

# 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* (Thüm.) 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. pedicariae* (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. rumicola* (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. gossypicola* (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 appianata* (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.

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## 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).

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 *Didymellaceae*. 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 *Chaetosphaerionema* (*Phaeosphaeriaceae*) (de Gruyter *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* remain unresolved (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 Höhnelt 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

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