).

Specimen examined: USA, Oregon, on Dactylis glomerata, 1973 (holotype CBS H-20237, culture ex-holotype CBS 124513 = PD 73/1414).

Didymella dimorpha (Aveskamp *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814101.

Basionym: Phoma dimorpha Aveskamp *et al.*, Stud. Mycol. 65: 29. 2010.

Description and illustration (Aveskamp et al. 2010).

Specimen examined: **Spain**, Canary Isles, Gran Canaria, from phyllocladium of *Opuntia* sp., Oct. 1979, J.A. von Arx (**holotype** CBS H-20234, culture exholotype CBS 346.82).

Didymella eucalyptica (Sacc.) Q. Chen & L. Cai, comb. nov. MycoBank MB814103.

Basionym: Phoma eucalyptica Sacc., Syll. Fung. 3: 78. 1884. ≡ Peyronellaea eucalyptica (Sacc.) Aveskamp et al., Stud. Mycol. 65: 32. 2010.

Description (de Gruyter & Noordeloos 1992).

Specimen examined: Australia, Western Australia, from a leaf of *Eucalyptus* sp., deposited in CBS Jun. 1991, CBS 377.91 = PD 79/210.

Notes: Phoma eucalyptica was recombined into *Peyronellaea* by Aveskamp *et al.* (2010), as *Pe. curtisii*, and we here introduce the new combination *Didymella eucalyptica* for this species based on its phylogenetic relationship.

Didymella exigua (Niessl) Sacc., Michelia 2: 57. 1880. Fig. 13.

Basionym: Didymosphaeria exigua Niessl, Oesterr. bot. Z. 25: 165. 1875.

≡ Cercidospora exigua (Niessl) Kuntze, Revis. gen. pl. 3: 454. 1898.

Description from ex-neotype culture (CBS 183.55): Ascomata subepidermal in the cortex of stems or in bracts of dead inflorescences, erumpent, subglobose to flattened, small, up to

170 µm diam, papillate; wall 10–15 µm thick, outer wall consisting of 2–3 layers of cells of *textura angularis*. *Pseudoparaphyses* hyaline, 1.5–2.5 µm diam, septate. *Asci* bitunicate, clavate to short cylindrical, 45–70 × 10–12 µm. *Ascospores* uni- to biseriate, ellipsoidal, straight to slightly curved, 12–16 × 4.5–6 µm, hyaline, smooth, apex obtuse, base broadly obtuse to subobtuse, medianly 1-septate, upper cell often wider than lower cell, slightly constricted at the septum.

Specimen examined: France, Menise sur Tholon, from Rumex arifolius, deposited in CBS May 1955, E. Müller (neotype CBS H-20123, culture exnectype CBS 183.55).

Note: Conidiomata *in vivo* and *in vitro* resemble ascomata in size, and give rise to conidia that are short cylindrical to bacilliform, 0(-1)-septate, hyaline, $9-13 \times 4-6 \mu m$ (Corbaz 1957).

Didymella gardeniae (S. Chandra & Tandon) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814104.

Basionym: Pyrenochaeta gardeniae S. Chandra & Tandon, Mycopathol. Mycol. Appl. 29: 274. 1966.

≡ *Phoma gardeniae* (S. Chandra & Tandon) Boerema, Verslagen Meded. Plantenziektenk. Dienst Wageningen 156: 27. 1980.

≡ *Peyronellaea gardeniae* (S. Chandra & Tandon) Aveskamp *et al.*, Stud. Mycol. 65: 32. 2010.

Description (de Gruyter & Boerema 2002).

Specimen examined: India, Allahabad, from the leaf of Gardenia jasminoides, deposited in CBS Sep. 1968, S. Chandra & R.N. Tandon (isotype CBS H-7605, culture ex-isotype CBS 626.68 = IMI 108771).

Didymella glomerata (Corda) Q. Chen & L. Cai, comb. nov. MycoBank MB814105.

Basionym: Coniothyrium glomeratum Corda, Icon. Fung. (Praque) 4: 39. 1840.

≡ *Phoma glomerata* (Corda) Wollenw. & Hochapfel, Z. Parasitenk. 3: 592. 1936.

≡ *Peyronellaea glomerata* (Corda) Goid. ex Togliani, Ann. Sperim. Agrar. III 6: 93. 1952.

Description (Boerema 1993).

Specimens examined: Romania, Bucuresti, from fresco in church, Nov. 1971, I. Ionita, CBS H-16340, culture CBS 133.72. The Netherlands, from *Chrysan-themum* sp., deposited in CBS Sep. 1963, CBS 528.66 = PD 63/590.

Didymella heteroderae (Chen *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814106.

Basionym: Phoma heteroderae Sen Y. Chen *et al.*, Mycologia 88: 885. 1996 (1997).

≡ *Peyronellaea heteroderae* (Sen Y. Chen *et al.*) Crous, Persoonia 32: 223. 2014.

= Phoma pomorum var. *calorpreferens* Boerema *et al.*, Persoonia 15: 207. 1993.

≡ *Phoma calorpreferens* (Boerema *et al.*) Aveskamp *et al.*, Mycologia 101: 370. 2009.

≡ Peyronellaea calorpreferens (Boerema *et al.*) Aveskamp *et al.*, Stud. Mycol. 65: 31. 2010.

Description (Boerema 1993).

Specimen examined: The Netherlands, from undefined food material, 1973, G.H. Boerema (holotype L 990.290.418, culture ex-holotype CBS 109.92 = PD 73/1405).

Notes: This species was treated as *Peyronellaea calorpreferens* (Aveskamp *et al.* 2010), which was later considered as a *nom. illeg.*, and then a new combination was introduced as *Pe. heteroderae*, citing the basionym as *Phoma heteroderae* (Crous *et al.* 2014).



Fig. 13. Didymella exigua (CBS 183.55). A. Ascomata on host. B. Surface view of ascoma. C–G. Asci with ascospores (arrow denotes pseudoparaphyse). H. Hyaline 1-septate ascospores. Scale bars: B–H = 10 µm.

Didymella lethalis (R. Stone) Sivan., Bitunicate Ascomycetes and their Anamorphs: 424. 1984.

Basionym: Mycosphaerella lethalis R. Stone, Ann. Mycol. 10: 587. 1912.

 = Ascochyta lethalis Ellis & Barthol., Fungi Columb. 1808. 1903.
 ≡ Peyronellaea lethalis (Ellis & Barthol.) Aveskamp, Gruyter & Verkley, Stud. Mycol. 65: 32. 2010.

Specimen examined: Unknown origin, from unknown substrate, deposited in CBS Sep. 1925, A.W. Archer, CBS 103.25.

Notes: Sivanesan (1984) published the link between *Ascochyta lethalis* and *Didymella lethalis*. However, this connection requires molecular verification. The phylogenetic data indicated that *Didymella lethalis* (CBS 103.25) is closely related to *D. pinodes* (CBS 525.77), but they differ in seven bp in four sequenced loci. Here we tentatively retain them as two distinct species. Clarification of the relationship between the two species awaits the examination of the type specimen of *Didymella lethalis*.

Didymella longicolla (Aveskamp *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814107.

Basionym: Phoma longicolla Aveskamp *et al.*, Stud. Mycol. 65: 49. 2010.

Description and illustration (Aveskamp et al. 2010).

Specimen examined: Spain, Canary Isles, from *Opuntia* sp., J. de Gruyter (holotype CBS H-20238, culture ex-holotype CBS 124514 = PD 80/1189).

Didymella macrostoma (Mont.) Q. Chen & L. Cai, comb. et stat. nov. MycoBank MB814108.

Basionym: Phoma macrostoma var. macrostoma Mont., Ann. Sci. Nat. Bot. III 11: 52. 1849.

= Polyopeus purpureus var. incoloratus A.S. Horne, J. Bot. 58: 240. 1920. ≡ Phoma macrostoma var. incolorata (A.S. Horne) Boerema & Dorenb., Persoonia 6: 55. 1970. (as "macrostomum var. incolorata")

Description (de Gruyter et al. 2002).

Specimens examined: Germany, near München, from the bark of Larix decidua, deposited in CBS Jun. 1995, L. Pehl, CBS 482.95. Switzerland, Vierwaldstättersee, near Brunnen, from a leaf of Acer pseudoplatanus, Oct. 1968, J. Gemmen, CBS H-16477, culture CBS 223.69. The Netherlands, Wageningen, from wood of Malus sylvestris, deposited in CBS Sep. 1969, G.H. Boerema, CBS H-16431, culture CBS 529.66 = PD 66/521. Unknown origin, from seed of Pinus nigra var. astriaca, deposited in CBS Aug. 1938, J.G. ten Houten, CBS 247.38.

Notes: The representative isolate of *Phoma macrostoma* var. *incolorata* (CBS 223.69) was genetically identical, and ecologically and morphologically highly similar to the representative isolates of *P. macrostoma* var. *macrostoma* (CBS 482.95, CBS 529.66). *Phoma macrostoma* var. *incolorata* only differs from the type variety in lacking hyphal pigmentation and having a negative reaction in NaOH (de Gruyter *et al.* 2002), which may be related to the production of cholesterol (Rajak & Rai 1983). Since these characteristics may vary under different incubation conditions and on different media for cultivation, we concluded that these two varieties should be combined to *Didymella mascrostoma*. Isolate CBS 247.38, which was received as *Phoma libertiana*, grouped with *D. macrostoma* in the same well-supported clade with identical sequences in all four loci, and we therefore reidentify it as *D. macrostoma*.

Didymella maydis (Arny & R.R. Nelson) Q. Chen & L. Cai, comb. nov. MycoBank MB814109.

Basionym: Phyllosticta maydis Arny & R.R. Nelson, Phytopathology 61: 1171. 1971.

- = Phoma zeae-maydis Punith., Mycopathologia 112: 50. 1990. (nom. nov. for Phyllosticta maydis in Phoma)
- ≡ *Peyronellaea maydis* (Arny & R.R. Nelson) Crous, Persoonia 32: 223. 2014.
- = *Mycosphaerella zeae-maydis* Mukunya & Boothr., Phytopathology 63: 530. 1973.

≡ *Didymella zeae-maydis* (Mukunya & Boothr.) Arx, Beih. Nova Hedwigia 87: 288. 1987.

≡ *Peyronellaea zeae-maydis* (Mukunya & Boothr.) Aveskamp *et al.,* Stud. Mycol. 65: 33. 2010.

Description (de Gruyter 2002).

Specimens examined: **USA**, New York, Aurora, Cornell University, from dead Zea mays, Apr. 1972, D.M. Mukuya & C.W. Boothroyd (**holotype** of *Mycosphaerella* zeae-maydis CUP 52727); Wisconsin, Hancock, from Zea mays, Aug. 1970, D.C. Arny, culture ex-holotype of "*Phyllosticta maydis*" CBS 588.69.

Notes: Mukunya & Boothroyd (1973) established the sexual and asexual connection between *Mycosphaerella zeae-maydis* and *Phyllosticta maydis*. This species was recombined into *Peyronellaea* as *Pe. zeae-maydis* by Aveskamp *et al.* (2010), and later this treatment was corrected as a new combination *Pe. maydis* (Crous *et al.* 2014). Here we treat it based on the asexual morph and introduce a new combination, *Didymella maydis*.

Didymella microchlamydospora (Aveskamp & Verkley) Q. Chen & L. Cai. **comb. nov.** MvcoBank MB814110.

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

Description and illustration (Aveskamp et al. 2009a).

Specimen examined: UK, from leaves of *Eucalyptus* sp., 1994, A.M. Ainsworth (holotype CBS H-20147, culture ex-holotype CBS 105.95).

Didymella molleriana (G. Winter) Q. Chen & L. Cai, comb. nov. MycoBank MB814102.

Basionym: Ascochyta molleriana G. Winter, Bol Soc. Brot. 1883: 26. 1884.

Phoma digitalis Boerema, Verslagen Meded. Plantenziektenk. Dienst Wageningen 153: 19. 1979.

Description (de Gruyter et al. 2002).

Specimens examined: **New Zealand**, Levin, from a leaf of *Digitalis purpurea*, Oct. 1973, G.H. Boerema, CBS H-16201, culture CBS 229.79 = LEV 7660. **The Netherlands**, Ommen, from *Digitalis* sp., deposited in CBS Jan. 2001, H. de Gruyter, CBS 109179 = PD 90/835-1.

Note: Ascochyta molleriana Wint. was a replaced synonym of *Phoma digitalis*, and we recombine this species into *Didymella* based on its phylogeny.

Didymella musae (P. Joly) Q. Chen & L. Cai, comb. nov. MycoBank MB814111.

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

Description (Boerema 1993).

Specimen examined: India, from fruit of Mangifera indica, deposited in CBS Jun. 1969, CBS 463.69.

Didymella negriana (Thüm.) Q. Chen & L. Cai, comb. nov. MycoBank MB814112.

Basionym: Phoma negriana Thüm. "Ph. negrianum", Die Pilze des Weinstockes, Vienna: 185. 1878.

≡ *Phyllosticta negriana* (Thüm.) Allesch., Rabenh. Krypt.-Fl. 1: 98. 1898. Description (de Gruyter *et al.* 1998).

Specimen examined: Germany, Oberdollendorf am Rhein, from Vitis vinifera, deposited in CBS Mar. 1971, L. Kiewnik, CBS H-16511, culture CBS 358.71.

Didymella nigricans (P.R. Johnst. & Boerema) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814113.

Basionym: Phoma nigricans P.R. Johnst & Boerema, New Zealand J. Bot. 19: 394. 1982.

≡ *Peyronellaea australis* Aveskamp *et al.*, Stud. Mycol. 65: 31. 2010. Description (de Gruyter *et al.* 1998).

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

Didymella pedeiae (Aveskamp *et al.*) Q. Chen & L. Cai, comb. nov. MycoBank MB814114.

Basionym: Phoma pedeiae Aveskamp *et al.*, Stud. Mycol. 65: 27. 2010.

Description and illustration (Aveskamp et al. 2010).

Specimen examined: **The Netherlands**, Aalsmeer region, on *Schefflera elegantissima*, 1992, isolated by J. de Gruyter (**holotype** CBS H-20239, culture exholotype CBS 124517 = PD 92/612A).

Didymella pinodella (L.K. Jones) Q. Chen & L. Cai, comb. nov. MycoBank MB814115.

Basionym: Ascochyta pinodella L.K. Jones, Bull. New York Agric. Exp. Sta., Geneva 547: 10. 1927.

≡ *Phoma medicaginis* var. *pinodella* (L.K. Jones) Boerema, Netherlands J. Pl. Pathol. 71: 88. 1965.

 \equiv *Phoma pinodella* (L.K. Jones) Morgan-Jones & K.B. Burch, Mycotaxon 29: 485. 1987.

≡ Peyronellaea pinodella (L.K. Jones) Aveskamp et al., Stud. Mycol. 65: 33. 2010.

Description (de Gruyter et al. 2002).

Specimens examined: The Netherlands, from a stem of *Pisum sativum*, deposited in CBS Jul. 1990, M.E. Noordeloos, CBS 318.90 = PD 81/729. USA, Minnesota, from *Trifolium pratense*, deposited in CBS Sep. 1966, CBS 531.66.

Didymella pinodes (Berk. & A. Bloxam) Petr., Ann. Mycol. 22: 16. 1924. Figs 14–15.

Basionym: Sphaeria pinodes Berk. & A. Bloxam, Ann. Mag. Nat. Hist., Ser. III 7: 454. 1861.

≡ *Mycosphaerella pinodes* (Berk. & A. Bloxam) Vestergr., Ann. Mycol. 10: 581. 1912.

≡ *Peyronellaea pinodes* (Berk. & A. Bloxam) Aveskamp *et al.*, Stud. Mycol. 65: 33. 2010.

= Ascochyta pinodes L.K. Jones, Bull. New York Agric. Exp. Sta., Geneva 547: 4. 1927.

Description from holotype (K 56275): Pseudothecia solitary, on the surface of stems, brown, uniloculate, subglobose to globose, $125-215 \times 100-205 \mu m$, ostiolate. Asci cylindrical to subclavate, $33-74 \times 10-15 \mu m$, 8-spored, biseriate. Ascospores broadly fusiform to ellipsoidal, $11-20 \times 4-8 \mu m$, smooth, straight or slightly curved, hyaline, 1-septate, slightly constricted at the septum, guttulate, upper cells usually broader and longer than the lower cells.

Description from ex-epitype culture (CBS 525.77): Conidiomata pycnidial, solitary or confluent, (sub-)globose, glabrous or with some hyphal outgrows, produced on the agar surface or immersed, $(130-)170-270(-320) \times 130-210(-235) \mu m$. Ostioles 1–2, papillate. Pycnidial wall pseudoparenchymatous, 3–5-layered, 14–23 µm thick, composed of oblong to isodiametric cells, outer wall 2–3-layered, pigmented. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, 6.5–8.5 × 5–6 µm.



Fig. 14. Didymella pinodes (K 56275). A. Type collection packet. B. Ascomata on host substrate. C. Ascomata. D. Ascospore. E. Section of ascomata. F. Asci. G. Ascus. Scale bar: B = 200 µm; C, E = 20 µm; D = 2.5 µm, F = 10 µm, G = 5 µm.

Conidia variable in shape and size, cylindrical, allantoid to fabiform, smooth- and thin-walled, hyaline, 0–2-septate, mostly 1-septate, 7–16.5 × 4–6 μ m, somewhat constricted at the septum, with 5–20 guttules per cell. *Conidial matrix* pale salmon.

Culture characteristics: Colonies on OA, 35–40 mm diam after 7 d, margin regular, white, floccose in concentric rings, with sparse mycelia near the centre, and an olivaceous background; reverse olivaceous, buff rings near the margin. Colonies on MEA 40–45 mm diam after 7 d, margin regular, white, with concentric rings; reverse concolourous. Colonies on PDA, 35–40 mm diam after 7 d, margin regular, densely covered by floccose, white, pale olivaceous near the centre; reverse white in outer ring, darkening towards the centre of the colony via buff, hazel to pale brown olivaceous. NaOH test negative.

Specimens examined: Belgium, Gembloux, from *Pisum sativum*, Sep. 1977, G. Sommereyns (epitype designated here CBS H-14681, MBT202499, culture exepitype CBS 525.77). UK, from stems of *Pisum sativum*, 1886 (holotype K 56275).

Notes: We only observed the sexual morph from the holotype specimen of *Didymella pinodes*. By comparing the morphological characters of the asexual morph (pycnidia, conidiogenous cells and conidia) of CBS H-14681 with the descriptions published by Punithalingam (1972) and Mel'nik (1977), we designate CBS H-14681 as epitype of this species.

Didymella pomorum (Thüm.) Q. Chen & L. Cai, comb. nov. MycoBank MB814116.

Basionym: Phoma pomorum Thüm., Fungi Pomicoli: 105. 1879.

≡ *Peyronellaea pomorum* var. *pomorum* (Thüm.) Aveskamp *et al.*, Stud. Mycol. 65: 33. 2010.

- = Peyronellaea circinata Kusnezowa, Novoste Sist. Nizsh. Rast. 8: 189. 1971.
 - ≡ Phoma jolyana var. circinata (Kusnezowa) Boerema. & Kesteren, Kew Bull. 31: 535. 1977.
 - ≡ *Phoma pomorum* var. *circinata* (Kusnezowa) Aveskamp *et al.*, Mycologia 101: 377. 2009.
 - ≡ Peyronellaea pomorum var. circinata (Kusnezowa) Aveskamp et al., Stud. Mycol. 65: 33. 2010.
- = Phoma cyanea Jooste & Papendorf, Mycotaxon 12: 444. 1981.
 - ≡ *Phoma pomorum* var. *cyanea* (Jooste & Papendorf) Aveskamp *et al.*, Mycologia 101: 377. 2009.
 - ≡ Peyronellaea pomorum var. cyanea (Jooste & Papendorf) Aveskamp et al., Stud. Mycol. 65: 32. 2010.
- = Phoma triticina E. Müll., Phytopathol. Z. 19: 413. 1952.
- Description (Boerema 1993).

Specimens examined: Russia, West Siberia, Novosibirsk, from Heracleum dissectum, deposited in CBS May 1976 (isotype of "Phoma pomorum var. circinata" CBS H-3747, culture ex-isotype CBS 285.76 = ATCC 26241 = IMI 176742 = VKM F-1843). South Africa, Heilbron, from straw of *Triticum* sp., 1972, W.J. Jooste (holotype of "Phoma pomorum var. cyanea" PREM 45736, culture ex-holotype CBS 388.80). Switzerland, Zürich, Oerlikon, from *Triticum* spelta, deposited in CBS Mar. 1952, E. Müller (culture ex-holotype of "Phoma triticina" CBS 354.52). The Netherlands, Wageningen, from *Polygonum* tataricum, deposited in CBS Sep. 1966, CBS H-16540, culture CBS 539.66 = ATCC 16791 = IMI 122266 = PD 64/914.

Notes: The isolates of the respective Phoma pomorum varieties, viz. vars. circinata (CBS 285.76), cyanea (CBS 388.80) and pomorum (CBS 539.66), and the species *P. triticina* (CBS 354.52), clustered in a well-supported clade. Sequences of these four isolates are nearly identical in all four loci, and these four taxa have only negligible differences in morphology. Thus, we



Fig. 15. Didymella pinodes (CBS 525.77). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidia. I. Section of pycnidium. J. Section of pycnidial wall. K. Conidia. Scale bars: G = 200 µm; H = 100 µm; I = 20 µm; J–K = 10 µm.

regarded these four taxa to be conspecific, and treat them as a single species, *Didymella pomorum*.

Didymella protuberans (Lév.) Q. Chen & L. Cai, comb. nov. MycoBank MB814117. Fig. 16.

Basionym: Phoma protuberans Lév., Ann. Sci. Nat. Bot. III 5: 281. 1846.

- ≡ Peyronellaea protuberans (Lév.) Aveskamp et al., Stud. Mycol. 65: 33. 2010.
- = Didymella alectorolophi Rehm, Hedwigia 64: 294. 1923.
- ≡ Peyronellaea alectorolophi (Rehm.) Aveskamp et al., Stud. Mycol. 65: 31. 2010.
- = Phoma alecotorolophi Boerema et al., Persoonia 16: 366. 1997.
- = Phoma obtusa Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 378. 1870.
 - ≡ *Peyronellaea obtusa* (Fuckel) Aveskamp *et al.*, Stud. Mycol. 65: 33. 2010.

Description from ex-neotype culture (CBS 381.96): Conidiomata pycnidial, solitary or aggregated, irregularly globose, glabrous or covered with some hyphal outgrowths, semi-immersed or immersed, $110-280(-350) \times 95-220(-295) \ \mu m$. Ostioles 1–2,

slightly papillate or non-papillate. *Pycnidial wall* pseudoparenchymatous, 5–7-layered, 15–25 µm thick, composed of oblong to isodiametric cells. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to doliiform, $3.5-5(-6) \times 3-4.5$ µm. *Conidia* ellipsoidal, hyaline, thin-walled, smooth, aseptate, $4.5-7.5 \times 3-5(-6.5)$ µm, egutullate or sometimes with 1(-3) small guttules. *Conidial matrix* whitish.

Culture characteristics: Colonies on OA, 55–60 mm diam after 7 d, margin regular, floccose, white to pale greenish olivaceous; reverse buff to white. Colonies on MEA 50–55 mm diam after 7 d, margin regular, white, with tufts of aerial mycelium; reverse olivaceous, greenish olivaceous near the centre. Colonies on PDA, 50–55 mm diam after 7 d, margin regular, white, floccose, pale leaden near the centre; reverse white to buff, olivaceous near the centre. NaOH spot test: a luteous discolouration on MEA, later changing to dull green to vinaceous-black, from the centre to outer ring.

Specimens examined: Germany, Hessen, from stalks of Daucus carota, K.W.G. Fuckel (holotype of "Phoma obtusa" G00266302 & G00266303). The Netherlands, from seed of Rhinanthus major, deposited in CBS Feb. 1996,



Fig. 16. Didymella protuberans (CBS 381.96). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidium. I. Conidia. Scale bars: G = 100 µm; H = 50 µm; H = 10 µm.

(holotype of "Phoma alecotorolophi" L 992.167.515, culture ex-holotype CBS 132.96 = PD 93/853); from a root of *Daucus carota*, deposited in CBS Jul. 1993, J. de Gruyter, CBS 377.93 = PD 80/976; from *Spinacia oleracea*, deposited in CBS Jul. 1993, J. de Gruyter, CBS 391.93 = PD 80/87; from a leaf of *Lycium halifolium*, deposited in CBS Apr. 1996 (neotype of *Phoma protuberans* designated here HMAS 246694, MBT202500, culture ex-neotype CBS 381.96 = PD 71/706).

Notes: The type specimen of *Phoma protuberans* could not be traced. The original description lacks conidial dimensions. In the specimen HMAS 246694, collected from *Lycium halifolium* in the Netherlands, the aseptate conidia measured $4.5-7.5 \times 3-5(-6.5) \mu m$, which is, in general agreement with the description by Boerema *et al.* (1997), $4-10.5 \times 2-5 \mu m$ *in vitro*. Therefore, HMAS 246694 is selected as neotype.

Strains CBS 132.96 (ex-holotype of "*Phoma alecotorolophii*"), CBS 377.93 and CBS 391.93, grouped in a well-supported clade together with the neotype of *Didymella protuberans*. Sequences used in the multi-locus analyses of these four strains are identical, and there is no detectable difference in morphology among them. Based on current data, we confirmed that these four strains represent the same species, for which the name *Didymella protuberans* is adopted.

Didymella rhei (Ellis & Everh.) Q. Chen & L. Cai, comb. nov. MycoBank MB814156.

Basionym: Ascochyta rhei Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 45: 160. 1893.

≡ Phoma rhei (Ellis & Everh.) Aa & Boerema, Persoonia 18: 42. 2002. Description (de Gruyter *et al.* 2002). Specimen examined: New Zealand, from a leaf of *Rheum rhaponticum*, deposited in CBS Jan. 2001, H. de Gruyter, CBS 109177 = LEV 15165 = PD 2000/9941.

Didymella rumicicola (Boerema & Loer.) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814118. Figs 17–18. *Basionym: Phoma rumicicola* Boerema & Loer., New Zealand J. Bot. 18: 473. 1980.

Description from holotype (PDD 50667): Conidiomata pycnidial, solitary or confluent, subglobose, glabrous, (100–) 145–335(-470) × (100–)145–240(-330) μ m. Ostioles 1–4, papillate or non-papillate. Pycnidial wall pseudoparenchymatous, 3–5-layered, 18–35 μ m thick, composed of isodiametric cells, outer wall 2–3-layered, pigmented. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, 3.5–5.5 × 3–4 μ m. Conidia ellipsoidal to cylindrical, smooth- and thin-walled, aseptate, 6.5–11.5 × 3–4.5 μ m, guttulate.

Description from ex-isotype culture (CBS 683.79): Conidiomata pycnidial, solitary or confluent, subglobose, glabrous, superficial or immersed, $(75-)345-480 \times (50-)250-370 \ \mu\text{m}$. Ostioles 1–4, papillate or non-papillate. *Pycnidial wall* pseudoparenchymatous, 2–4-layered, 20–31 $\ \mu\text{m}$ thick, composed of isodiametric cells, outer cell layer pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform, $3.5-8.5 \times 3-7 \ \mu\text{m}$. *Conidia* ellipsoidal to cylindrical, thin-walled, smooth, aseptate, $4.5-9(-12.5) \times 2.5-5 \ \mu\text{m}$, with many minute guttules, *ca.* 5–25 guttules. *Conidial matrix* yellowish cream.



Fig. 17. Didymella rumicicola (PDD 50667). A. Type collection packet. B. Pycnidia on dried culture. C. Pycnidia. D. Section of pycnidial wall. E–F. Conidiogenous cells. G. Conidia. Scale bars: B = 100 µm; C = 50 µm; D, G = 10 µm; E–F = 2.5 µm.

Culture characteristics: Colonies on OA, 60–65 mm diam after 7 d, margin regular, felty, olivaceous; reverse concolourous. Colonies on MEA 55–60 mm diam after 7 d, margin regular, wooly, white, grey olivaceous near the margin; reverse buff, pale grey olivaceous near the margin. Colonies on PDA, 55–60 mm diam after 7 d, margin regular, floccose, white, abundant black pycnidia visible, giving an iron-black colour near the centre and margin; reverse dark olivaceous with some white zones. NaOH test negative.

Specimen examined: New Zealand, Levin, from *Rumex obtusifolius*, deposited in CBS Nov. 1979, G.F. Laundon (holotype PDD 50667, isotype CBS H-7627, culture ex-isotype CBS 683.79 = LEV 15094).

Notes: The isotype of *Didymella rumicicola* clustered in a wellsupported clade with CBS 179.97 (*D. acetosellae*, originally identified as *Phoma acetosellae*) without any difference in the sequenced loci. These two species were both initially isolated from *Rumex* spp. However, *D. rumicicola* is distinguished from *D. acetosellae* in the faster growing rate (60–65 mm vs. 20–30 mm after 7 d on OA), and the smaller conidiogenous cells (3.5–8.5 × 3–7 µm in *D. rumicicola* vs. 5–13 × 6–12 µm in *D. acetosellae*; Boerema *et al.* 1980). Since CBS 179.97 is not the ex-type culture of *D. acetosellae*, the potential conspecificity of *D. rumicicola* and *D. acetosellae* remains to be confirmed.

Didymella sancta (Aveskamp *et al.*) Q. Chen & L. Cai, comb. nov. MycoBank MB814119.

Basionym: Phoma sancta Aveskamp *et al.*, Mycologia 101: 377. 2009.

≡ *Peyronellaea sancta* (Aveskamp *et al.*) Aveskamp *et al.*, Stud. Mycol. 65: 33. 2010.

Description and illustration (Aveskamp et al. 2009a).

Specimen examined: South Africa, from dead branches of Ailanthus altissima, Oct. 1982, C. Jansen (holotype CBS H-16332, culture ex-holotype CBS 281.83).

Didymella senecionicola Q. Chen & L. Cai, **nom. nov.** MycoBank MB814120.

≡ Phoma senecionis P. Syd., Hedwigia. 38: 136. 1899, non Didymella senecionis Hollós, 1908.

Description (de Gruyter et al. 1993).

Specimen examined: New Zealand, Raetihi, from a stem of Senecio jacobaea, deposited in CBS Jan. 1978, G.H. Boerema, CBS 160.78 = LEV 11451.

Notes: As the epithet "senecionis" was occupied in *Didymella*, a new name is proposed for this species. The name *Didymella* senecionis was based on the sexual morph, producing uniseptate ascospores arranged uniseriately into the clavate asci (Saccardo & Trotter 1913). *Didymella senecionicola* is presently only known from its asexual morph, producing aseptate, oblong to ellipsoidal conidia (de Gruyter et al. 1993).

Didymella sp. 1

Specimen examined: The Netherlands, Wageningen, Alphen aan de Rijn, from a leaf of *Pteris* sp., deposited in CBS Apr. 1996, CBS 379.96.

Notes: This isolate was incorrectly identified as "*Didymella adianticola*", as it is phylogenetically distant from the authentic strains of *D. adianticola* (CBS 187.83 and CBS 260.92). It is probably a novel species, and will be treated after further study.

Didymella sp. 2

Specimen examined: Germany, Berlin, from a flower-stalk of Chrysanthemum roseum, deposited in CBS Sep. 1958, R. Schneider, CBS 115.58 = DSM 62044.



Fig. 18. Didymella rumicicola (CBS 683.79). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Section of pycnidial wall. I. Conidia. Scale bars: G = 200 µm; H–I = 10 µm.

Notes: CBS 115.58 was originally received as "*Ascochyta pyr-ethri*", and clustered in a distinct lineage (Fig. 1). Since the type of *As. pyrethri* is not available for comparison, we are unsure if CBS 115.58 represents a new species or is conspecific to *As. pyrethri*. This isolate awaits further study.

Didymella subglomerata (Boerema *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814121.

Basionym: Phoma subglomerata Boerema et al., Persoonia 15: 204. 1993.

≡ *Peyronellaea subglomerata* (Boerema *et al.*) Aveskamp *et al.*, Stud. Mycol. 65: 33. 2010.

Description (Boerema 1993).

Specimen examined: USA, North Dakota, from *Triticum* sp., deposited in CBS Sep. 1992, J. de Gruyter, CBS 110.92 = PD 76/1010.

Didymella subherbarum (Gruyter *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814122.

Basionym: Phoma subherbarum Gruyter *et al.*, Persoonia 15: 387. 1993.

Description (de Gruyter et al. 1993).

Specimens examined: Canada, Ontario, from overwintered seeds of Zea mays, deposited in CBS May 1992, J. de Gruyter (holotype L 992.177.439, culture ex-holotype CBS 250.92 = DAOM 171914 = PD 92/371). Peru, from Solanum sp., deposited in CBS May 1992, J. de Gruyter, CBS 249.92 = PD 78/1088.

Didymella viburnicola (Oudem.) Q. Chen & L. Cai, comb. nov. MycoBank MB814123.

Basionym: Phoma viburnicola Oudem., Ned. Kruidk. Arch. 2: 247. 1900.

Description (de Gruyter & Noordellos 1992).

Specimen examined: **The Netherlands**, Wageningen, Aboretum, from *Viburnum* cassioides, deposited in CBS May 1973, CBS H-16605, culture CBS 523.73 = PD 69/800.

Notes: Phoma viburnicola was first collected on Viburnum oxycoccus from the Netherlands, with conidia measuring $5-6 \times 3.5 \ \mu m$ (Saccardo 1902). De Gruyter & Noordeloos (1992) confirmed the conidial size of the representative isolates as $3.5-5.5 \times 1.6-2.2 \ \mu m$, which agrees with the original description. We herewith treat this species as a new combination in *Didymella*.

Clade 7: Paraboeremia

Paraboeremia Q. Chen & L. Cai, gen. nov. MycoBank MB814061.

Etymology: Morphologically resembling the genus *Boeremia*, but being phylogenetically distinct.

Conidiomata pycnidial, globose to subglobose, or irregular shaped, superficial on or immersed into the agar, solitary or confluent, ostiolate, sometimes with a short neck around the ostioles. *Pycnidial wall* pseudoparenchymatous, 3–6-layered, outer layers pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, globose to flask-shaped. *Conidia* ellipsoidal, sometimes curved, hyaline, smooth- and thin-walled, generally aseptate, guttulate, sometimes with greenish colour. *Ascomata* pseudo-thecial, subglobose to pyriform, ostiolate. *Asci* 8-spored, bitunicate. *Ascospores* subcylindrical, hyaline, 1-septate, the upper cell wider than the lower cell, constricted at the septum.

Type species: Paraboeremia selaginellae (Sacc.) Q. Chen & L. Cai.

Paraboeremia adianticola (Aa & Boerema) Q. Chen & L. Cai, comb. nov. MycoBank MB814124. Fig. 19.

Basionym: Didymella adianticola Aa & Boerema, Verslagen Meded. Plantenziektenk. Dienst Wageningen 159 (Jaarboek 1982): 25. 1983.

Phyllosticta adianticola E. Young, Mycologia 7: 144. 1915.
 Phoma adianticola (E. Young) Boerema, Verslagen Meded. Plantenziektenk. Dienst Wageningen 159 (Jaarboek 1982): 25. 1983.

Description from culture (CBS 260.92): Conidiomata pycnidial, solitary, globose to subglobose, glabrous, semi-immersed or immersed, $(150-)170-265 \times (120-)140-245 \ \mu m$. Ostioles 1–3, spalely papillate. Pycnidial wall pseudoparenchymatous, 4–6-layered, 13–24 μm thick, composed of isodiametric cells, outer layer brown. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to dolliform, 5.5–7 × 3–6.5 μm . Conidia ellipsoidal to cylindrical, smooth- and thin-walled, aseptate, 4–7 × 2–2.8 μm , with 2 large polar guttules. Conidial matrix white.

Culture characteristics: Colonies on OA, 55–60 mm diam after 7 d, margin regular, buff to salmon, abundant pycnidia visible; reverse pale salmon. Colonies on MEA 20–25 mm diam after 7 d, margin regular, aerial mycelium sparse, pale saffron to brown, grey near the centre; reverse pale saffron, pale brown near the centre. Colonies on PDA, 35-40 mm diam after 7 d, margin regular, floccose, white or somewhat pale pink; reverse saffron. Application of NaOH results in a greenish olivaceous discolouration of the agar.

Specimens examined: **Unknown origin**, from *Pteris ensiformis*, deposited in CBS May 1992, J. de Gruyter, CBS 260.92 = PD 86/1103. **USA**, Florida, from a leaf of *Polystichum adiantiforme*, deposited in CBS Feb. 1983, G.H. Boerema, CBS H-16142, culture CBS 187.83 = PD 82/128.

Notes: Our taxonomic treatment was based on the sexual morph. Boerema (1983) connected the sexual (*Didymella adianticola*) and asexual (*Phoma adianticola*) morphs, which however requires molecular verification.

Paraboeremia putaminum (Speg.) Q. Chen & L. Cai, comb. nov. MycoBank MB814125.

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

Description (de Gruyter & Noordeloos 1992).

Specimens examined: **Denmark**, from the rhizosphere of *Malus sylvestris*, deposited in CBS Feb. 1969, E. Sønderhousen, CBS 130.69 = CECT 20054 = IMI 331916. **The Netherlands**, from a branch of *Ulmus* sp., deposited in CBS Jun. 1991, G.H. Boerema, CBS 372.91 = PD 75/960.

Notes: The two representative cultures of "*Phoma putaminum*" (CBS 130.69 and CBS 372.91) clustered in the *Paraboeremia* clade, and thus a new combination *Paraboeremia putaminum* is proposed. This species has identical LSU sequence with the type species, *Pa. selaginellae*, but is distinct in two bp and three bp in ITS and *tub2* sequences respectively. The clarification of their relationship awaits further study.

Paraboeremia selaginellae (Sacc.) Q. Chen & L. Cai, comb. nov. MycoBank MB814126. Fig. 20.

Basionym: Phyllosticta selaginellae Sacc., Malpighia 11: 304. 1897. = Phoma selaginellicola Gruyter et al., Persoonia 15: 399. 1993. Description from ex-neotype culture (CBS 122.93): Conidiomata pycnidial, solitary, globose to obpyriform, glabrous, semiimmersed or immersed, $130-360 \times 120-320 \mu m$. Ostioles 2–3, slightly papillate. Pycnidial wall pseudoparenchymatous, 4–7-layered, 16–23 μm thick, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, 5–6.5 × 3.5–5.5 μm . Conidia ellipsoidal to cylindrical, hyaline, smooth- and thin-walled, aseptate, 2.5–5 × 1–2 μm , sometimes with 1–2 guttules. Conidial matrix whitish.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular, floccose, grey olivaceous, white near the margin; reverse grey olivaceous to buff near the centre. Colonies on MEA 35–40 mm diam after 7 d, margin crenate, aerial mycelium sparse, olivaceous, white near the centre; reverse concolourous. Colonies on PDA, 35–40 mm diam after 7 d, margin crenate, floccose, with concentric rings, white to pale olivaceous; reverse olivaceous to pale brown, dull green near the centre. Application of NaOH results in a brown discolouration of the agar.

Specimen examined: **The Netherlands**, from a leaf of Selaginella sp., deposited in CBS Jan 1993, J. de Gruyter (**neotype of** *Phyllosticta selaginellae* designated here HMAS 246693, MBT202501, culture ex-neotype CBS 122.93 = PD 77/1049).

Notes: The type specimen of *Phyllosticta selaginellae* could not be located, and is presumably lost. The strain CBS 122.93 from *Selaginella* sp. had ellipsoidal to cylindrical conidia, $2.5-5 \times 1-2 \mu m$, which is in agreement with the original description based on *Selaginella helvetica*, and hence this collection is designated as neotype.

Paraboeremia selaginellae has a close phylogenetic relationship to *Pa. putaminum*, but can be distinguished by its narrower conidia ($2.5-5 \times 1-2 \mu m$). Conidia of *Pa. putaminum* are guttulate, $3-4 \times 2-2.5 \mu m$, and conspicuous greenish in colour (de Gruyter & Noordeloos 1992).

Clade 8: Macroventuria

Macroventuria Aa, Persoonia 6: 359. 1971.

Ascomata perithecial, globose, ostiolate, erumpent on the agar surface, setose in the upper part. Asci ellipsoidal or saccate, bitunicate, 8-spored. Ascospores mostly hyaline, ellipsoidal, 2-celled (from van der Aa 1971).

Type species: Macroventuria anomochaeta Aa, Persoonia 6: 362. 1971.

Notes: This genus was established by van der Aa (1971), accommodating two species in the family *Venturiaceae* which produced relatively large, nearly hyaline, two-celled ascospores, differing from *Leptosphaerulina* (van der Aa 1971). Later *Macroventuria* was placed in *Pseudosphaeriaceae* by Barr (1982) and then in *Pleosporaceae* by Eriksson & Hawksworth (1986) (Kodsueb *et al.* 2006). In the study of Aveskamp *et al.* (2010) this genus was accommodated in the *Didymellaceae*, which is confirmed in the present study.



Fig. 19. Paraboeremia adianticola (CBS 260.92). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidia. I. Section of pycnidia. J. Section of pycnidial wall. K–L. Conidiogenous cells. M. Conidia. Scale bars: G = 100 μm; H–I = 50 μm; J, K, M = 10 μm; L = 5 μm.

Macroventuria anomochaeta Aa, Persoonia 6: 362. 1971.

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

Notes: Strain CBS 502.72, which was also received as "*M. anomochaeta*" appears to be phylogenetically distinct from the ex-holotype (CBS 525.71). Genetically, CBS 502.72 differs from CBS 525.71 in only three bp in the four loci sequenced. As we have not examined the morphology of CBS 502.72, its classification awaits further study. The type of *M. wentii* (CBS 526.71) differs from that of *M. anomochaeta* (CBS 525.71) in 19 bp in the four loci sequenced.

Macroventuria wentii Aa, Persoonia 6: 361. 1971.

Specimen examined: USA, Nevada, Death Valley, from plant litter, 1970, F.W. Went (holotype CBS H-14195, culture ex-holotype CBS 526.71).

Clade 9: Ascochyta

Ascochyta Lib., Pl. crypt. Arduenna, fasc. 1: no. 59. 1830. emend. Q. Chen & L. Cai.

Conidiomata pycnidial, subglobose or ampulliform to mammiform, sometimes irregularly shaped, superficial on or immersed into the agar, solitary or confluent, ostiolate or poroid opening formed at the end of the growing process. *Pycnidial wall* pseudoparenchymatous, 1–8-layered, outer wall pigmented. *Conidiogenous cells* annellidic or phialidic, hyaline, smooth, variable in shape, *i.e.* subglobose, cylindrical, flask-shaped, obpyriform, ampulliform to doliiform. *Conidia* variable in shape, *i.e.* ovoid, oblong, subcylindrical, ellipsoidal, cymbiform, allantoid, straight or slightly curved, hyaline or sometimes slightly coloured (yellow to pale brown), smooth- and thinwalled, aseptate or septate, mostly uniseptate, sometimes 2–3-septate, eguttulate or guttulate (Boerema & Bollen 1975, Boerema *et al.* 2004). *Chlamydospores* occasionally occur in old cultures. *Ascomata* pseudothecial, immersed or erumpent,



Fig. 20. Paraboeremia selaginellae (CBS 122.93). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidium. I. Section of pycnidial wall. J. Conidiogenous cells. K. Conidia. Scale bars: G = 200 µm; H = 100 µm; I–J = 10 µm; K = 5 µm.

subglobose to flattened, or irregular, solitary or confluent, ostiolate, sometimes developing an elongated neck. *Asci* subcylindrical to subclavate, or saccate, sometimes slightly curved, 8-spored, bitunicate, sometimes short-stipitate. *Pseudoparaphyses* filamentous, hyaline, thin-walled, septate, conspicuous in immature fructifications, and disappear at maturity. *Ascospores* ovoid to ellipsoidal, slightly biconic, hyaline to yellowish into the ascus, may become brown when released, smooth, 1septate, sometimes 3-septate, symmetrical or asymmetrical, constricted at the septum, uniseriate or biseriate (Jellis & Punithalingam 1991, Trapero-Casas & Kaiser 1992, Kaiser *et al.* 1997, Chilvers *et al.* 2009).

Type species: Ascochyta pisi Lib., Pl. crypt. Arduenna, fasc. 1: no. 59. 1830.

Notes: In most cases, the host ranges of species belonging to this genus are rather restricted, occurring mostly on the *Campanulaceae*, *Chenopodiaceae*, *Leguminosae*, *Poaceae*, *Solanaceae* and *Umbelliferae*. Some species are associated with one specific host, but may also be found on other related species of the same genus or family (Boerema & Bollen 1975). As the sexual morphs of several *Ascochyta* species were linked to their asexual morphs (Kaiser *et al.* 1997, Chilvers *et al.* 2009, Woudenberg *et al.* 2009), we incorporated these features into the generic circumscription.

Ascochyta fabae Speg. Anales Mus. Nac. Hist. Nat. Buenos Aires 6: 321. 1898–1899.

= *Ascochyta pisi* f. *foliicola* Sacc. & Marchal, Rev. Mycol. (Toulouse) 7: 148. 1885.

= Didymella fabae G.J. Jellis & Punith, Pl. Pathol. 40: 151. 1991.

Description from holotype of Didymella fabae (IMI 336944): Ascomata arranged in rows on bean straw of Vicia faba. Ascomata pseudothecial, immersed, becoming partially erumpent, dark brown to blackish brown, subglobose, solitary or confluent, 180-240 × 130-150 µm, with short necks, ostiolate. Ostiole nearly circular, 35–50 µm wide, surrounded by dark brown cells. Ascomatal wall pseudoparenchymatous, of textura angularis, 5-8 layered, outer wall 3-4-layered, dark brown. Asci arranged in a relatively flat layer, hyaline, cylindrical to subclavate, 8spored, 55-70 × 10-14 µm, usually constricted near the base to form a distinct foot. Pseudoparaphyses hyaline, thin-walled, septate, 1-2 µm, conspicuous in immature fructifications. Ascospores irregularly biseriate, hyaline, smooth, slightly biconic, broadly ellipsoidal, 1-septate, constricted at the septum, with the upper cell broader than the lower cell, $15-18 \times 5.5-6.5 \ \mu m$. Naturally discharged ascospores on bean straw later turn yellowish brown to dark brown and sometimes 2-septate (from Jellis & Punithalingam 1991).

Specimens examined: **Belgium**, Gembloux, from *Phaseolus vulgaris*, Sep. 1977, G. Sommereyns, CBS H-8998, culture CBS 524.77. **The Netherlands**, Randwijk, from a leaf of *Vicia faba*, deposited in CBS Oct. 1971, G.H. Boerema, CBS 649.71; from *Phaseolus vulgaris*, PD 83/492. **UK**, Great Britain, from a dead stem of *Vicia faba*, Jan. 1990, G.J. Jellis (**holotype** of "*Didymella fabae*" IMI 336944).

Notes: The sexual morph of *Ascochyta fabae* was published by Jellis & Punithalingam (1991) as *Didymella fabae*, which was recorded on overwintering bean straw of *Vicia faba* in Cambridge. *Ascochyta viciae* (CBS 451.68) is phylogenetically closely related to *As. fabae*, but they are distinguishable based on morphology. Conidia of *As. viciae* are much longer and narrower than those of *As. fabae* (30–60 × 2.5 µm vs. $10-25 \times 5-6$ µm) (Saccardo 1884, Saccardo 1902).

Ascochyta herbicola (Wehm.) Q. Chen & L. Cai, comb. nov. MycoBank MB814127.

Basionym: Phoma herbicola Wehm., Mycologia 38: 319. 1946. Description (de Gruyter *et al.* 1998).

Specimens examined: **USA**, Montana, Missoula, head of Seeley Lake, from water, deposited in CBS Mar. 1997, CBS H-16581, culture CBS 629.97 = PD 76/ 1017; Wyoming, Jackson, Glory Mountain, from stems of *Syntheris dissecta*, Jul. 1040, L.E. Wehmeyer (**holotype** 1032b).

Ascochyta lentis Vassiljevsky, Acta Inst. Bot. Acad. Sci. Pl. Crypt, ser II: 358. 1938.

= Didymella lentis W.J. Kaiser, B.C. Wang & J.D. Rogers, Pl. Dis. 81: 815. 1997.

Specimen examined: Unknown origin, from seeds of *Lens culinaris*, deposited in CBS Sep. 1984, G.H. Boerema, CBS H-9060, culture CBS 370.84 = PD 81/783.

Ascochyta medicaginicola var. medicaginicola Q. Chen & L. Cai, nom. nov. MvcoBank MB814129.

≡ *Phoma medicaginis* var. *medicaginis* Malbr. & Roum., Rev. Mycol. 8: 91. 1886.

Description (de Gruyter et al. 2002).

Specimens examined: Czech Republic, from Medicago sativa, deposited in CBS Jul. 1990, M.E. Noordeloos, CBS 316.90 = CCM F-187. France, Rounen, from Medicago sativa, Oct. 1885, C. Roumeguère (isotype BR 5020155793119).

Notes: Ascochyta medicaginicola var. macrospora and As. medicaginicola var. medicaginicola clustered in the same branch without any difference in four sequenced loci. However, these two varieties could be distinguished based on morphology and physiology. Ascochyta medicaginicola var. medicaginicola usually produces aseptate conidia measuring (4.2–) 5.7-7.2(-12.7) × (1.4-)2.1-2.3(-3.5) µm, that differ from variety A. medicaginicola var. macrospora which produces 1-3-septate, larger conidia [(2.8-)6.3-11.1(-27.8) × (1.4-)2.1-2.9(-5.8) µm] (Boerema et al. 1993), especially when incubated at low temperature. Additionally, As. medicaginicola var. macrospora showed relatively stronger specific pathogenicity to the primary host of both varieties, lucerne (Medicago sativa), than As. medicaginicola var. medicaginicola (Boerema et al. 1993). Hence, we maintain these two varieties and propose two new names.

Ascochyta medicaginicola var. *macrospora* (Boerema *et al.*) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814128.

■ Phoma medicaginis var. macrospora Boerema et al., Netherlands J.
 Pl. Pathol. 99 (Suppl. 1): 19. 1993.
 Description (de Gruyter et al. 2002).

Specimens examined: Canada, Saskatchewan, Saskatoon, from seed of *Medicago sativa*, deposited in CBS Jun. 1965, G.H. Boerema, CBS 404.65 = IMI 116999. USA, Minnesota, from *Medicago sativa*, Sep. 1953, M.F. Kernkamp (holotype CBS H-16487, culture ex-holotype CBS 112.53).

Note: As the epithet "*medicaginis*" was occupied in *Ascochyta*, we introduce the new epithet "*medicaginicola*" for the varieties of *Phoma medicaginis* (see above).

Ascochyta nigripycnidia (Boerema et al.) Q. Chen & L. Cai, comb. nov. MycoBank MB814130.

Basionym: Phoma nigripycnidia Boerema *et al.*, Persoonia 16: 356. 1997.

Description (Boerema et al. 1997).

Specimen examined: Czech Republic, from a leaf of *Vicia cracca*, deposited in CBS Jan 1996, M. Ondrej (holotype L 992.163.150, culture ex-holotype CBS 116.96 = CCMF 243 = PD 95/7930).

Ascochyta phacae (Corbaz) Q. Chen & L. Cai, comb. nov. MycoBank MB814131. Fig. 21.

Basionym: Didymella phacae Corbaz, Sydowia 9: 229. 1955.

Description from holotype (ZT Myc 54988): Pseudothecia on stems of Phaca alpina, solitary, brown to black, uniloculate, subglobose to globose, $110-255 \times 110-245 \mu m$, ostiolate single. Ascomatal wall pseudoparenchymatous, of textura angularis, 3-5-layered, $18-23.5 \mu m$ thick. Asci cylindrical to subclavate, $40-60 \times 11.5-15 \mu m$, 8-spored, biseriate. Ascospores broadly fusiform, $11.5-14.5 \times 4.5-6.5 \mu m$, smooth, hyaline, uniseptate, slightly constricted at the septum, guttulate, upper cells usually broader than the lower cells.

Specimens examined: Switzerland, Valais, Gabi, Feehrbergen, from dead stems of *Phaca alpina*, deposited in CBS May 1955, E. Müller (holotype ZT Myc 54988, culture ex-holotype CBS 184.55).

Notes: Didymella phacae was linked to an ascochyta-like asexual morph (Corbaz 1955, 1957, Corlett 1981), but this morph was not formally named and described. A new combination is proposed here, as *Ascochyta phacae*.

Ascochyta pisi Lib., Pl. crypt. Arduenna, fasc. 1: no. 59. 1830. Figs 22-23.

≡ Septoria leguminum var. pisorum (Lib.) Desm., Ann. Sci. Nat. Bot., sér. 2, 19: 344. 1843.

= Didymella pisi Chilvers et al., Mycol. Res. 113: 396. 2009.

Description from isotype (BR 5020059493320): Leaf spots elliptical to circular, brown to black. Pycnidia on bean pod surface of Laburnum anagyroides, solitary or confluent, subglobose, $65-210 \times 45-185 \mu m$. Ostiole single. Pycnidial wall pseudo-parenchymatous, 3-4-layered, $14-24 \mu m$ thick, composed of isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, doliiform. Conidia fusiform to cylindrical, smooth- and thin-walled, hyaline, uniseptate, $11-18.5 \times 3-5 \mu m$, with 2-5 guttules.

Description from holotype of Didymella pisi: Ascomata pseudothecial, globose to irregular, 200–400 µm diam, with inconspicuous ostiole, brown to blackish, soft. Asci bitunicate, cylindrical to saccate, 8-spored, 46–168 × 10–15 µm. Ascospores usually uniseriately arranged, hyaline, more or less equally bicellular, constricted at the septum, rounded at both ends or with one end more acute, smooth, 12–17.5 × 6.5–8.5 µm. Hamathecial elements sparse or absent. Pseudothecia formed on pea stems only when opposite mating types were present (from Chilvers *et al.* 2009).



Fig. 21. Ascochyta phacae (ZT Myc 54988). A. Type collection packet. B. Pseudothecium. C. Section of pseudothecial wall. D. Pseudothecia on host substrate. E. Asci. F. Ascospores. Scale bars: B-C = 20 µm; D = 200 µm; E = 10 µm; F = 5 µm.

Description from ex-epitype culture (CBS 122785): Conidiomata pycnidial, solitary, globose to subglobose, with some hyphal outgrows, produced on the agar surface and immersed, $90-195 \times 75-160 \mu$ m. Ostiole single, slightly papillate or nonpapillate. Pycnidial wall pseudoparenchymatous, 3-4 layered, $14.5-29 \mu$ m thick, composed of isodiametric cells. Conidiogenous cells annellidic, hyaline, smooth, flask-shaped to obpyriform, $5.5-8.5 \times 4.5-8 \mu$ m. Conidia oblong to cylindrical, thin-walled, smooth, mainly uniseptate, incidentally aseptate or 2-septate, $7-16 \times 3-5 \mu$ m, always somewhat constricted at the septum, with (4-)6-14(-16) guttules. Conidial matrix pale pink.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular, floccose, white, slight grey near the centre; reverse buff to pale salmon, somewhat pale olivaceous near the centre. Colonies on MEA 35–40 mm diam after 7 d, margin regular floccose, white, sparse near the margin; reverse white, pale green near the centre. Colonies on PDA, 25–30 mm diam after 7 d, margin regular, wooly, white; reverse white, buff to amber near the centre. NaOH test negative.

Specimens examined: Belgium, from pods of Pisum sativum (isotype of Ascochyta pisi BR 5020059493320). Canada, Saskatoon, from Pisum sativum, B. Gossen, CBS 122751 = ATCC 201620. The Netherlands, Venlo, from Pisum sativum, M.M.J. Dorenbosch (epitype designated here of Ascochyta pisi, HMAS 246705, MBT202502, culture ex-epitype CBS 122785 = PD 78/517); from Pisum sativum, deposited in CBS Qct. 1954, J.A. von Arx, CBS 126.54; from Juglans regia, deposited in CBS Mar. 1949, PD, CBS 108.49 = DSM 62041. USA, Idaho, from Pisum sativum, 1995, D. Webster, CBS 122750 = ATCC 201619.

Notes: Ascochyta pisi was originally described from *Pisum sativum* in Ardenne, on the borders of France and Belgium (Saccardo 1884). The conidia observed on the isotype (11–18.5 × 3–5 µm) and epitype (7–16 × 3–5 µm) of *As. pisi* are congruent with that of the original description (14–16 × 4–6 µm). Therefore, the specimen HMAS 246705 (ex CBS 122785) is designated as epitype for this species.

Didymella pisi was confirmed to be the sexual morph of *As. pisi* from the cross between two *As. pisi* isolates (CBS 122750 and CBS 122751; Chilvers *et al.* 2009). CBS 122750 has four bp differences in *tub2* sequence from other isolates, but is identical in other loci. The isolate CBS 108.49 was initially identified as *Ascochyta juglandis* when deposited in CBS, but clustered with other *As. pisi* strains in a well-supported clade with sequences of four loci being identical to other strains in the clade. Therefore, we reclassified this strain as *As. pisi*.

Ascochyta rabiei (Pass.) Labr., Rev. Pathol. Vég. Entomol. Agric. France 18: 228. 1931.

Basionym: Zythia rabiei Pass., Comment. Soc. Crittog. Ital. 2: 437. 1867.

- ≡ Phoma rabiei (Pass.) Khune ex Gruyter, Persoonia 18: 89. 2002.
- *Mycosphaerella rabiei* Kovatsch. The blight of chick pea: 70. 1936.
 Didymella rabiei (Kovatsch.) Arx, Beitr. Kryptogamenfl. Schweiz 11: 364. 1962.



Fig. 22. Ascochyta pisi (BR 5020059493320). A. Type collection packet. B. Pycnidia on host substrate. C. Conidia. D. Pycnidia. E. Section of pycnidium. Scale bars: B = 100 µm; C-D = 10 µm; E = 20 µm.

Specimens examined: **Bulgaria**, from *Cicer arietinum*, deposited in CBS Feb. 1937, I.C. Kovachevsky, **ex-holotype** CBS 237.37. **India**, from the seeds of *Cicer arietinum*, deposited in CBS Jun. 1965, S. Sinha, CBS 534.65. **Unknown origin**, from an unknown substrate, deposited in CBS Feb. 1930, F. Labrousse, CBS 206.30.

Ascochyta sp. 1

Specimens examined: Australia, from a leaf of *Pisum sativum*, deposited in CBS Sep. 1984, G.H. Boerema, CBS 372.84 = PD 80/1246; from a leaf of *Pisum sativum*, deposited in CBS Sep. 1984, G.H. Boerema, CBS H-9078, culture CBS 373.84 = PD 80/1247.

Notes: These two strains were deposited as "*Ascochyta fabae*", but phylogenetically they are distinct from the authentic cultures of *As. fabae* (CBS 524.77, CBS 649.71 and PD 83/492). This species is probably a novel species, and will be described after further study.

Ascochyta sp. 2

Specimens examined: Sweden, Uppland, from Lathyrus vernus, May 1987, K. & L. Holm, CBS 113797 = UPSC 2222.



Fig. 23. Ascochyta pisi (CBS 122785). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidia. I. Section of pycnidium. J–K. Conidiogenous cells. L. Conidia. Scale bars: G = 200 µm; H–I = 20 µm; J–K = 5 µm; L = 10 µm.

Notes: Isolate CBS 113797 was received as "*Didymella astragalina*". However, it was distant from other *Didymella* species in the multi-locus phylogenetic tree, and clustered in the *Ascochyta* clade. The original host of *D. astragalina* is *Astragalus cicer*. Since the type of *D. astragalina* was unavailable for examination, it still needs to be confirmed if CBS 113797 represents a new species or is conspecific to *D. astragalina*.

Ascochyta syringae Bres., Hedwigia 33: 207. 1894.

Specimen examined: The Netherlands, from seed capsule of Syringa vulgaris, P.D. Wageningen, deposited in CBS Jul. 1972, G.H. Boerema, CBS 545.72.

Ascochyta versabilis (Boerema *et al.*) Q. Chen & L. Cai, comb. nov. MycoBank MB814132.

Basionym: Phoma versabilis Boerema *et al.*, Persoonia 16: 154. 1996.

Description (Boerema & de Gruyter 1998).

Specimens examined: Germany, Westfalen, Oberdresselendorf, from stems of *Cardamine impatiens*, Oct. 1925, A. Ludwig (holotype L 995.229.369). The Netherlands, Wageningen, from a stem of *Silene* sp., deposited in CBS Jun. 1997, CBS 876.97 = PD 82/1008.

Notes: An authentic isolate of *Phoma versabilis* (CBS 876.97), which morphologically agrees well with the original description of this species (Boerema *et al.* 2004), grouped in the *Ascochyta* clade. Thus, *Ascochyta versabilis* was introduced as a new combination.

Ascochyta viciae Lib., Pl. crypt. Arduenna, fasc. 4: no. 356. 1837.

≡ Septoria viciae (Lib.) Westend., Herb. crypt. Belg.: no. 1151. 1857.
 ≡ Phyllosticta viciae (Lib.) Cooke, Handb., Brit. Fungi 1: 452. 1871.

Specimen examined: The Netherlands, Baarn, Praamgracht, from a leaf of Vicia sepium, Jun. 1968, H.A. van der Aa, CBS H-9121, culture CBS 451.68.

Ascochyta viciae-pannonicae Odřej, Biológia (Bratislava) 25: 685. 1970.

Specimen examined: Czech Republic, from a leaf of Vicia pannonica, deposited in CBS May 1992, CBS 254.92 = CCM F-241.

Clade 10: Phomatodes

Phomatodes Q. Chen & L. Cai, gen. nov. MycoBank MB814062.

Etymology: Name after its phoma-like conidia.

Conidiomata pycnidial, globose to subglobose, on agar surface or immersed, solitary or confluent, ostiolate. *Pycnidial wall* pseudoparenchymatous, 3–5-layered, outer wall pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to doliiform. *Conidia* cylindrical to allantoid, hyaline, thin-walled, smooth, aseptate, guttulate.

Type species: Phomatodes aubrietiae (Moesz) Q. Chen & L. Cai.

Phomatodes aubrietiae (Moesz) Q. Chen & L. Cai, comb. nov. MycoBank MB814133. Fig. 24.

Basionym: Sclerophomella aubrietiae Moesz, Choroby Szkodn. Rosl. 3: 144. 1926.

= Phoma aubrietiae (Moesz) Boerema, Gewasbescherming 1: 66. 1970.

Description from ex-epitype culture (CBS 627.97): Conidiomata pycnidial, solitary, globose to subglobose, glabrous, semiimmersed or immersed, $110-255(-290) \times 90-215(-245) \mu m$. Ostiole single, slightly papillate. Pycnidial wall pseudoparenchymatous, 4–6 layered, 18–24.5 µm thick, composed of isodiametric cells, Conidiogenous cells phialidic, hyaline, smooth, ampulliform to dolliform, 4.5–6.5 × 3.5–5 µm. Conidia ellipsoidal to cylindrical, smooth- and thin-walled, aseptate, 6–8.5 × 2.5–3 µm, with 2(–4) large polar guttules. Conidial matrix white.

Culture characteristics: Colonies on OA, 25–30 mm diam after 7 d, margin regular, with concentric rings, woolly, grey to pale olivaceous; reverse olivaceous. Colonies on MEA 15–20 mm diam after 7 d, margin regular, fluffy, greenish olivaceous to olivaceous; reverse concolourous. Colonies on PDA, 35–40 mm diam after 7 d, margin regular, floccose, smoke-grey; reverse dark olivaceous. NaOH test negative.

Specimens examined: Albania, from dead stalks of Aubrietia gracilis (holotype BP 12773). The Netherlands, Bodegraven, from seed of Aubrietia hybrida cv. Superbissima, deposited in CBS Aug. 1967, G.H. Boerema, CBS H-16154, culture CBS 383.67 = PD 65/223; from a stem of Aubrietia sp., Mar. 1997, J. de

Gruyter (epitype designated here CBS H-16155, MBT202503, culture exepitype CBS 627.97 = PD 70/714).

Notes: The holotype of Sclerophomella aubrietiae was collected from Aubrietia gracilis in Albania, with conidia measuring $5-10 \times 2-3 \mu m$ (Boerema & Valckx 1970). The conidial dimensions of our selected epitype (CBS H-16155, ex-epitype culture CBS 627.97) agree well with that of the original description.

Phomatodes nebulosa (Pers.) Q. Chen & L. Cai, comb. nov. MycoBank MB814134. Fig. 25.

Basionym: Sphaeria nebulosa Pers., Observ. Disp. Mycol. 2: 69. 1800.

≡ Phoma nebulosa (Pers.) Berk., Outl. Brit. Fung. (London): 314. 1860.

Description from culture (CBS 100191): Conidiomata pycnidial, solitary or aggregated, globose to subglobose, glabrous, produced on the agar surface or immersed. 125–185 × 105–135 µm. Ostiole single, conspicuously papillate. Pycnidial wall pseudoparenchymatous, 3-5-layered, 20-37 µm thick, brown, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, 7-9 × 4.5-8(-9.5) µm. Conidia cylindrical, smooth- and thin-walled, aseptate, $5-7 \times 1.5-2.5 \mu m$, with (1-)2-6(-8)large polar guttules. Conidial exudates not recorded.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular, floccose, greenish olivaceous, abundant pycnidia visible near the centre of colony; reverse dark olivaceous, pale greenish olivaceous near the margin. Colonies on MEA 40–45 mm diam after 7 d, margin regular, white with a greenish olivaceous concentric ring; reverse concolourous. Colonies on PDA, 40–45 mm diam after 7 d, margin regular, floccose, white, abundant pycnidia near the centre; reverse white in outer ring, darkening towards the centre of the colony via buff, hazel to black. NaOH test negative.

Specimens examined: **Poland**, near Gryfice, from *Thlaspi arvense*, deposited in CBS Dec. 1997, collected by J. Marcinkowska, CBS 100191. **The Netherlands**, from a stem of *Mercurialis perennis*, deposited in CBS Jan 1993, J, de Gruyter, CBS 117.93 = PD 83/90; from a leaf of *Armoracia rusticana*, deposited in CBS Jul. 1996, collected by H.A. van der Aa, CBS 740.96.

Notes: Isolates CBS 100190 and CBS 100191 were identified as "*Didymella macropodii*" in Boerema *et al.* (2004), and two other isolates obtained in this study (CBS 740.96, PD 84/512) were also received as "*D. macropodii*". In the phylogenetic analyses, CBS 100191 and CBS 740.96 clustered with the reference culture of *Phomatodes nebulosa* (CBS 117.93), but are distant from reference culture of *D. macropodii* (CBS 100190, data not shown). In addition, the morphological features of this isolate (CBS 100191) are essentially similar to that of *Phomat. nebulosa* (de Gruyter *et al.* 1993, Boerema *et al.* 2004), and different from *D. macropodii* (Boerema & de Gruyter 1998, Boerema *et al.* 2004), thus we concluded that cultures CBS 100191 and CBS 740.96 were more appropriately classified as *Phomat. nebulosa*.

Clade 11: Calophoma

Calophoma Q. Chen & L. Cai, gen. nov. MycoBank MB814063.



Fig. 24. Phomatodes aubrietiae (CBS 627.97). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidium. I–J. Conidiogenous cells. K. Conidia. Scale bars: G = 100 µm; H = 20 µm; I–K = 5 µm.

Etymology: Calo = $\kappa \dot{\alpha} \lambda \lambda \sigma \zeta$ in Greek, beauty kalos (Greek), beautiful, good; *phoma* = phoma-like morphology.

Conidiomata pycnidial, subglobose to irregular, on agar surface or immersed, solitary or confluent, ostiolate, or with an elongate neck in older cultures. *Micropycnidia* present. *Pycnidial wall* pseudoparenchymatous, 2–6-layered, outer wall pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, globose to flaskshaped, ampulliform to doliiform. *Conidia* variable in size and shape, *i.e.* subglobose, subcylindrical, ellipsoidal, somewhat obclavate-fusiform, hyaline or becoming slightly brown, smoothand thin-walled, aseptate, occasionally large 1-septate conidia occur that are eguttulate or guttulate. *Chlamydospores* only occur in one species, uni- or multicellular, unicellular intercalary, guttulate, thick-walled, multicellular irregular dictyo/phragmosporous, somewhat botryoid and in combination with unicellular chlamydospores.

Type species: Calophoma clematidina (Thüm.) Q. Chen & L. Cai.

Calophoma aquilegiicola (M. Petrov) Q. Chen & L. Cai, comb. nov. MycoBank MB814135.

Basionym: Phoma aquilegiicola M. Petrov, Trudy Bot. Inst. Akad. Nauk S.S.S.R, Ser. 1, Fl. Sist. Vyssh. Rast : 281. 1933. Description (Boerema *et al.* 1997).

Specimens examined: **New Zealand**, Auckland, from fading leaves of *Thalictrum dipterocarpum*, Jul. 2004, C.F. Hill, CBS 116402. **The Netherlands**, from a stem of *Aconitum pyramidale*, deposited in CBS Jan 1996, CBS 107.96 = PD 73/598; from a stem of *Aquilegia* sp., deposited in CBS Jan 1996, CBS 108.96 = PD 79/611; from a stem of *Aquilegia* sp., deposited in CBS Jan 1996, CBS 109.96 = PD 83/832. **Unknown origin**, from *Aquilegia* sp., deposited in CBS Jan 1996, CBS Jul. 1931, R. Laubert, CBS 107.31.

Notes: The holotype of *Phoma aquilegiicola* was from dry stalks of *Aquilegia vulgaris* collected in Russia. Isolate CBS 107.31 was originally identified as *Ascochyta aquilegiae*, but in the phylogenetic analysis it appears indistinguishable from four representative cultures of *Calophoma aquilegiicola*. This species is morphologically and phylogenetically closely related to *Ca. glaucii*. Clarification of their relationship awaits future studies.

Calophoma clematidina (Thüm.) Q. Chen & L. Cai, comb. nov. MycoBank MB814136. Fig. 26.

Basionym: Ascochyta clematidina Thüm., Bull. Soc. Imp. Naturalistes Moscou 55: 98. 1880.

≡ Phoma clematidina (Thüm.) Boerema, Verslagen Meded. Plantenziektenk. Dienst Wageningen (Jaarboek 1978) 153: 17. 1979.

Description from ex-epitype culture (CBS 108.79): Conidiomata pycnidial, solitary, globose to subglobose, mostly with some hyphal outgrows, produced on the agar surface or immersed, (120-)135-165 × 85-130 µm. Ostioles 1(-3), conspicuously papillate. Pycnidial wall pseudoparenchymatous, 2-4-layered, 13-21 µm thick, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, 5.5-7.5 × 4-7 µm. Conidia ellipsoidal to cylindrical, smooth- and thin-walled, aseptate or occasionally 1-septate, $4.5-7 \times 2-3 \mu m$, with (0-)2-4(-8) polar guttules. Conidial matrix pale pink. Chlamydospores usually scanty, uni- or multicellular, unicellular intercalary, guttulate, thick-walled, greenbrown, 8-10 µm diam, multicellular irregular dictyo/phragmosporous, somewhat botryoid and in combination with unicellular chlamydospores, tan to dark brown, 3-50 × 12-25 µm (Woudenberg et al. 2009).



Fig. 25. Phomatodes nebulosa (CBS 100191). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidial section. I. Section of pycnidial wall. J–K. Conidiogenous cells. L. Conidia. Scale bars: G = 200 µm; H = 20 µm; I–L = 10 µm.

Culture characteristics: Colonies on OA, 25–30 mm diam after 7 d, margin regular, felty, white, pale brown grey towards the centre; reverse buff with a hazel centric ring in the middle. Colonies on MEA 30–35 mm diam after 7 d, margin regular, wooly, white, olivaceous near the centre; reverse concolourous. Colonies on PDA, 20–25 mm diam after 7 d, margin regular, felty; white reverse buff in outer ring, darkening towards the centre of the colony via hazel to brown olivaceous. NaOH test negative.

Specimens examined: **The Netherlands**, Spaubeek, from the stem of *Clematis* sp., deposited in CBS Jan 1979, G.H. Boerema (**epitype** CBS H-16193, culture ex-epitype CBS 108.79 = PD 78/522). **UK**, England, from *Clematis* sp., deposited in CBS Jan. 1966, F.T. Last, CBS 102.66.

Notes: Woudenberg et al. (2009) designated an epitype (CBS H-16193 with culture CBS 108.79) for *Phoma clematidina*. *Clematis* spp. are susceptible to different *Phoma s. lat.* species. *Calophoma clematidina* (syn. *Phoma clematidina*) has shown host specificity to *Clematis* hybrids, while *Didymella vitalbina* was isolated exclusively from *Cl. vitalba*, and such isolates were initially misidentified as *Phoma clematidina* (Woudenberg *et al.* 2009).

Calophoma clematidis-rectae (Petr.) Q. Chen & L. Cai, comb. nov. MycoBank MB814137. Fig. 27.

Basionym: Coniothyrium clematidis-rectae Petr., Feddes Repert Spec. Nov. Regni Veg. Beih. 42: 356. 1927.

≡ *Phoma clematidis-rectae* (Petr.) Aveskamp *et al.*, Stud. Mycol. 65: 25. 2010.

Description (Aveskamp et al. 2010).

Specimen examined: The Netherlands, Boskoop, from *Clematis* sp., deposited in CBS Nov.1963, collected by G.H. Boerema, CBS H-20275, culture CBS 507.63 = PD 07/03486747 = MUCL 9574.

Note: Aveskamp *et al.* (2010) recombined *Coniothyrium clematidis-rectae* into *Phoma*, and we propose a new combination for this species here, *Calophoma clematidis-rectae*.



Fig. 26. Calophoma clematidina (CBS 108.79). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia sporulating on OA. H. Pycnidium. I. Swollen cells. J. Vertical section of pycnidium. K. Section of pycnidial wall. L. Conidia. M–N. Conidiogenous cells. Scale bars: G = 200 µm; H–I = 100 µm; K–M = 10 µm; N = 5 µm.

Calophoma complanata (Tode) Q. Chen & L. Cai, comb. nov. MycoBank MB814138.

Basionym: Sphaeria complanata Tode, Fung. Mecklenb. Sel. (Lüneburg) 2: 21. 1791.

≡ Phoma complanata (Tode) Desm., Ann. Sci. Nat. Bot. 16: 299. 1851. Description (Boerema & de Gruyter 1998).

Specimens examined: **The Netherlands**, Tilburg, from a stem of *Heracleum* sphondy/ium, Nov. 1997, H.A. van der Aa, CBS H-16194, culture CBS 100311; from a stem of *Angelica sylvestris*, deposited in CBS Jun. 1992 J. de Gruyter, CBS 268.92 = PD 75/3.

Calophoma glaucii (Brunaud) Q. Chen & L. Cai, comb. nov. MycoBank MB814139.

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

Description (Boerema et al. 1997).

Specimens examined: **The Netherlands**, near Lisse, from *Dicentra* sp., deposited in CBS Jan 1996, CBS 112.96 = PD 79/765; Wageningen, from a leaf of *Chelidonium majus*, deposited in CBS Jan 1996, CBS 114.96 = PD 94/888.

Calophoma sp. 1

Specimen examined: Switzerland, Gabi am Simplon, from Vincetoxicum officinale, deposited in CBS May 1955, E. Müller, CBS 186.55.

Notes: This isolate resided in a single lineage, which is phylogenetically distinct from other species, and was originally identified as "*Didymella vincetoxici*". Since the type of *D. vincetoxici* was unavailable for study, we are unsure if CBS 186.55 represents a new species or is conspecific to *D. vincetoxici*.

Calophoma vodakii (E. Müll.) Q. Chen & L. Cai, comb. nov. MycoBank MB814140.

Basionym: Didymella vodakii E. Müll., Sydowia 7: 332. 1953.

Specimen examined: Switzerland, Kt. Wallis, Brig, from *Hepatica triloba*, deposited in CBS Jun. 1953, E. Müller (holotype ZT Myc 54939, culture exholotype CBS 173.53).

Notes: The specimen information of CBS 173.53, such as host, locality, collection date and collector are the same as those given in the original description of *Didymella vodakii* when it was published as a novel species (Müller 1953). It is therefore concluded that isolate CBS 173.53 represents the ex-holotype culture of *D. vodakii*.

Clade 12: Phoma

Phoma Sacc., Michelia 2: 4. 1880. emend. Q. Chen & L. Cai. = Atradidymella M.L. Davey & Currah, Amer. J. Bot. 96: 1283. 2009.

Conidiomata pycnidial, sub-globose to elongated, superficial on or immersed into the agar, solitary or confluent, ostiolate. *Pyc-nidial wall* pseudoparenchymatous, 3–7-layered, outer wall pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform. *Conidia* oblong to cylindrical, ellipsoidal, sometimes



Fig. 27. Calophoma clematidis-rectae (CBS 507.63). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia sporulating on OA. H. Pycnidia. I. Conidiogenous cells. J. Section of pycnidial wall. K. Conidia. Scale bars: G = 200 µm; H = 40 µm; I = 5 µm; J–K = 10 µm.

fusiform, hyaline, smooth- and thin-walled, aseptate, guttulate. *Ascomata* pseudothecial, erumpent, subglobose to pyriform, solitary, setose around ostiole, with a short neck. *Hamathecium* pseudoparenchymatous in young ascomata, persisting as septate filamentous remnants in mature ascomata. *Asci* cylindrical to clavate, 8-spored, bitunicate. *Ascospores* fusiform, brown, 1-septate, smooth, slightly constricted at the septum, biseriate or triseriate (Davey & Currah, 2009).

Type species: Phoma herbarum Westend., Bull. Acad. Roy. Sci. Belgique, Cl. Sci. 19: 118. 1852.

Notes: As the sexual morph (*Atradidymella*) of *Phoma herbarum*, type species of the genus *Phoma*, was linked here, the generic features were emended and supplemented with the characters of sexual morph.

Phoma herbarum Westend., Bull. Acad. Roy. Sci. Belgique, Cl. Sci. 19: 118. 1852. emend. Q. Chen & L. Cai. Figs 29–30.

= Atradidymella muscivora M.L. Davey & Currah, Amer. J. Bot. 96: 1283. 2009.

= Phoma muscivora M.L. Davey & Currah, Amer. J. Bot. 96: 1283. 2009.

= Phoma cruris-hominis Punith., Nova Hedwigia 31: 135. 1979.

Description from isotype (BR 5020153305384): Leaf spots elliptical to circular, black. Conidiomata pycnidial, solitary, subglobose,

130–220 × 55–170 μm. Ostiole single. Pycnidial wall pseudoparenchymatous, 3–5-layered, 10–30 μm thick, composed of isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, doliiform. Conidia oblong to ellipsoidal, smooth- and thin-walled, hyaline, sometimes 1-septate, 5–7.5 × 2.5–3.5 μm.

Description of sexual morph: Ascomata pseudothecial, solitary, erumpent from underlying host cell, dark brown, uniloculate, subglobose to ellipsoidal or pyriform, $(75-115 \times 58-95 \ \mu\text{m})$ with short concolourous, occasionally septate setae around ostiole. *Peridium* wall pseudoparenchymatous, 3-layered, 10 μ m thick. *Hamathecium* pseudoparenchymatous in young ascomata, persisting as septate filamentous remnants (1-3 μ m) in mature ascomata. *Asci* cylindrical to clavate, 8-spored, bitunicate, 6–13 μ m, grouped in a small fascicle of 10–20 at base of pseudothecium. *Ascospores* broadly fusiform, golden brown to dark brown, smooth, straight to allantoid, 1-septate, 14–20 × 4–5.5 μ m, slightly constricted at septum, the upper cell sometimes shorter and broader than the lower, biseriate or triseriate (from Davey & Currah 2009).

Description from culture (CBS 615.75): Conidiomata pycnidial, solitary, globose to subglobose, glabrous, semi-immersed or immersed, $130-265 \times 120-240 \ \mu m$. Ostioles 1–2, slightly papillate. Pycnidial wall pseudoparenchymatous, 3–5-layered,



Fig. 28. Phoma neerlandica (CBS 134.96). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H–I. Pycnidia. J. Section of pycnidial wall. K. Conidia. Scale bars: G = 200 µm; H–I = 50 µm; J–K = 10 µm.

14–22 µm thick, composed of isodiametric cells. *Conidiogenous cells* phialidic, hyaline, smooth, dolliform, 5–6.5 × 4–5.5 µm. *Conidia* ellipsoidal to ovoid, smooth- and thin-walled, aseptate, 4.5–6 × 2–3 µm, with 1–2 guttules. *Conidial matrix* white.

Culture characteristics: Colonies on OA, 30–35 mm diam after 7 d, margin regular, abundant pycnidia in concentric rings, giving a salmon colour to the colonies, pale brown near the centre; reverse pale greenish olivaceous in outer ring, towards the centre of the colony via buff to olivaceous. Colonies on MEA 35–40 mm diam after 7 d, margin irregular, flattened, white to greenish olivaceous; reverse greenish olivaceous, white near the margin. Colonies on PDA, 35–40 mm diam after 7 d, margin regular, flattening towards the centre, via hazel to grey-brown; reverse hazel to brown. NaOH test negative.

Specimens examined: **Belgium**, Vlaams-Brabant, Tervuren, from a stem of Solanum lycopersicum (**isotype** of *Phoma herbarum* BR 5020153305384). **Switzerland**, Kt. Graubünden, from *Achillea millefolium*, deposited in CBS Mar. 1951, E. Müller, CBS 304.51. **The Netherlands**, Emmeloord, from the stem of *Rosa multiflora* cv. Cathayensis, deposited in CBS Dec. 1975, G.H. Boerema, CBS 615.75 = PD 73/ 665 = IMI 199779; Naaldwijk, from a stem base of *Nerium* sp., deposited in CBS Sep. 1991, J. de Gruyter, CBS 502.91 = PD 82/276. **UK**, from a leg of woman, Apr. 1977, Y.M. Clayton, **holotype** of "*Phoma cruris-hominis*" IMI 213845; culture ex-holotype of "*Phoma cruris-hominis*" IMI 213845; near Dumfries, from die-back of *Picea excelsa*, deposited in CBS Oct. 1937, T.R. Peace, CBS 274.37. **USA**, Michigan, Wolf Lake, from dried gametophytes of *Funaria hygrometrica*, 2008, M.L. Davey, culture **ex-holotype** of "*Atradidymella muscivora*" UAMH 10909 = CBS 127589; from gametophytes of *Polytrichum juniperinum* growing on the base of an uprooted *Picea mariana* tree, 2008, M.L. Davey, culture ex-holotype of "*Atradidymella muscivora*" UAMH 10909 = CBS 127589 = Pj8-D.

Notes: Atradidymella muscivora was introduced as the sexual morph of a new species "Phoma muscivora", which is

morphologically similar to P. herbarum (Davey & Currah 2009). However, based on the description of P. muscivora, there are no significant morphological differences from P. herbarum, thus we conclude that they are conspecific. Phoma muscivora and At. muscivora are treated as synonyms of Phoma herbarum here, which by default makes it the first report of a sexual morph of the type species of the genus Phoma. The culture exholotype of Phoma cruris-hominis (CBS 377.92), isolated from a lesion on the leg of a woman in London (Punithalingam 1979b), was shown to be genetically identical to the ex-type species of P. herbarum. Two isolates deposited as Phoma acuum (CBS 274.37) and Leptosphaeria millefolii (CBS 304.51) clustered with P. herbarum in the phylogenetic tree, with only two bp differences in tub2 from the authentic strains of P. herbarum (CBS 502.91, CBS 615.75). Due to the similarity based on their DNA sequences, we re-identified these isolates as P. herbarum.

Phoma neerlandica Q. Chen & L. Cai, **sp. nov.** MycoBank MB814141. Fig. 28.

Etymology: Epithet derived from the country of origin, the Netherlands.

Description from ex-holotype culture (CBS 134.96): Conidiomata pycnidial, solitary or aggregated, globose to subglobose, glabrous, produced on the agar surface or immersed, $95-350(-430) \times 80-300 \ \mu\text{m}$. Ostioles 1-2(-3), papillate. Pycnidial wall pseudoparenchymatous, 5-7-layered, $20-35 \ \mu\text{m}$ thick, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, $4-7 \times 3-6.5 \ \mu\text{m}$. Conidia ellipsoidal to cylindrical, sometimes fusiform, smoothand thin-walled, aseptate, occasionally 1-septate, $4.5-8.5(-12) \times 2-3.5 \ \mu\text{m}$, with $1-6 \ \text{minute guttules}$. Conidial matrix rosy-buff to pale salmon.

Culture characteristics: Colonies on OA, 40–45 mm diam after 7 d, margin regular, flattened, olivaceous to grey, abundant pycnidia produced in concentric rings; reverse alternate olivaceous and salmon concentric rings. Colonies on MEA 40–45 mm diam after 7 d, margin regular, wooly, dull green; reverse concolourous. Colonies on PDA, 35–40 mm diam after 7 d, margin regular, woily, pale olivaceous to hazel, white near the margin, black pycnidia produced in some sectors; reverse pale brown olivaceous with salmon patches, white near the margin. NaOH test negative.

Specimen examined: **The Netherlands**, Emmeloord, from a leaf of *Delphinium* sp., deposited in CBS Feb. 1996 (**holotype** HMAS 246691, culture ex-holotype CBS 134.96 = PD 84/676).

Notes: Isolate CBS 134.96 was initially identified as "*Phoma delphinii*". However, we have been unable to trace the type material. In the original description, conidial dimensions of *Phoma delphinii* were given as $3-4 \times 2 \mu m$, while Boerema *et al.* (1997) indicated that conidia of CBS 134.96 were notably variable in shape and size, mostly $4-15 \times 1.5-5 \mu m$, and including some 1-septate large conidia ($15.5-22 \times 4-5 \mu m$). In our observations, the conidial size of CBS 134.96 agrees with that reported by Boerema *et al.* (1997). Since the conidial dimensions of CBS 134.96 and *Phoma delphinii* differ markedly, we prefer to describe this isolate as a new species, *Phoma neerlandica*.

Phoma neerlandica is phylogenetically most closely related to the type species of *Phoma*, *P. herbarum*. They can be morphologically distinguished from each other by the longer, uniseptate conidia in *P. neerlandica* [$4.5-8.5(-12) \times 2-3.5 \mu m$] compared to the aseptate conidia in *P. herbarum* ($4.5-6 \times 2-3 \mu m$).

Clade 13: Leptosphaerulina

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

Ascomata pseudothecial, immersed or erumpent, obpyriform to subglobose, ostiolate. Asci clavate to ovoid, or obovoid, saccate, oblong, bitunicate, 8-spored. Ascospores muriform, oblong, ellipsoidal to obovoid, subfusoid, hyaline to brown, 1(-6)-septate, slightly constricted at the septum, biseriate or triseriate (Saccardo 1905, Inderbitzin et al. 2000, Abler 2003, Crous et al. 2011).

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

Notes: The genus *Leptosphaerulina* was introduced to accommodate the type species *L. australis* (McAlpine 1902), which was isolated from *Prunus armeniaca* (Saccardo 1905). The genus currently comprises about 25 species (McAlpine 1902, Graham & Luttrell 1961, Irwin & Davis 1985, Roux 1986, Inderbitzin *et al.* 2000). *Leptosphaerulina* was first accommodated in the *Pleosporaceae* (Inderbitzin *et al.* 2000, Kodsueb *et al.* 2006), but later found to be related to *Didymella* (Kodsueb *et al.* 2006). Our analysis showed that *Leptosphaerulina* grouped in a distinct clade in the *Didymellaceae*, but that it is distant from *Didymella*.

Leptosphaerulina americana (Ellis & Everh.) J.H. Graham & Luttr., Phytopathology 51: 686. 1961.

Basionym: Pleospora americana Ellis & Everh., N. Amer. Pyren. (Newfield): 336. 1892.

Specimen examined: USA, Georgia, from Trifolium pratense, deposited in CBS May 1955, E.S. Luttrell, CBS 213.55.

Leptosphaerulina arachidicola W.Y. Yen et al., J. Agric. Forest. 10: 167. 1956.

Specimen examined: China, Taiwan, from a leaf of Arachis hypogaea, deposited in CBS May 1959, K.T. Huang, CBS 275.59 = ATCC 13446.

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

On synthetic nutrient-poor agar: Ascomata pseudothecial, solitary to aggregated in clusters, brown, superficial on agar medium, obpyriform to subglobose, $100-150 \times 150-200 \mu m$; ostiole central, up to $30 \mu m$ diam; outer wall covered with short, brown hyphal setae, $5-15 \times 3-5 \mu m$, with obtuse ends. Asci $100-120 \times 35-45 \mu m$, 8-spored, hyaline, obovoid, bitunicate with strongly developed apical chamber, $5-7 \times 2-3 \mu m$. Ascospores multiseriate in asci, hyaline, smooth, with mucoid sheath, 4 transverse septa, and 2-3 vertical, and 1-2 oblique septa, constricted at second vertical septum from apex, ellipsoidal to obovoid,



Fig. 29. Phoma herbarum (BR 5020153305384). A. Type collection packet. B. Pycnidia on host substrate. C. Section of pycnidia. D. Pycnidium with conidia. E. Conidia. F. Section of pycnidial wall. Scale bars: C = 20 µm; D, F = 10 µm; E = 5 µm.

tapering from middle of upper part of ascospore (widest point) to an acutely rounded apex, base obtusely rounded; hamathecial tissue dissolving among asci, and pseudoparaphyses not observed, $(32-)33-27(-40) \times (12-)13-14(-15) \mu m$.

Culture characteristics: Colonies on OA, 20–25 mm diam after 7 d, lobate margins, dirty white near the centre, olivaceous grey to iron-grey near the margin. Colonies on MEA, 20–25 mm diam after 7 d, lobate margins, dirty white near the centre, sienna near the margin; reverse sienna. Colonies on PDA, 20–25 mm diam after 7 d, lobate margins, dirty white near the centre, olivaceous grey near the margin; reverse iron-grey (from Crous *et al.* 2011).

Specimen examined: Kenya, on leaves of *Protea* sp., 1999, culture CBS 116307 = CPC 3712. Indonesia, Lampung, from *Eugenia aromatica*, Dec. 1982, H. Vermeulen, CBS 317.83.

Notes: Leptosphaerulina australis was originally isolated from *Prunus armeniaca* in Australia (Saccardo 1905). The culture collected from Kenya is the first record from *Proteaceae* (Crous *et al.* 2011).

Leptosphaerulina trifolii (Rostr.) Petr., Sydowia 13: 76. 1959.

Basionym: Sphaerulina trifolii Rostr., Bot. Tidsskr. 22: 265. 1899.

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

Clade 14: Neoascochyta

Neoascochyta Q. Chen & L. Cai, **gen. nov.** MycoBank MB814064.

Etymology: Morphologically resembling the genus *Ascochyta*, but phylogenetically distinct.

Conidiomata pycnidial, globose to subglobose, or irregularly shaped, superficial on or immersed into the agar, solitary or confluent, ostiolate, sometimes with a short neck. *Pycnidial wall* pseudoparenchymatous, 2–7-layered, outer wall pigmented, thick. *Conidiogenous cells* phialidic, hyaline, smooth, globose to flask-shaped, short obpyriform, or ampulliform to doliiform. *Conidia* variable in shape, hyaline, smooth- and thin-walled, *i.e.* fusoid to cylindrical, obclavate-ovoid to ellipsoidal, incidentally slight curved, uniseptate or aseptate, eguttulate or guttulate. *Ascomata* pseudothecial immersed or erumpent, solitary or confluent, globose to subglobose, ostiolate. *Asci* cylindrical to subclavate, slightly curved, short pedicellate or sessile, 8-spored, bitunicate. *Ascospores* cylindrical to ovoid, ellipsoidal, hyaline, 1-septate, symmetrical or asymmetrical, constricted at the septum, biseriate or irregular uniseriate.

Type species: Neoascochyta exitialis (Morini) Q. Chen & L. Cai.

Neoascochyta desmazieri (Cavara) Q. Chen & L. Cai, comb. nov. MycoBank MB814142. Fig. 31.

Basionym: Ascochyta desmazieri Cav., Z. Pflanzenkrankh 3: 21. 1893. (as "desmazieresii").

Description from ex-neotype culture (CBS 297.69): Conidiomata pycnidial, solitary or sometimes aggregated, globose to subglobose, mostly with some hyphal outgrows, immersed, 115–280 × 95–165(–235) µm. Ostiole single, papillate or nonpapillate. Pycnidial wall pseudoparenchymatous, 2–4(–5)layered, 15–28 µm thick, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, 6–8.5 × 7.5–11 µm. Conidia cylindrical, hyaline, smooth- and thin-walled, mostly 1-septate, 8.5–18 × 2.5–4 µm, with 4–10(–13) guttules per cell. Conidial exudates not recorded.



Fig. 30. Phoma herbarum (CBS 615.75). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidia. I. Section of pycnidial wall. J. Conidiogenous cells. K. Conidia. Scale bars: G = 100 µm; H = 50 µm; I, K = 10 µm; J = 5 µm.

Culture characteristics: Colonies on OA, 20–25 mm diam after 7 d, margin regular, felty, with concentric rings, white, pale greenish olivaceous near the centre; reverse white in outer ring, darkening towards the centre of the colony via pale salmon, buff to hazel. Colonies on MEA 35–40 mm diam after 7 d, margin regular, felty, whitish, grey greenish olivaceous near the centre; reverse white in outer ring, darkening towards the centre of the colony via buff, hazel to olivaceous. Colonies on PDA, 35–40 mm diam after 7 d, margin regular, similar as on MEA. NaOH test negative.

Specimens examined: Austria, Landwirtschaftl, from *Poaceae*, Mar. 1979, E. Lengauer, CBS H-8993, culture CBS 247.79. Germany, Hohenlieth, from *Lolium perenne*, deposited in CBS Apr. 1969, U.G. Schlösser (neotype designated here HMAS 246690, MBT202505, culture ex-neotype CBS 297.69). Norway, Oclo, from hay, Feb. 1997, M. Torp, CBS H-8935, culture CBS 758.97.

Notes: Attempts to locate the type specimen of *Ascochyta desmazieri* were unsuccessful. This species was first published as *Septoria graminium* var. *Iolii* based on the examination of PI. crypt. No. 1919 of Desmazières, and later was placed in *Asco-chyta* by Cavara (1893) as *As. desmazieri*, with conidia measuring 20–30 × 2 µm. Sprague (1944) emended the conidial range of *As. desmazieri* as 15–20 × 2.8–3.5 µm after examining Desmazières's exsiccatum No. 2169 (Punithalingam 1979a). Punithalingam (1979a) clarified the confusion surrounding *As.*

desmazieri, Septoria sp. and Phoma Iolii, and suggested to retain As. desmazieri as a single species. The morphology of the neotype (HMAS 246690; $8.5-18 \times 2.5-4 \mu m$), which we designated here, agrees with the description of As. desmazieri by Sprague (1944).

The sole isolate deposited in CBS as "Ascochyta agrostidis" (CBS 758.97) was genetically identical to the culture ex-neotype of *Neoascochyta desmazieri* (CBS 297.69). Therefore, we reclassify isolate CBS 758.97 as *Neoa. desmazieri*.

Neoascochyta exitialis (Morini) Q. Chen & L. Cai, comb. nov. MycoBank MB814143. Fig. 32.

Basionym: Sphaerella exitialis Morini, Nuovo Glorn. Bot. Ital. 18: 37. 1886.

≡ Didymella exitialis (Morini) E. Müll., Phytopathol. Z. 19: 407. 1952.

Description from culture (CBS 389.86): Conidiomata pycnidial, solitary, globose to subglobose, mostly with some hyphal outgrows, superficial on or immersed into the agar, $95-150 \times 75-120 \mu m$. Ostiole single, papillate or non-papillate. Pycnidial wall pseudoparenchymatous, 3-5-layered, $22-40 \mu m$ thick, composed of isodiametric or sometimes irregular cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, $6-8 \times 6-9.5 \mu m$. Conidia broadly fusoid to cylindrical, incidentally slightly curved, smooth- and thin-walled, hyaline, uniseptate,



Fig. 31. Neoascochyta desmazieri (CBS 297.69). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidia. I. Section of pycnidium. J. Section of pycnidial wall. K–L. Conidiogenous cells. M. Conidia. Scale bars: G = 200 µm; H = 100 µm; I = 20 µm; J, M = 10 µm; K–L = 5 µm.

 $15.5-25 \times 4-7 \mu m$, with many minute guttules, *ca.* 15-30 guttules per cell. Conidial exudates not recorded.

Culture characteristics: Colonies on OA, 20–25 mm diam after 7 d, margin regular, floccose, white, grey olivaceous near the margin; reverse white in outer ring, olivaceous near the centre. Colonies on MEA 35–40 mm diam after 7 d, margin regular, wooly, pale greenish olivaceous, olivaceous near the centre; reverse concolourous. Colonies on PDA, 30–35 mm diam after 7 d, margin regular, wooly, whitish, hazel near the centre; reverse dull green. NaOH test negative.

Specimens examined: Germany, Monheim, from a leaf of Secale cereale, May 1984, M. Hossfeld, CBS 811.84; from a leaf of *Hordeum vulgare*, deposited in CBS Dec. 1984, CBS H-8939, culture CBS 812.84. Sweden, Uppland, from *Allium* sp., Sep. 1986, O. Constantinescu, CBS 113693 = UPSC 1929. Switzerland, Utzenstorf, from *Triticum aestivum*, deposited in CBS Sep. 1986, CBS 389.86 = INIFAT C86 = MW I 1343. The Netherlands, Gelderland, Laren, from *Triticum* sp. variety Tower, deposited in CBS Mar. 2002, I. de Vires, CBS

110124. **Unknown origin**, unknown substrate, deposited in CBS Aug. 1940, K. Röder, CBS 118.40.

Notes: Isolate CBS 118.40 was initially identified as "*D. arcuata*", CBS 811.84 and CBS 812.84 as "*As. avenae*", CBS 110124 as "*As. skagwayensis*", and CBS 113693 as "*As. allii*". The multilocus analysis revealed no phylogenetic differences among these isolates. Genetically there was nearly no difference among these strains, except a single bp difference of CBS 113693 in tub2. Here we reclassified all these isolates as *Neoascochyta exitialis*.

Neoascochyta graminicola (Punith.) Q. Chen & L. Cai, comb. nov. MycoBank MB814144. Fig. 33. *Basionym: Didymella graminicola* Punith., Mycol. Pap. 119: 2. 1970.

Description from culture (CBS 102789): Conidiomata pycnidial, solitary, subglobose, glabrous, superficial on or immersed into the agar, $195-325 \times 145-270(-300) \mu m$. Ostioles 1–2, slightly



Fig. 32. Neoascochyta exitialis (CBS 389.86). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidia. I. Pycnidial section. J. Section of pycnidial wall. K–L. Conidiogenous cells. M. Conidia. Scale bars: G = 200 μm; H–I = 20 μm; J–M = 10 μm.

papillate. *Pycnidial wall* pseudoparenchymatous, 3–5-layered, 17–24 µm thick, composed of isodiametric cells. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to dolliform, 8.5–10.5 × 6.5–9.5 µm. *Conidia* cylindrical, smooth- and thinwalled, 1-septate, 12.5–17.5 × 4.5–6.5 µm, with 4–8 guttules. *Conidia matrix* white.

Culture characteristics: Colonies on OA, 15–20 mm diam after 7 d, margin regular, floccose, white to hazel, pale olivaceous near the centre; reverse pale olivaceous, white near the margin. Colonies on MEA 15–20 mm diam after 7 d, margin crenate, flattened, pale greenish olivaceous; reverse concolourous. Colonies on PDA, 35–40 mm diam after 7 d, margin dendritic, floccose, white to pale greenish olivaceous; reverse olivaceous. NaOH test negative.

Specimens examined: Belgium, Gembloux, from Hordeum vulgare, deposited in CBS Sep. 1979, J. Fraselle, CBS H-9007, culture CBS 586.79. Germany, Kiel-

Kitzeberg, Schlosskoppelweg, from seeds of *Lolium perenne* or *L. multiflorum*, 1968, U.G. Schlösser (**holotype** IMI 136404); from seed of *Lolium multiflorum*, deposited in CBS Apr. 1969, U.G. Schlösser, CBS 301.69; from *Triticum aestivum*, Apr. 1982, G.M. Hoffmann, CBS H-1614, culture CBS 447.82; Eschweiler, from a leaf of *Hordeum vulgare*, May 1984, M. Hossfeld, CBS H-9017, culture CBS 815.84; Monheim, from a leaf of *Hordeum vulgare*, May 1984, M. Hossfeld, CBS H-9016, culture CBS 816.84. **New Zealand**, Canterbury Province, from a leaf of *Lolium perenne*, Dec. 1999, S. Ganev, culture CBS 102789.

Notes: According to the original literature (Punithalingam 1969), the holotype of *Didymella graminicola* was collected from *Lolium perenne* or *L. multiflorum* in Germany. The culture CBS 301.69 was previously deposited as "Ascochyta sorghi", CBS 447.82 as "*D. exitialis*", CBS 586.79 as "As. graminea", CBS 815.84 and CBS 816.84 as "As. hordei var. americana". In the phylogenetic analysis, these cultures clustered together in a well-supported clade and their sequences of four loci are genetically identical to the authentic culture of *Neoascochyta graminicola* (CBS 102789). As *As. sorghi* was reported to be restricted to sorghum



Fig. 33. Neoascochyta graminicola (CBS 102789). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidium. I–J. Conidiogenous cells. K. Conidia. Scale bars: G = 100 µm; H = 50 µm; I–J = 5 µm; K = 10 µm.

(Punithalingam 1979a), isolate CBS 301.69 from Lolium multiflorum was misidentified. Isolate CBS 447.82 clustered distantly from the ex-type of D. exitialis (CBS 389.86). Ascochyta graminea was originally reported from Cynodon dactylon in Italy (Punithalingam 1979a), whereas the isolate CBS 586.79 was from a different host, Hordeum vulgare, which belongs to the same host family as Neoa. graminicola (syn. D. graminicola). According to the original description of As. hordei var. americana, its conidia ($15-20 \times 4-5(-5.5) \mu m$; Punithalingam 1979a) are hyaline to yellowish brown, wider than those of Neoa. graminicola (hyaline, $14-18(-20) \times 3-4 \mu m$; Punithalingam 1969), which suggests that they are two distinct species. Although isolates CBS 815.84 and CBS 816.84 were both isolated from Hordeum vulgare, the same host of As. hordei var. americana, they were phylogenetically identical to Neoa. graminicola, and reidentified as such.

Neoascochyta europaea (Punith.) Q. Chen & L. Cai, comb. et stat. nov. MycoBank MB814145. Figs 34–35. *Basionym: Ascochyta hordei* var. *europaea* Punith., Mycol. Pap. 142: 95. 1979.

Description from holotype (IMI 164252): Leaf spots elliptical to circular, rosy buff with brown border. *Pycnidia* immersed in leaf surface of *Hordeum vulgaris*, solitary or confluent, subglobose,

50–290 × 40–250 µm. Ostioles 1(–2) on a short neck. Pycnidial wall pseudoparenchymatous, 2-layered, composed of isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, doliiform. Conidia fusoid to cylindrical, sometimes ellipsoidal, smooth- and thin-walled, hyaline to pale brown, 1-septate, 12.5–19.5 × 3–5 µm, with 2–10 guttules per cell.

Description from ex-epitype culture (CBS 820.84): Pycnidia mostly solitary or sometimes confluent, globose to subglobose, with some hyphal outgrows, produced on the agar surface or immersed, $(190-)215-450(-565) \times (150-)200-350(-420) \mu m$. Ostioles 1–4 on a short neck. Pycnidial wall pseudoparenchymatous, 3–5-layered, 27–50 µm thick, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, 7.5–11.5 × 6–9 µm. Conidia fusoid to cylindrical, incidentally slight curved, smooth- and thinwalled, hyaline to pale buff, 1-septate, 14.5–20.5 × 4–5 µm, with many minute guttules, ca. 10–20 guttules per cell. Conidial exudates not recorded.

Culture characteristics: Colonies on OA, 40–45 mm diam after 7 d, margin regular, floccose, dark grey, pycnidia semi-immersed in concentric rings near the margin, grey olivaceous; reverse concolourous. Colonies on MEA 35–40 mm diam after 7 d, margin regular, wooly, pale greenish, olivaceous near the centre,



Fig. 34. Neoascochyta europaea (IMI 164252). A. Type collection packet. B. Pycnidia. C. Pycnidia on host substrate. D. Conidia. Scale bars: B = 50 µm; C = 200 µm; D = 10 µm.

white near the margin; reverse concolourous. Colonies on PDA, 40–45 mm diam after 7 d, margin regular, floccose, smoke-grey with a pale ring near the margin, black pycnidia produced near the centre and a concentric ring; reverse dull green. NaOH test negative.

Specimens examined: Germany, Eschweiler, from a leaf of Hordeum vulgare, May 1984, M. Hossfeld, CBS H-9024, culture CBS 819.84; from a leaf of Hordeum vulgare, May 1984, M. Hossfeld (epitype designated here CBS H-9025, MBT202506, culture ex-epitype CBS 820.84). UK, from leaves of Hordeum vulare., Feb. 1972, T. Fozzard (holotype IMI 164252).

Notes: Conidia from the holotype are mostly 1-septate, $12.5-19.5 \times 3-5 \mu m$, hyaline to pale brown, which agrees well with the original description with conidia $14-16 \times 3-4.5(-5) \mu m$. The morphology of specimens selected in this study agrees with the type as well, and thus CBS H-9025 is chosen as epitype, with the living culture ex-epitype CBS 820.84. *Neoascochyta europaea* mainly occurs in Europe and especially in Great Britain on barley, rye and wheat (Punithalingam 1979a).

Neoascochyta paspali (P.R. Johnst.) Q. Chen & L. Cai, comb. nov. MycoBank MB814147.

Basionym: Phoma paspali P.R. Johnst., New Zealand J. Bot. 19: 181. 1981.

Description (de Gruyter et al. 1998).

Specimen examined: New Zealand, Auckland, Kaikohe, from a dead leaf of *Paspalum dilatatum*, Jan. 1979, P.K. Buchanan (isotype CBS H-7623, culture exisotype CBS 560.81 = PD 92/1569).

Neoascochyta sp. 1

Specimen examined: Argentina, Tandil, from a leaf of *Triticum aestivum*, Oct. 2002, CBS 112524.

Notes: CBS 112524 was initially identified as "*Ascochyta hordei*" and grouped in the same clade with CBS 516.81, another misidentified culture, in the phylogenetic tree. Since the type material of *As. hordei* could not be obtained, the identity of CBS 112524 remains uncertain, and requires further study.



Fig. 35. Neoascochyta europaea (CBS 820.84). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidium. I. Pycnidial section. J. Section of pycnidial wall. K. Conidiogenous cells. L. Conidia. Scale bars: G = 200 μm; H = 100 μm; I = 20 μm; J–L = 10 μm.

Neoascochyta sp. 2

Specimen examined: Italy, Cenreo Richerche sul riso, Mortara, from Oryza sativa, Aug. 1981, CBS H-11964, culture CBS 516.81.

Notes: This isolate was incorrectly identified as "*Didymella graminicola*", and is phylogenetically distant from the authentic culture of this species (CBS 102789). This is a potential new species, and will be described elsewhere.

Neoascochyta sp. 3

Specimen examined: Norway, Oslo, from hay, deposited in CBS Apr. 1997, M. Torp, CBS H-9005, culture CBS 689.97.

Notes: Isolate CBS 689.97 was deposited as "*Ascochyta festu-cae*" and represents a single branch, which was distant from other species in the tree. Since the type of *As. festucae* is unavailable, we could not confirm if CBS 689.97 represents a new species, or is conspecific to *As. festucae*.

Neoascochyta sp. 4

Specimen examined: South Africa, Heilbron, from *Triticum aestivum*, deposited in CBS Sep. 1974, W.J. Jooste, CBS H-9008, culture CBS 544.74.

Notes: Isolate CBS 544.74, originally identified as "*Ascochyta hordei*", clustered sister to *Neoascochyta* sp. 5. This culture was collected from *Triticum aestivum*, while the type of *As. hordei* was from *Hordeum sativum* (Punithalingam 1979a). Since the type material of *As. hordei* was unavailable, the identity of this isolate remains uncertain.

Neoascochyta sp. 5

Specimen examined: South Africa, Potchefstroom, from straw, deposited in CBS Oct. 1972, M.C. Papendorf, CBS H-8974, culture CBS 876.72.

Notes: Isolate CBS 876.72, originally identified as "Ascochyta brachypodii", clustered sister to Neoascochyta sp. 4, which is distinct from other species in the phylogenetic tree. Since the

type material of *As. brachypodii* was unavailable, the identity of this isolate remains uncertain.

Clade 15: Xenodidymella

Xenodidymella Q. Chen & L. Cai, **gen. nov.** MycoBank MB814065.

Etymology: Xeno = $\xi \epsilon vo \zeta$ in Greek, alien, distinct; *didymella* = didymella-like conidia.

Conidiomata pycnidial, globose to subglobose, on agar surface or immersed, solitary or confluent, ostiolate. *Pycnidial wall* pseudo-parenchymatous, 3–9-layered, outer wall pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, globose to flask-shaped, ampulliform. *Conidia* variable in shape, hyaline, smooth-and thin-walled, *i.e.* ellipsoidal to allantoid, subcylindrical, oblong, pyriform, usually aseptate or occasionally 1-septate *in vivo*, mostly guttulate. *Chlamydospores* occasionally present, brown, intercalary, in spiral chains, unicellular, globose to subglobose. *Ascomata* pseudothecial, immersed or erumpent, globose to subglobose, solitary or confluent, ostiolate or poroid. *Asci* cylindrical to subclavate, 8-spored, bitunicate. *Ascospores* obovoid to oblong, clavate, ellipsoidal, sometimes slightly curved, hyaline, 1-septate, symmetrical or asymmetrical, constricted at the septum, biseriate.

Type species: Xenodidymella applanata (Niessl) Q. Chen & L. Cai.

Xenodidymella applanata (Niessl) Q. Chen & L. Cai, comb. nov. MycoBank MB814148. Figs 36–37.

Basionym: Didymosphaeria applanata Niessl, Oesterr. Bot. Z. 25: 129. 1875.

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

= *Phyllosticta argillacea* Bres., Hedwigia 33: 206. 1894.

≡ Phoma argillacea (Bres.) Aa & Boerema, Persoonia 18: 17. 2002.

Description from holotype (M 0275818): Leaf spots circular, brown to black. *Pseudothecia* on leaf surface, solitary, globose to subglobose, $225-265 \times 210-260 \mu m$. *Ostioles* single. *Asci* cylindrical, $50-60 \times 10.5-14.5 \mu m$, 8-spored, biseriate. *Pseudothecia wall* pseudoparenchymatous, composed of isodiametric cells, 5-7-layered, $30-41 \mu m$ thick. *Ascospores* broadly fusiform, $11.5-15.5 \times (4-)5.5-7.5 \mu m$, smooth, straight or slightly curved, hyaline, 1-septate, slightly constricted at the septum, upper cells usually broader than the lower cells.

Description from ex-epitype culture (CBS 195.36): Conidiomata pycnidial, solitary, globose to subglobose, glabrous, produced on the agar surface or semi-immersed, $85-175 \times 60-145 \mu m$. Ostiole single, slightly papillate. Pycnidial wall pseudoparenchymatous, 5-7-layered, $20-25 \mu m$ thick, composed of isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to dolliform, $5.5-8 \times 4.5-6 \mu m$. Conidia ellipsoidal to ovoid, smooth- and thin-walled, aseptate, $5-7 \times 2-3 \mu m$, with several guttules. Conidia matrix white.

Culture characteristics: Colonies on OA, 20–25 mm diam after 7 d, margin regular, crenate, floccose, white, pale olivaceous near the centre; reverse buff to pale brown. Colonies on MEA, 15–20 mm diam after 7 d, margin regular, floccose, white, pale greenish olivaceous near the margin; reverse buff. Colonies on

PDA, 15–20 mm diam after 7 d, margin regular, floccose, white; reverse pale brown olivaceous. Application of NaOH results in a pale reddish discolouration of the agar.

Specimens examined: Germany, near Köningstein, from leaves of Rubus idaeus, Aug. 1893, W. Krieger (holotype of "Phyllosticta argillacea" Fungi saxon. 1187, S). Sweden, Umeå, Västerhiske, from a shoot of Rubus idaeus, Jan. 2000, S. Hellqvist, CBS 115577; from Rubus arcticus subsp. × stellarcticus, Jan. 2000, S. Hellqvist, CBS 115578. The Netherlands, Baarn, from Rubus idaeus cv. 'Rode Radbout', deposited in CBS Apr. 1963, J.A. von Arx, CBS H-11941, culture CBS 205.63; Breda, from stem of Rubus idaeus, 1936, Rietsema (epitype of Didymosphaeria applanata designated here HMAS 246688, MBT202507, culture exepitype CBS 195.36). UK, Shrewsbury, from Rubus idaeus, 1875, Plowright (holotype of Didymosphaeria applanata M 0275818).

Notes: A phoma-like asexual morph of *Didymella applanata* has been described by Corbaz (1957) and Corlett (1981), and later identified by de Gruyter *et al.* (2002) as *Phoma argillacea*. The original description of the asexual morph reported a conidial size of $6-9 \times 2-3 \mu m$, which agrees with the epitype $(5-7 \times 2-2.8 \mu m)$ designated in the present study. *Xenodidymella applanata* is a pathogen of raspberry (*Rubus idaeus*) that was in the past commonly recorded as a sexual morph on this host. Furthermore, it also occasionally occurred on other species of *Rubus* (de Gruyter *et al.* 2002). Strain CBS 115578 showed certain distance from the other three representative strains of *Xenodidymella applanata*, with two bp differences in four sequenced loci.

Xenodidymella asphodeli (E. Müll.) Q. Chen & L. Cai, comb. nov. MycoBank MB814149. Figs 38–39.

Basionym: Didymella asphodeli E. Müll., Sydowia 12: 245. 1958 (1959).

= Ascospora solieri Mont., Ann. Sci. Nat. Bot., sér. 3, 11: 48. 1849. ≡ Phoma solieri (Mont.) Sacc., Michelia 1: 525. 1879.

Description from holotype (ZT Myc 56445): Leaf spots elliptical, pale brown to black. *Pycnidia* abundant, on leaf surface of *Asphodelus albus*, solitary, globose, $(85-)180-280(-360) \times (70-)150-320 \mu m$. Ostiole single, distinctly papillate. *Pycnidial wall* pseudoparenchymatous, 3–4-layered, 15–30 μm thick, composed of oblong to isodiametric cells, outer wall 2–3-layered, brown. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform. *Conidia* broad cylindrical, smooth- and thin-walled, aseptate, 16.5–26 × 5.5–8 μm , guttulate.

Description from ex-epitype culture (CBS 375.62): Conidiomata pycnidial, solitary, globose, with some hyphal outgrows, superficila on or immersed into the agar, 160-385(-445) × 135-350(-400) µm. Ostiole single, distinct papillate. Pycnidial wall pseudoparenchymatous, 3-7-layered, 30-65 µm thick, composed of oblong to isodiametric cells, outer wall twolayered, brown. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, 8.5-12 × 6.5-11 µm. Conidia variable in shape and size, broadly obovoid, pyriform to cylindrical, smoothand thin-walled, aseptate, $14-27(-34) \times 4.5-11(-15) \mu m$, with 20-40 large guttules. Conidial matrix pale pink. Chlamydospores unicellular, produced in and on the agar, brown, intercalary, in spiral chains, globose to subglobose, 14.5-41.5 × 10-37 µm, thick-walled.

Culture characteristics: Colonies on OA, 40–45 mm diam after 7 d, margin regular, flattened, olivaceous, black pycnidia



Fig. 36. Xenodidymella applanata (M 0275818). A. Type collection packet. B. Pseudothecia on host substrate. C. Pseudothecium. D. Section of pseudothecial wall. E. Asci. F. Ascospores. Scale bars: B = 100 µm; C, D = 50 µm; E-F = 5 µm.

produced in concentric rings; reverse iron-grey to olivaceous in concentric rings. Colonies on MEA 35–40 mm diam after 7 d, margin regular, floccose, greenish olivaceous to dark leadenblack, white tufts near the centre; reverse greenish olivaceous to dark leaden-black, hazel near the centre. Colonies on PDA, 40–45 mm diam after 7 d, margin regular, floccose, white to ironblack; reverse hazel to iron-black in concentric rings. NaOH test negative.

Specimens examined: France, Aples Maritimes, Tende, from Asphodelus albus, deposited in CBS Jan. 1962, E. Müller (epitype of *Didymella asphodeli* designated here HMAS 246689, MBT202508, culture ex-epitype CBS 375.62). Italy, Sardinie, from a wilting leaf of *Asphodelus ramosus*, May 1974, W. Gams & J. Stalpers, CBS 499.72. Switzerland, Monte Generoso, Bella Vista, from dead

stems of Asphodelus albus, May 1956, Kt. Tessin (holotype of Didymella asphodeli ZT Myc 56445).

Notes: When Didymella asphodeli was introduced, a description of a sexual morph was provided (Müller 1958). However, in the examination of the holotype, we only observed the asexual morph with large conidia, $16.5-26 \times 5.5-8 \mu m$, which agrees with the conidial morphology of the epitype designated here, $14-27(-34) \times 4.5-11(-15) \mu m$. Müller (1958) also reported a connection between *D. asphodeli* and a pycnidial fungus which was identified as *Phyllostictina solieri* (currently *Phoma solieri*). However, this sexual-asexual link requires molecular verification. The two isolates (CBS 375.62 and CBS 499.72) showed certain



Fig. 37. Xenodidymella applanata (CBS 195.36). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidium. I–J. Conidiogenous cells. K–L. Conidia. Scale bars: G = 100 µm; H = 50 µm; I–L = 5 µm.

distance in phylogeny, and further study is needed to confirm if the two strains represent different species.

Xenodidymella catariae (Cooke & Ellis) Q. Chen & L. Cai, comb. nov. MycoBank MB814150.

Basionym: Sphaeria catariae Cooke & Ellis, Grevillea 5: 95. 1877.

- ≡ *Didymella catariae* (Cooke & Ellis) Sacc., Syll. Fung. (Abellini) 1: 557. 1882.
- = Ascochyta nepeticola Melnik, Novosti Sist. Nizsh. Rast. 5: 178. 1968.
 ≡ Phoma nepeticola (Melnik) Dorenb. & Gruyter, Persoonia 18: 18. 2002.

Description (de Gruyter et al. 2002).

Specimen examined: **The Netherlands**, from the stem of *Nepeta catenaria*, deposited in CBS Mar. 2000, CBS 102635 = PD 77/1131.

Notes: This species was first reported from *Nepeta catenaria* in New Jersey, with ascospores described as biseriate, ellipsoidal, uniseptate, $20 \times 8 \ \mu m$ (Cooke & Ellis 1877). The asexual and the sexual morphs were reported from the same host, with conidia $(4-)5-7(-11.5) \times 2.5-5 \ \mu m$ *in vitro*, and $8-15(-17) \times (2.5-) 3-(4.5-)5 \ \mu m$ *in vivo* (de Gruyter *et al.* 2002).

Xenodidymella humicola (J.C. Gilman & E.V. Abbott) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814151. *Basionym: Phoma humicola* J.C. Gilman & E.V. Abbott, Iowa

State Coll. J. Sci. 1: 266. 1927. Description (de Gruyter *et al.* 1998). Specimen examined: **USA**, Nevada, Death Valley, from a dead leaf of *Franseria* sp., deposited in CBS Apr. 1985, G.H. Boerema, CBS H-16390, culture CBS 220.85 = PD 71/1030.

Clade 16: Neodidymelliopsis

Neodidymelliopsis Q. Chen & L. Cai, gen. nov. Myco-Bank MB814066.

Etymology: Neo = $v \epsilon o$ in Greek, new; in reference to the morphologically similarity with the genus *Didymella*.

Conidiomata pycnidial, globose to subglobose, ellipsoidal, later irregular, superficial on or immersed into the agar, solitary or confluent, ostiolate, or with an elongated neck. Pycnidial wall pseudoparenchymatous, 2-7-layered, outer wall pigmented. Conidiogenous cells phialidic, hyaline, smooth, flask-shaped, ampulliform to short cylindrical. Conidia variable in shape, smooth- and thin-walled, i.e. ovoid to ellipsoidal, cylindrical, allantoid, hyaline to pale brown, or pale yellowish, usually aseptate or occasionally 1-septate in vivo, mostly guttulate. Chlamydospores observed in some species, intercalary or terminal, globose to oval, single or in chains, brown, smooth, sometimes dictyochlamydospores. Ascomata pseudothecial, immersed or erumpent, subglobose to pyriform, solitary or confluent, ostiolate. Asci cylindrical to clavate, sessile or stipitate, 8-spored, bitunicate. Pseudoparaphyses filamentous, 0(-3)-septate. Ascospores subovoid to oblong, ellipsoidal, hyaline, smooth, 1(-3)-septate, symmetrical or asymmetrical, constricted at the septum, bi- to triseriate.



Fig. 38. Xenodidymella asphodeli (ZT Myc 56445). A. Type collection packet. B. Pycnidia on host substrate. C. Pycnidium. D. Section of pycnidial wall. E. Conidia. Scale bars: C = 20 µm; D-E = 10 µm.

Type species: Neodidymelliopsis cannabis (G. Winter) Q. Chen & L. Cai.

Neodidymelliopsis cannabis (G. Winter) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814152.

Basionym: Sphaerella cannabis G. Winter, Hedwigia 11: 145. 1872. ≡ Didymella cannabis (G. Winter) Arx, Beitr. Kryptogamenfl. Schweiz 11: 365. 1962.

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

≡ Phoma cannabis (L.A. Kirchn.) McPartl., Mycologia 86: 871. 1994.

= Didymella urticicola Aa & Boerema, Trans. Brit. Mycol. Soc. 67: 303. 1976.

= Phoma urticicola Aa & Boerema, Trans. Brit. Mycol. Soc. 67: 303. 1976. Description and illustrations (McPartland 1994).

Specimens examined: **The Netherlands**, Baarn, from a leaf of *Urtica dioica*, Dec. 1967, H.A. van der Aa, CBS H-11956, culture CBS 591.67; Wageningen, from a dead stem tip of *Urtica dioica*, Mar. 1973, G.H. Boerema (**holotype** of "*Didymella urticicola*" CBS H-11971, culture ex-holotype CBS 121.75 = ATCC 32164 = IHEM 3403 = IMI 194767 = PD 73/584); Zeist, from packing material, Nov. 1976, G.A. Harrewijn, CBS H-11959, culture CBS 629.76. **Unknown origin**, from *Cannabis sativa*, deposited in CBS Oct. 1937, K. Röder, CBS 234.37.

Notes: Cannabis is the only known host of Neod. cannabis, and records of this species are mainly from countries in Eurasia and North America (McPartland 1994). Initially isolates CBS 121.75 and CBS 591.67 were respectively identified as "Didymella urticicola" and "D. eupyrena". Sequences of all four loci were identical to that of the authentic cultures of Neod. cannabis (CBS 629.76 and CBS 234.37). Furthermore, morphologically there were no significant differences between D. urticicola [conidia $(3-)4-6.5(-8.5) \times (1.5-)2-3(-3.5) \mum$; Boerema 1976] and D. cannabis (conidia $3-8 \times 2-3 \mum$; McPartland 1994). We re-

identified CBS 121.75 and CBS 591.67 as *Neod. cannabis*, and treated *Didymella urticicola* and its asexual morph *Phoma urticicola* as synonyms of *Neod. cannabis*. This new combination was proposed based on the sexual morph of the taxon, and the sexual-asexual connection should be further confirmed. A neotype of the asexual morph of *Neod. cannabis* was designated by McPartland (1994), which was from Germany and deposited in BPI. The asexual stage of *Neod. cannabis* often produces septate conidia *in vivo*, which was considered as a "pseudo-ascochyta" form. Although the oldest epithet for this species is that of *Depazea cannabis* L.A. Kirchn. 1856, we have been unable to confirm this synonymy.

Neodidymelliopsis polemonii (Cooke) Q. Chen & L. Cai, comb. nov. MycoBank MB814153. Figs 40–41. *Basionym: Phoma polemonii* Cooke, Grevillea 13: 94. 1885.

Description from isotype (K 197453): Caulicolous, associated with stem lesions. Conidiomata pycnidial, ellipsoidal to subglobose, on the surface of stems, 148–388 × 120–287 µm. Ostiole single, papillate. Pycnidial wall pseudoparenchymatous, 3–5-layered, 14.5–30.5 µm thick, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, 3.5–5.5 × 3.5–5 µm. Conidia ellipsoidal to cylindrical, thin-walled, smooth, hyaline, 4.5–7 × 2–3 µm, eguttulate.

Description from ex-epitype culture (CBS 109181): Conidiomata pycnidial, solitary or confluent, globose to subglobose, or irregular, covered with hyphal outgrowths, semiimmersed or immersed, $100-340 \times 75-235$ µm. Ostioles


Fig. 39. Xenodidymella asphodeli (CBS 375.62). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H–I. Pycnidia. J. Pycnidial section. K. Section of pycnidial wall. L. Chlamydospores in chains. M–N. Conidiogenous cells. O. Conidia. Scale bars: G = 200 µm; H–J, L = 50 µm; K = 20 µm; M–N = 5 µm; O = 10 µm.



Fig. 40. Neodidymelliopsis polemonii (K 197453). A, D. Type collection packet. B. Pycnidia on host substrate. C. Pycnidium. E. Conidiogenous cells. F. Section of pycnidial wall. G. Section of pycnidium. H. Conidia. Scale bars: B = 200 μm; C = 50 μm; E = 2.5 μm; F-G = 10 μm; H = 5 μm.

1–3, with wide openings or developing to elongated necks, slightly papillate or non-papillate. *Pycnidial wall* pseudoparenchymatous, 2–7-layered, 14–19 µm thick, composed of oblong to isodiametric cells, outer layers pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to doliiform, $3.5-7 \times 2.5-6$ µm. *Conidia* ellipsoidal to cylindrical, sometimes allantoid, hyaline, smooth- and thin-walled, aseptate, $5.5-7(-7.5) \times 1.5-3$ µm, with 2(–4) small polar guttules. *Conidial matrix* whitish.

Culture characteristics: Colonies on OA, 30–35 mm diam after 7 d, margin regular, floccose, white, hazel near the colony margin; reverse buff, pale brown near the margin. Colonies on MEA 25–30 mm diam after 7 d, margin regular, floccose, white to pale olivaceous; reverse olivaceous. Colonies on PDA, 20–25 mm diam after 7 d, margin regular, floccose, white to pale greenish olivaceous; reverse dull green. NaOH test negative.

Specimens examined: **The Netherlands**, from *Polemonium caeruleum*, deposited in CBS Jan. 2001, H. de Gruyter, (epitype designated here HMAS 246687, MBT202509, culture ex-epitype CBS 109181 = PD 83/757); Valkenswaard, from *Polemonium caeruleum*, Oct. 1967, H.A. van der Aa, CBS H-9081, culture CBS 375.67. **UK**, Surrey, from stems of *Polemonium coeruleum*, Mar. 1885, M.C. Cooke (isotype K 197453).

Notes: According to the original literature, *Phoma polemonii* was described from the stems of *Polemonium caeruleum* in the UK, with ellipsoidal conidia, $10 \times 3 \mu m$. The conidial dimensions observed in the type specimen in K are $4.5-7 \times 2-3 \mu m$, which is quite different from the original description. We have repeated the measurement several times using 90 conidia in total, and confirmed the conidial dimensions of the isotype as

4.5–7 × 2–3 µm. Morphological characters of our selected epitype (HMAS 246687, ex-epitype CBS 109181) from *Polemonium caeruleum* are consistent with the isotype specimen, although 1-septate, larger conidia occasionally occur. Isolate CBS 375.67 was initially identified as "*Ascochyta polemonii*", but phylogenetically it clustered with *Neodidymelliopsis polemonii*, and was morphologically similar and from the same host, *Polemonium caeruleum*. Therefore, we re-identified this isolate as *Neod. polemonii*.

Neodidymelliopsis sp. 1

Specimen examined: Canada, British Columbia, from a leaf of Achlys triphylla, Jun. 1976, J. Gremmen, CBS 256.77.

Notes: Isolate CBS 256.77, originally identified as "*Ascochyta achlydis*", was phylogenetically distinct from other species in the genus *Neodidymelliopsis*. This isolate occurred on *Achlys triphylla*, which is the same original host of *Ascochyta achlydis*. Since the type of *Ascochyta achlydis* was unavailable, it was unclear if CBS 256.77 represented a new species, or was conspecific to *As. achlydis*.

Neodidymelliopsis sp. 2

Specimen examined: Israel, En Avdat, Negev desert, from soil in desert, Feb. 1996, A. van Iperen, CBS 382.96.

Notes: Isolate CBS 382.96, deposited as "Ascochyta scotinospora", represented a distinct lineage in the phylogenetic tree. Since the type of As. scotinospora was unavailable, it was



Fig. 41. Neodidymelliopsis polemonii (CBS 109181). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse). G. Pycnidia forming on OA. H. Pycnidia. I. Section of pycnidium. J. Conidiogenous cells. K. Conidia. Scale bars: G = 200 µm; H = 100 µm; I = 20 µm; J–K = 10 µm.

unclear if CBS 382.96 represented a new species, or was conspecific to As. scotinospora.

Neodidymelliopsis xanthina (Sacc.) Q. Chen & L. Cai, comb. nov. MycoBank MB814154. Fig. 42.

Basionym: Phoma xanthina Sacc., Michelia 1: 359. 1878.

≡ Macrophoma xanthina (Sacc.) Berl. & Voglino, Atti Soc. Veneto-Trentino. Sci. Nat. Padova 10: 181. 1887.

≡ Ascochyta xanthina (Sacc.) Petr. & P. Syd., Ann. Mycol. 22: 347. 1924.

Description from ex-neotype culture (CBS 383.68): Conidiomata pycnidial, solitary or confluent, globose to subglobose, glabrous, superficial on or immersed into the agar, (310-) 345-535(-600) × 285-530(-565) µm. Ostioles single, papillate. Pycnidial wall pseudoparenchymatous, 2-3-layered, 13-31 µm thick, composed of oblong to isodiametric cells. Conidiogenous cells phialidic, hyaline, smooth, ampulliform, 7-12.5 × 5.5-12.5 µm. Conidia ellipsoidal to allantoid, incidentally slight curved, smooth- and thin-walled, hyaline to pale yellowish, mainly aseptate, $(5-)6.5-11.5 \times 2-4.5 \mu m$, with (0-)2-12(-15) minute polar guttules, occasionally with larger 1septate conidia. Conidial matrix pale brown.

Culture characteristics: Colonies on OA, 45–50 mm diam after 7 d, margin regular, floccose, white, pale grey to olivaceous near

the centre; reverse grey-brown to hazel, white near the margin. Colonies on MEA 40–45 mm diam after 7 d, margin regular, floccose, white, pale greenish olivaceous near the centre; reverse concolourous. Colonies on PDA, 35–40 mm diam after 7 d, margin regular, floccose, whitish, black pycnidia visible near the centre and concentric rings; reverse buff in outer ring, darkening towards the centre of the colony via amber, hazel to brown zones. Application of NaOH resulted in a slight greenish to reddish discolouration.

Specimens examined: **The Netherlands**, Baarn, from leaves of *Delphinium* sp., May 1968, H.A. van der Aa (**neotype designated here** CBS H-8938, MBT202512, culture ex-neotype CBS 383.68); from a leaf of *Delphinium* sp., Jun. 1969, H.A. van der Aa, CBS H-8939, culture CBS 168.70.

Notes: The type of *Phoma xanthina* was from *Delphinium* sp. in France. Loan requests for the type specimen were unsuccessful, and we assume that it has been lost. De Gruyter (2002) provided a description of a representative culture of *P. xanthina* (CBS 383.68 from *Delphinium* sp. in the Netherlands), which was also examined in the present study. CBS 383.68 is chosen as neotype due to its morphological congruence with the original description of this species.

Isolate CBS 168.70 was previously identified as "Ascochyta aquilegiae", and found to cluster with Neod. xanthina in the



Fig. 42. Neodidymelliopsis xanthina (CBS 383.68). A–B. Colony on OA (front and reverse). C–D. Colony on MEA (front and reverse). E–F. Colony on PDA (front and reverse).
G. Pycnidia forming on OA. H. Pycnidia. I. Conidiogenous cells. J. Conidia. Scale bars: G = 200 μm; H = 100 μm; I–J = 10 μm.

present phylogenetic study. Hence, it is considered as conspecific to *Neod. xanthina*.

Clade 17: Nothophoma

Nothophoma Q. Chen & L. Cai, **gen. nov.** MycoBank MB814060.

Etymology: *Notho* = nothus in Greek, fake, close but different; *phoma* = phoma-like morphology.

Conidiomata pycnidial, globose to elongated, or irregular, superficial on or immersed into the agar, solitary or confluent, ostiolate, sometimes with a short neck. *Pycnidial wall* pseudo-parenchymatous, 2–9-layered, outer wall pigmented. *Conidiogenous cells* phialidic, hyaline, smooth, ampulliform to doliiform, sometimes flask-shaped. *Conidia* variable in shape, hyaline but incidentally brown, smooth- and thin-walled, aseptate, *i.e.* ovoid, oblong to ellipsoidal, eguttulate or guttulate.

Type species: Nothophoma infossa (Ellis & Everh.) Q. Chen & L. Cai.

Nothophoma anigozanthi (Tassi) Q. Chen & L. Cai, comb. nov. MycoBank MB814084. Figs 11–12.

Basionym: Phoma anigozanthi Tassi, Bull. Labor. Ort. Bot. Siena 2: 148. 1899.

≡ *Phyllosticta anigozanthi* (Tassi) Allesch, Rabenh. Krypt.-FI. [ed. 2], Pilze 7: 754. 1903.

Description from holotype (N 3622): Leaf spots elliptical to circular, black. *Pseudothecia* solitary, on the surface of leaves, brown, uniloculate, subglobose to globose, $85-125 \times 70-100 \mu m$, ostiolate. *Asci* obpyriform to fusiform, $55-73 \times 17-26 \mu m$, 8-spored, irregular uniseriate. *Ascospores* broadly fusiform to ellipsoidal, $14-20 \times 3.5-5.5 \mu m$, smooth, straight or slightly curved, hyaline, uniseptate, slightly constricted at the septum, guttulate, upper cells usually broader and longer than the lower cells.

Description from ex-epitype culture (CBS 381.91): Conidiomata pycnidial, solitary or aggregated, globose to subglobose, glabrous, olivaceous buff, superficial on or semi-immersed in the agar, $(65-)70-130 \mu m$ diam; conidiomata with age becoming black, broadly globose to irregular, with some white hyphal outgrows and with a clear elongated neck around the ostioles, (145-) 155–280(-300) × $(120-)140-230(-250) \mu m$. Ostioles 1-4(-6), on a distinctly elongated neck (up to 170 μm). Pycnidial wall pseudoparenchymatous, 3-6-layered, $16-41 \mu m$ thick, composed of isodiametric cells, outer wall 2–3-layered, pigmented. Conidiogenous cells phialidic, hyaline, smooth, ampulliform to doliiform, $5-9 \times 4.5-7.5 \mu m$. Conidia ellipsoidal, smoothand thin-walled, aseptate, $3.5-5 \times 1.5-2.5 \mu m$, sometimes with several very small guttules. Conidial matrix creamy white.

Culture characteristics: Colonies on OA, 40–45 mm diam after 7 d, margin regular, powdery due to the abundant pycnidia produced in concentric rings, olivaceous to grey olivaceous; reverse concolourous. Colonies on MEA 40–45 mm diam after

7 d, margin regular, flattened, greenish olivaceous, pale salmon near the margin; reverse concolourous. Colonies on PDA, similar as on OA, but somewhat slower growing, 30–35 mm diam after 7 d, hazel to olivaceous. NaOH spot test: a luteous discolouration on MEA, later changing to dull green to vinaceous-black, from the centre to outer ring.

Specimen examined: Italy, on leaves of Anigozanthos flavidus, Feb. 1862 (holotype N 3622 in SIENA). The Netherlands, from a leaf of Anigozanthus maugleisii, deposited in CBS Jun. 1991, H. Cevat (epitype designated here CBS H-5199, MBT202498, culture ex-epitype CBS 381.91 = PD 79/1110).

Notes: The original description of *Phoma anigozanthi* indicated that this fungus produces aseptate conidia, $4-4.5 \times 2 \mu m$, which is in agreement with our observation of the specimen CBS H-5199 ($3.5-5 \times 1.5-2.5 \mu m$). CBS H-5199 is therefore designated as epitype. *Sphaerella millepunctata* was recorded as the spermogonial state of *Nothophoma anigozanthi* (syn. *Phoma anigozanthi*; Saccardo 1902), and we did observe the asci and ascospores from the holotype of "*Phoma anigozanthi*" from *Anigozanthos flavidus* preserved in herbarium SIENA in Italy. An emended description of the sexual morph of *P. anigozanthi* is therefore provided.

Nothophoma arachidis-hypogaeae (V.G. Rao) Q. Chen & L. Cai, **comb. nov.** MycoBank MB814085.

Basionym: Phyllosticta arachidis-hypogaeae V.G. Rao, Sydowia 16: 275. 1962 (1963).

≡ Phoma arachidis-hypogaeae (V.G. Rao) Aa & Boerema, Persoonia 15: 388. 1993.

Description (de Gruyter et al. 1993).

Specimens examined: India, Poona, from leaves of Arachis hypogaea, Sep. 1962, V. Rao (holotype M.A.C.S. No. 134); Madras, from a leaf of Arachis hypogaea, deposited in CBS Jan 1993, J, de Gruyter, CBS 125.93 = PD 77/1029.

Notes: Nothophoma arachidis-hypogaeae clustered with No. infossa (CBS 123395), but they can be distinguished based on morphology and phylogeny. Conidia of No. arachidis-hypogaeae are narrower than that of No. infossa ($3.2-5.2 \times 1.8-2.4 \mu m vs. 4.5-6 \times 2.5-3.5 \mu m$) (de Gruyter *et al.* 1993, Aveskamp *et al.* 2009a). In the four sequenced loci, CBS 125.93 differs from CBS 123395 in 20 bp.

Nothophoma gossypiicola (Gruyter) Q. Chen & L. Cai, comb. nov. MycoBank MB814087.

Basionym: Phoma gossypiicola Gruyter, Persoonia 18: 96. 2002. Description (de Gruyter 2002).

Specimen examined: USA, Texas, from a leaf of Gossypium sp., deposited in CBS Aug. 1967, G.H. Boerema, CBS H-9006, culture CBS 377.67.

Notes: This species was first described as *Ascochyta gossypii* Woron. in 1914, the holotype of which was collected by N. Woronichin on leaves of *Gossypium* sp. near Abazinka, the former Soviet Union (de Gruyter 2002). However, this name was illegitimate and replaced by a *nomen novum*, *Phoma gossypii-cola* (de Gruyter 2002). Here this species is transferred to the new genus *Nothophoma*.

Nothophoma infossa (Ellis & Everh.) Q. Chen & L. Cai, comb. nov. MycoBank MB814088.

Basionym: Phoma infossa Ellis & Everh., J. Mycol. 4: 102. 1888.

Description and illustrations (Aveskamp et al. 2009a).

Specimen examined: **Argentina**, Buenos Aires Province, La Plata, from leaves of *Fraxinus pennsylvanica*, 2008, A.E. Perello (**neotype** CBS H-20145, culture exneotype CBS 123395).

Nothophoma quercina (Syd.) Q. Chen & L. Cai, comb. nov. MycoBank MB814086.

Basionym: Cicinobolus quercinus Syd., Ann. Mycol. 13: 42. 1915.

≡ Ampelomyces quercinus (Syd.) Rudakov, Mikol. Fitopatol. 13: 109. 1979.

≡ Phoma fungicola Aveskamp *et al.*, Stud. Mycol. 65: 26. 2010. Description (Aveskamp *et al.* 2010).

Specimen examined: Ukraine, Crimea, in the vicinity of Feodosiya, on *Microsphaera alphitoides* from *Quercus* sp., deposited in CBS Dec. 1992, CBS H-20276, culture CBS 633.92 = ATCC 36786 = VKM MF-325.

Notes: This species, originally published as *Cicinobolus quercinus*, was transferred to *Ampelomyces*, and later treated as a *nomen novum* in the genus *Phoma* by Aveskamp *et al.* (2010). According to the phylogenetic analysis in the present study, it clustered in the *Nothophoma* clade, and thus *Nothophoma quercina* was proposed as a new combination.

Microsphaeropsidaceae Q. Chen, L. Cai & Crous, fam. nov. MycoBank MB814155.

Conidiomata pycnidial, immersed or erumpent, subglobose, solitary or confluent, ostiolate. *Pycnidial wall* of *textura angularis*. Conidiogenous cells phialidic, hyaline, ampulliform to doliiform or subcylindrical, or somewhat irregular. Conidia thinwalled, smooth or (sometimes) with ornamentations, pale brown to yellowish or greenish brown, variable in shape, ovoid, globose, cylindrical to bacilliform, ellipsoidal to oblong, 0–1-septate.

Type genus: Microsphaeropsis Höhn., Hedwigia 59: 267. 1917.

Microsphaeropsis Höhn., Hedwigia 59: 267. 1917.

Conidiomata pycnidial, immersed or erumpent, subglobose, solitary or confluent, ostiolate. *Pycnidial wall* of *textura angularis*. *Conidiogenous cells* phialidic, hyaline, ampulliform to doliiform or subcylindrical, with a prominent apical periclinal thickening. *Conidia* thin-walled, smooth or finely roughened, hyaline when young, becoming pale brown to yellowish or greenish brown, variable in shape, ovoid, globose, cylindrical to bacilliform, ellipsoidal to oblong, straight to slightly curved, 0–1-septate.

Type species: Microsphaeropsis olivacea (Bonord.) Höhn., Hedwigia 59: 267. 1917.

Notes: Microsphaeropsis was established by von Höhnel, and was originally placed in the *Montagnulaceae* (von Höhnel 1917). Our phylogenetic analysis clearly indicated that *Microsphaeropsis* is basal to *Didymellaceae*, from which it appears to have a significant evolutionary distance. Conidia of *Microsphaeropsis* usually differ from those of *Didymellaceae* in surface ornamentation and darker colour. For this reason the



Fig. 43. *Microsphaeropsis olivacea* (BPI 797151). A. Conidiomata on host tissue. B. Section through conidiomatal wall, showing chains of chlamydospores. C–E. Conidiogenous cells. F. Brown, 0(–1)-septate conidia. G. Aseptate conidia. Scale bars: A = 200 μm; B–G = 10 μm.

Microsphaeropsidaceae is herewith introduced to accommodate *Microsphaeropsis*.

Microsphaeropsis olivacea (Bonord.) Höhn., Hedwigia 59: 267. 1917. Fig. 43.

Basionym: Coniothyrium olivaceum Bonord., Jahrb. Nassauischen Vereins Naturk. 23–24: 377. 1869.

Description from holotype (BPI 797151): Conidiomata pycnidial, up to 200 µm diam, solitary, dark brown, immersed, becoming erumpent and somewhat papillate at central ostiole, up to 80 µm diam. *Pycnidial* wall pseudoparenchymatous, 4–8-layered, of *textura angularis*, brown, giving rise to chains of brown chlamydospores extending into the host tissue, brown, smooth, thickwalled, ellipsoidal to globose, 6–10 µm diam. *Conidiophores* reduced to conidiogenous cells lining the inner cavity of conidioma. *Conidiogenous cells* hyaline, smooth, subcylindrical to doliiform, 5–7 × 4–7 µm; apex with prominent periclinal thickening. *Conidia* solitary, initially hyaline, smooth, becoming pale brown and finely roughened, 1–2-guttulate, ellipsoidal to subcylindrical with obtuse ends, straight to slightly curved, 0(–1) septate, $(5-)6-7(-8.5) \times (3-)3.5-4$ µm.

Specimens examined: Austria, on stem of *Hedera helix* (holotype BPI 797151, ex herb. Fuckel, ex herb. Boiss). France, Nancy, from needles of *Pirus laricio*, deposited in CBS Apr. 1977, M. Morelet, CBS H-10854, culture CBS 233.77. The Netherlands, Valkenswaard, from dead twigs and pods of *Sarothamnus* sp., Feb 1971, H.A. van der Aa, CBS H-10870, culture CBS 432.71.

Notes: The two cultures studied here closely resemble *M. olivacea*, in having smooth to finely roughened, pale brown, ellipsoidal to subcylindrical, straight to slightly curved conidia, $(5-)6-7 \times 3-4 \mu m$ (*in vitro*). Because they occur on different hosts, however, we refrain from designating any one of these isolates as ex-epitype.

Microsphaeropsis proteae (Crous & Denman) Crous & Denman, Persoonia 27: 32. 2011.

Basionym: Coniothyrium proteae Crous & Denman, S. African J. Bot. 64: 139. 1998.

Description and illustrations (Crous et al. 2011).

Specimen examined: South Africa, Western Cape Province, from *Protea nitida*, Aug. 1996, S. Denman (culture ex-type CBS 111319 = CPC 1425).

DISCUSSION

This study was prompted by the question of how to delineate natural genera in the *Ascochyta-Didymella-Phoma* complex, which represents a dilemma to plant pathologists and mycologists alike (Chilvers *et al.* 2009, Aveskamp *et al.* 2010, Hyde *et al.* 2013). Based on the previous studies by Aveskamp *et al.* (2009a, b, 2010) and de Gruyter *et al.* (2009, 2012), we combined the multi-locus data of *rpb2* with LSU, ITS and *tub2* for phylogenetic analysis, and added more isolates of previously unstudied species. The topology of the single *rpb2* phylogeny is highly similar to the combined four loci tree. In this regard, the *rpb2* gene showed better resolution at the species and generic level than ITS, LSU or *tub2.* Unfortunately, the success rate of the amplification of *rpb2* was not satisfactory.

The family *Didymellaceae* was established to accommodate the majority of species in Phoma s. lat. and related genera by de Gruyter et al. (2009), based on its type genus Didymella. Aveskamp et al. (2010) revised the taxonomy of some monophyletic clades in Didymellaceae. An interesting result generated in the present study was that a well-supported clade comprising Microsphaeropsis species clustered outside the Didymellaceae. That was inconsistent with previous studies, which indicated that the type species of Microsphaeropsis, Mi. olivacea, grouped in Didymellaceae (de Gruyter et al. 2009, 2012, Aveskamp et al. 2010). This is not so surprising, as previous studies were mostly based on LSU / SSU (e.g. de Gruyter et al. 2009) which lacked necessary resolution at genus level and resulted in unresolved polytomies (e.g. Aveskamp et al. 2010). Microsphaeropsis is characterised by small, predominantly aseptate conidia, formed on pycnidial phialides, which are morphologically similar to some species of Phoma and Coniothyrium (Jones 1976, Carisse & Bernier 2002). However, Microsphaeropsis produces pale greenish brown, finely roughened conidia, that differ significantly from the mainly hyaline, smooth conidia observed in Phoma species, and the usually 0-1-septate, verrucose conidia produced from annellides in Coniothyrium s. str. (Morgan-Jones 1974, Carisse & Bernier 2002, Aveskamp et al. 2010, de Gruyter et al. 2012). Additionally, in the study of de Gruyter et al. (2012), Coniothyrium s. str. clustered with the type genus Leptosphaeria in Leptosphaeriaceae, which was in agreement with the results obtained in the present study. Since many species of Microsphaeropsis are still unknown from culture or DNA sequence, further work is needed to resolve species boundaries in this genus.

The genera Boeremia, Leptosphaerulina, Macroventuria and Stagonosporopsis cluster in Didymellaceae, which agrees with the results of Aveskamp et al. (2010). Five Phoma species lacking of chlamydospores were also included in Epicoccum. Species in the former genus Peyronellaea and some that resided in several other lineages (named Groups G, H, I, J sensu Aveskamp et al. 2010) were recombined into Didymella. Furthermore, we demarcated the genera Ascochyta. Didymella and Phoma on the basis of their phylogeny of their respective generic type species, whilst we also introduced nine new genera, which were wellsupported in the molecular phylogenetic analyses, i.e. Allo-Calophoma, Heterophoma, Neoascochyta, Neophoma, didymelliopsis, Nothophoma, Paraboeremia, Phomatodes and Xenodidymella. Among the currently studied 17 genera in Didymellaceae, with the exception of Didymella, the sexual morph is only known from nine genera, *i.e.* Ascochyta, Leptosphaerulina, Macroventuria. Neoascochyta, Neodidymelliopsis, Paraboeremia, Phoma, Stagonosporopsis and Xenodidymella. Presently, all former Didymella species are known from their sexual morphs, although this will change as asexual taxa can now also be accommodated in this genus. The delimitation of Ascochyta, Didymella and Phoma is clarified by the present findings, in which the type species are separated into distinct monophyletic lineages, and all three genera were linked to sexual morphs.

The genera Ampelomyces, Ascochyta (de Gruyter et al. 2009, Aveskamp et al. 2010), Boeremia (Aveskamp et al. 2010), Chaetasbolisia (de Gruyter et al. 2009, Aveskamp et al. 2010, Wijayawardene et al. 2012, Zhang et al. 2012), Dactuliochaeta (Wijayawardene et al. 2012, Zhang et al. 2012), Didymella, Epicoccum, Leptosphaerulina, Macroventuria, Microsphaeropsis, Peyronellaea, Phoma (Aveskamp et al. 2010), Piggotia, Pithoascus (Wijayawardene et al. 2012, Zhang et al. 2012) and Stagonosporopsis (Aveskamp et al. 2010) were formerly placed in the family Didymellaceae. However, Ampelomyces, with the type species Ampelomyces guisgualis, was accommodated in Phaeosphaeriaceae (de Gruyter et al. 2009); Chaetasbolisia needs to be restudied including more taxa (Aveskamp et al. 2010); Microsphaeropsis grouped sister to the Didymellaceae in the Microsphaeropsidaceae in the present study; Pithoascus was recently placed in Microascaceae (Sandoval-Denis et al. 2016); while Dactuliochaeta and Piggotia require more molecular data to validate their taxonomic placements (Hyde et al. 2013). Hence, it was not possible to presently accept these three doubtful genera (Chaetasbolisia, Dactuliochaeta and Piggotia) in Didymellaceae. Moreover, Platychora was previously assigned to Venturiaceae (Barr 1968), but in a later study by Winton et al. (2007) and Zhang et al. (2012), the generic type Platychora ulmi was shown to cluster in Didymellaceae. This genus and the type species should also be reevaluated based on new collections and epitypification (Zhang et al. 2012). We concluded that 17 genera viz. Allophoma, Ascochyta, Boeremia, Calophoma, Didymella, Epicoccum, Heterophoma, Leptosphaerulina, Macroventuria, Neoascochyta, Neodidymelliopsis, Nothophoma, Paraboeremia, Phoma, Phomatodes, Stagonosporopsis and Xenodidymella can presently be supported as members of Didymellaceae.

Morphological characteristics have proven to be relatively conserved in *Phoma s. lat.*, including features such as shape and dimensions of pycnidia, conidiogenous cells and conidia. The relatively simple asexual morphological features of these species could not provide sufficient distinctions for species delimitation. Although these species clustered in different phylogenetic lineages, they share some overlapping morphological features (Table 2), which is similar to the situation in the genus *Septoria* for which it was concluded that reliable identification in future should be based on DNA sequence data linked to morphology and ecology (Quaedvlieg *et al.* 2013, Verkley *et al.* 2013).

In previous years, conidiogenesis and conidial septation used to be regarded as the most important criteria to discriminate species of Phoma and allied genera, especially between Ascochyta and Phoma (Morgan-Jones 1974, Boerema & Bollen 1975, Jones 1976, Punithalingam 1979a, de Gruyter et al. 2009, 2012, Aveskamp et al. 2010). However, conidiogenesis of species in the same genus was later found to differ, such as the annellidic conidiogenous cells in As. pisi (Boerema & Bollen 1975), versus the phialidic conidiogenous cells in As. fabae (Punithalingam 1975). Punithalingam (1979a) elucidated that the annellidic state was the initial stage during pycnidial development in Ascochyta, and that the phialidic state was the final stage that could be observed once pycnidia matured. Under the conditions employed in the present study, we observed all species accommodated in the Didymellaceae to exhibit phialidic conidiogenesis.

Several species belonging to phoma-related genera are known to exhibit some level of host-specificity. For instance, Ascochyta fabae showed pathogenic specialisation for faba bean (Vicia faba), while As. lentis is specific to lentil (Lens culinaris) (Kaiser et al. 1997), Nothophoma infossa (syn. Phoma infossa) is often associated with ash trees (Fraxinus sp.) and No. gossypiicola (syn. Phoma gossypiicola) is reported only on cotton plants (Gossypium spp.) (Aveskamp et al. 2010). However, not all fungal-host associations in Didymellaceae are clearly defined. Although the strains used in the present study were collected globally, cultures for each species are still limited in number and mainly arise from collections made in Europe and the USA. Generally, Asia, Africa and Latin America have been rather poorly represented in previous studies. For many old names, extype cultures are lacking, and holotype specimens could not be traced. To truly elucidate the taxonomy of phoma-like genera, therefore, a conserted global effort is called for not only to recollect previously described species, but also to add isolates from continents that have been largely neglected or undersampled by mycologists and plant pathologists in the past.

ACKNOWLEDGEMENTS

This study was financially supported by the National Natural Science Foundation of China (NSFC 31322001), China. Qian Chen acknowledges the external Cooperation Program of the Chinese Academy of Sciences (GJHZ1310) and NSFC (31110103906) for supporting her visit to CBS. The CBS-KNAW is acknowledged for providing cultures to facilitate this study. Drs Joyce HC Woudenberg, JZ (Ewald) Groenewald and Lorenzo Lombard, and Ms Mieke Starink-Willemse are thanked for support to Q.C. during her visit to CBS. The various fungaria cited in the Materials and Methods section are acknowledged for providing specimens for morphological studies.

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