

**Mycosphere Essays 19: Recent advances and future challenges in taxonomy of
coelomycetous fungi**

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Abstract

The application of molecular phylogenetic methods has provided a better understanding of the taxonomy and evolution of coelomycetous fungi. Providing taxonomic placements for orphan genera, re-visiting historic genera, resolving species complexes and polyphyletic genera are progressing with new data continually immersing. Taxonomists need to implement the usage of adopted names of pleomorphic fungi after the introduction of Art. 59.1. In this paper, we summarize the recent advances and future potentials of taxonomic studies of coelomycetous studies.

Keywords – morphology – phylogeny – pleomorphism – species complexes

Introduction

Hyde et al (2011) asked the question if morphology was still relevant in the molecular world. Since then, the application of DNA and protein sequence data in fungal taxonomy has become common practice amongst mycologists and a standard in most publications (Hyde et al. 2013, Ariyawansa et al. 2015). Within the coelomycetous fungi, introduction of new genera or species (Maharachchikumbura et al. 2012, Crous et al. 2015a, b, c, 2016, Li et al. 2015, 2016, Dai et al. 2016, Hyde et al. 2016, Wijayawardene et al. 2016, Tibpromma et al. 2017), resolving species complexes (Phillips et al. 2012, Alves et al. 2014, Damm et al. 2014) and linking sexual-asexual genera (Wijayawardene et al. 2014b, Rossman et al. 2015a, b) or linking asexual-asexual genera (i.e. synasexual) (Crous et al. 2009) are now almost entirely based on sequence analyses. Sequence data analyses have enabled more accurate and reliable delimitation of generic and species boundaries. However, despite these revolutionary approaches in fungal taxonomy, morphology remains important when introducing new taxa, as many coelomycetous genera lack sequence data and have yet to be re-visited since their introduction.

In this paper, we discuss recent advances in taxonomy of coelomycetous fungi and outline future directions.

Species complexes – Cryptic species

Recent phylogenetic analyses have shown that some species are a complex of often morphologically cryptic species, which means that species differentiation is problematic when relying only on morphological characters (Phillips et al. 2008, 2012, Yang et al. 2009, Alves et al. 2014, Damm et al. 2014, Jayawardena et al. 2016). The concept of cryptic species has been discussed in different life modes, including lichen-forming taxa (Crespo & Lumbsch 2010), plant pathogens (Phillips et al. 2012, Damm et al. 2014, Alves et al. 2014, Hyde et al. 2014), and saprobes (Udayanga et al. 2012, 2014). Jeewon & Hyde (2016) provide guidelines to the considerations needed when introducing a new species.

Sequence based taxonomic studies have revealed that several coelomycetous taxa are species complexes, which have now been split into several new species (Maharachchikumbura et al. 2012, Udayanga et al. 2012). Most of these species complexes appear to occur within plant pathogens and thus, recent advances in taxonomy can directly impact on other disciplines such as quarantine/biosecurity and agriculture. Recent changes in the taxonomy of some *Colletotrichum* and *Neofusicoccum* taxa and the bar code gene regions used to differentiate the species complexes are outlined in Table 1.

Although there was a suggestion that *Colletotrichum siamense* is a species complex (Sharma et al. 2015), Liu et al. (2016) tested this hypothesis using a global strain collection based on the GCPSR and coalescent methods. It was reported that their analyses did not support the recognition of any independent evolutionary lineages within *C. siamense sensu lato* as distinct species. They concluded that reproductive isolation, geographic and host plant barriers to gene flow are absent in *C. siamense sensu lato*. Consequently, *Colletotrichum communis*, *C. dianesei*, *C. endomangiferae*, *C. hymenocallidis*, *C. jasmini-sambac* and *C. murrayae* were synonymised under *C. siamense*. It may be highlighted here that although Liu et al. (2016) employed sophisticated phylogenetic and statistical methods, the main dataset had only 161 informative characters. It remains to be seen whether the hypothesis, that *C. siamense* is a single species, will pass through genome-wide sequence analysis in coming years.

Polyphyletic genera and morphologically similar genera

Some genera (e.g. *Camarosporium*, *Phoma*) have been shown to be polyphyletic, being linked to more than one sexual morph or have been placed in more than one family (Kirk et al. 2008, Schoch et al. 2009, de Gruyter et al. 2013, Aveskamp et al. 2010, Hyde et al. 2011, Wijayawardene et al. 2012). Other genera such as *Cytoplea* and *Cyclothyrium* share close morphological characters, and establishing generic boundaries was difficult (Sutton 1980, Wijayawardene et al. 2016).

a. *Camarosporium* Schulzer

The heterogenic nature of *Camarosporium* was mentioned by Sutton (1980). *Camarosporium sensu stricto* resides in *Pleosporineae*, *Pleosporales* (Wijayawardene et al. 2014a, 2016) but Wijayawardene et al. (2014c) showed that an isolate of *C. propinquum* from Italy resided in *Didymosphaeriaceae*, *Massarineae*, *Pleosporales*. Hence, Wijayawardene et al. (2014c) introduced *Pseudocamarosporium* to accommodate *C. propinquum* and four other species of *Pseudocamarosporium*.

Crous et al. (2013) introduced *C. psoraleae* Crous & M.J. Wingf., however, this species has paraphyses and produces microconidia in culture, features that have not been reported in *Camarosporium sensu stricto* (Sutton 1980). In phylogenetic analyses, Wijayawardene et al. (2014c) showed that *C. psoraleae* belongs in *Didymosphaeriaceae* and is a sister clade to *Pseudocamarosporium*; therefore, *Paracamarosporium* was introduced as a new genus.

Table 1 Recently resolved species complexes within *Colletotrichum* spp. and *Neofusicoccum* spp. and gene regions used

Species complex	Currently known species	Gene regions used	References
<i>C. acutatum</i>	31	ITS, ACT, TUB2, CHS-1, GAPDH, HIS3	Damm et al. 2012a
<i>C. boninense</i>	15	ITS, ACT, TUB2, CHS-1, GAPDH, HIS3, CAL	Damm et al. 2012b
<i>C. destructivum</i>	16	ITS, GAPDH, CHS-1, HIS3, ACT, TUB2	Damm et al. 2014
<i>C. gloeosporioides</i>	22 and one sub species	ACT, CAL, CHS-1, GAPDH, ITS	Weir et al. 2012
<i>Neofusicoccum parvum</i>	7	ITS, tef, tub2	Phillips et al. 2012, Dissanayake et al. 2016

Crous et al. (2015b) found that several *Paraconiothyrium* species grouped with *Paracamarosporium* and *Pseudocamarosporium*. Thus, the generic boundaries of *Paracamarosporium* and *Pseudocamarosporium* was expanded to include paraconiothyrium-like taxa. *Neocamarosporium* is not congeneric with *Camarosporium sensu stricto*, and Wijayawardene et al. (2016) showed that it resides in *Pleosporaceae*.

Camarosporium hederiae, introduced by Ellis & Everhart (1900), has brown, phragmosporous conidia, but *Camarosporium sensu stricto* has muriform conidia (Sutton 1980). Wijayawardene et al. (2015) examined two taxa from China and Germany that were morphologically close to *C. hederiae*. However, phylogenetic studies showed that these taxa reside in *Lentitheciaceae*, *Pleosporales*, and they were placed in the new genus *Phragmocamarosporium*, typified with *P. platani* Wijayaw.

Suttonomyces Wijayaw. et al. (in *Massarinaceae fide* Wijayawardene et al. 2015), *Didymello camerosporium* Wijayaw. et al. (in *Didymellaceae fide* Wijayawardene et al. 2016), and *Melanocamarosporium* Wijayaw. et al. (in *Melanommataceae fide* Wijayawardene et al. 2016) have also been introduced to accommodate morphologically similar, but phylogenetically distinct, camarosporium-like taxa. Wanasinghe et al. (2014) introduced *Murilentithecium* Wanasinghe et al. (*Lentitheciaceae*) with *Camarosporium*-like asexual morph.

Unfortunately, the type species of *Camarosporium*, *C. quaternatum* (Hazsl.) Schulz. does not have ex-type strains and thus needs to be epitypified. More than 500 species epithets are listed in Index Fungorum (2017), many of which are based on host association. To confirm their correct generic placement, they would all need to be re-collected, epitypified and sequenced. DNA sequence analyses show the placements of Camarosporium-like taxa in *Pleosporales* (Fig. 1).

Phoma-like taxa

Phoma is a significant plant pathogenic genus and comprises many species epithets (Index Fungorum 2017). Saccardo (1884) and Sutton (1980) broadly defined the generic concept as thin-walled pycnidia containing aseptate, hyaline, short conidia produced by monophialidic, doliiform to flask-shaped conidiogenous cells occurring on herbaceous substrates. However, in its broad definition, *Phoma* also harbours taxa with thick-walled pycnidia, or even septate conidia and also elongate conidia in axenic culture (Boerema 1997, Boerema et al 2004). Moreover, *Phoma* was divided into nine sections by Boerema et al. (2004): sect. *Phoma*, *Heterospora*, *Paraphoma*, *Peyronellaea*, *Phyllostictoides*, *Sclerophomella*, *Plenodomus*, *Macrospora* and *Pilosa*.

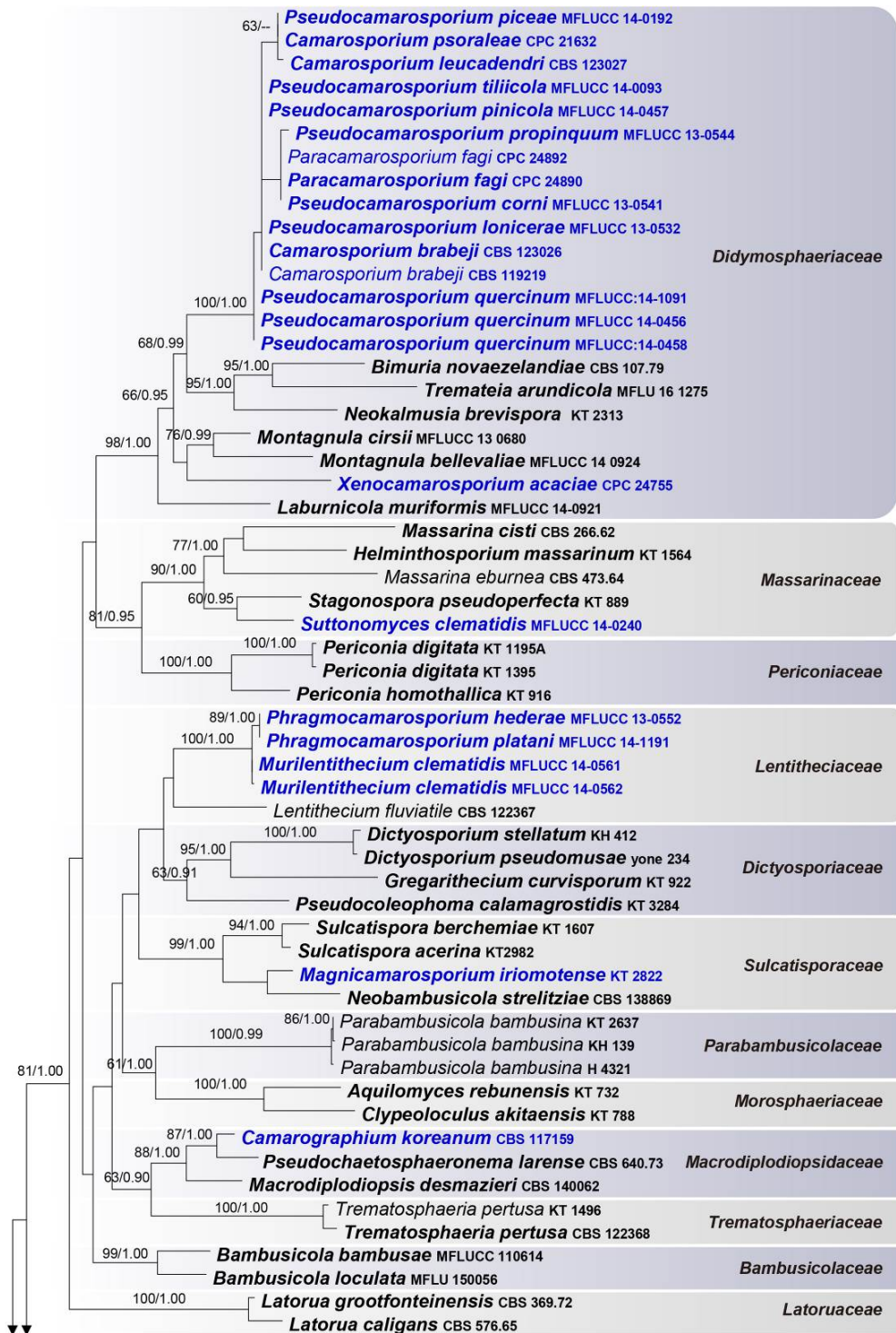


Fig. 1 – The best scoring RAXML tree of distribution of Camarosporium-like taxa generated from analyses of combined of LSU, SSU and TEF1- α sequence data. Bootstrap values of ML analyses (>60 %) resulting from 1000 bootstrap replicates and Bayesian posterior probabilities above 0.95 resulting from 5,000,000 replicates are given at the nodes. The original strain numbers are given after the species names. Classes are differentiated with alternative colours in the right justified column. The tree is rooted to *Hysterium pulicare* (CBS 123337) and *Hysterobrevium mori* (CBS 123563).

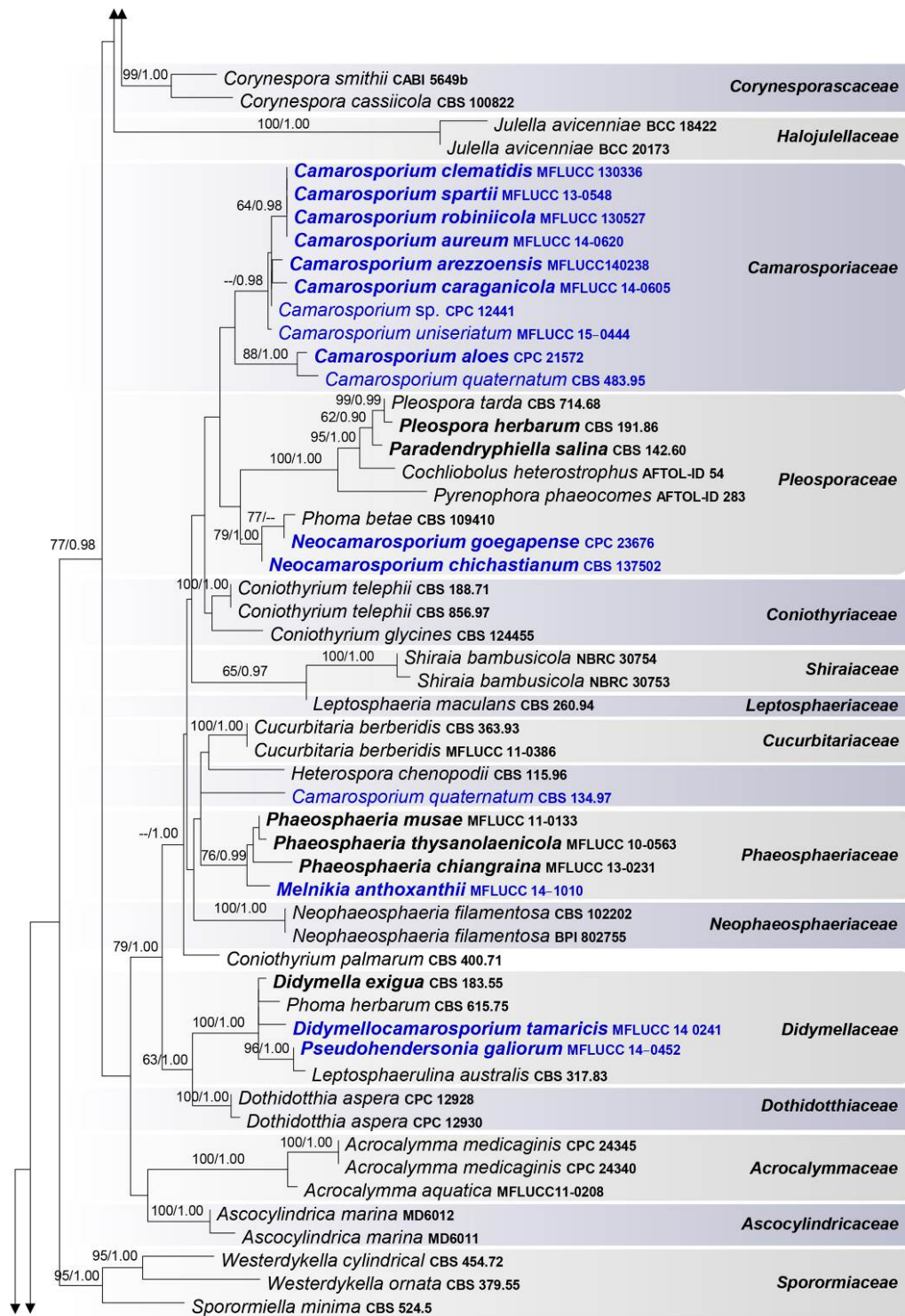


Fig. 1– Continued

Phoma-like asexual morphs are one of the most abundant fungal taxa and can be treated as one of the most common asexual morph of *Pleosporinae* in *Pleosporales*; the largest order of *Dothideomycetes* (de Gruyter et al. 2009, 2010, Aveskamp et al. 2010; Hyde et al. 2011, 2013, Wijayawardene et al. 2012). The phylogenetic placement of *Phoma sensu stricto* was confirmed in *Didymellaceae* (de Gruyter et al. 2009, Aveskamp et al. 2010).

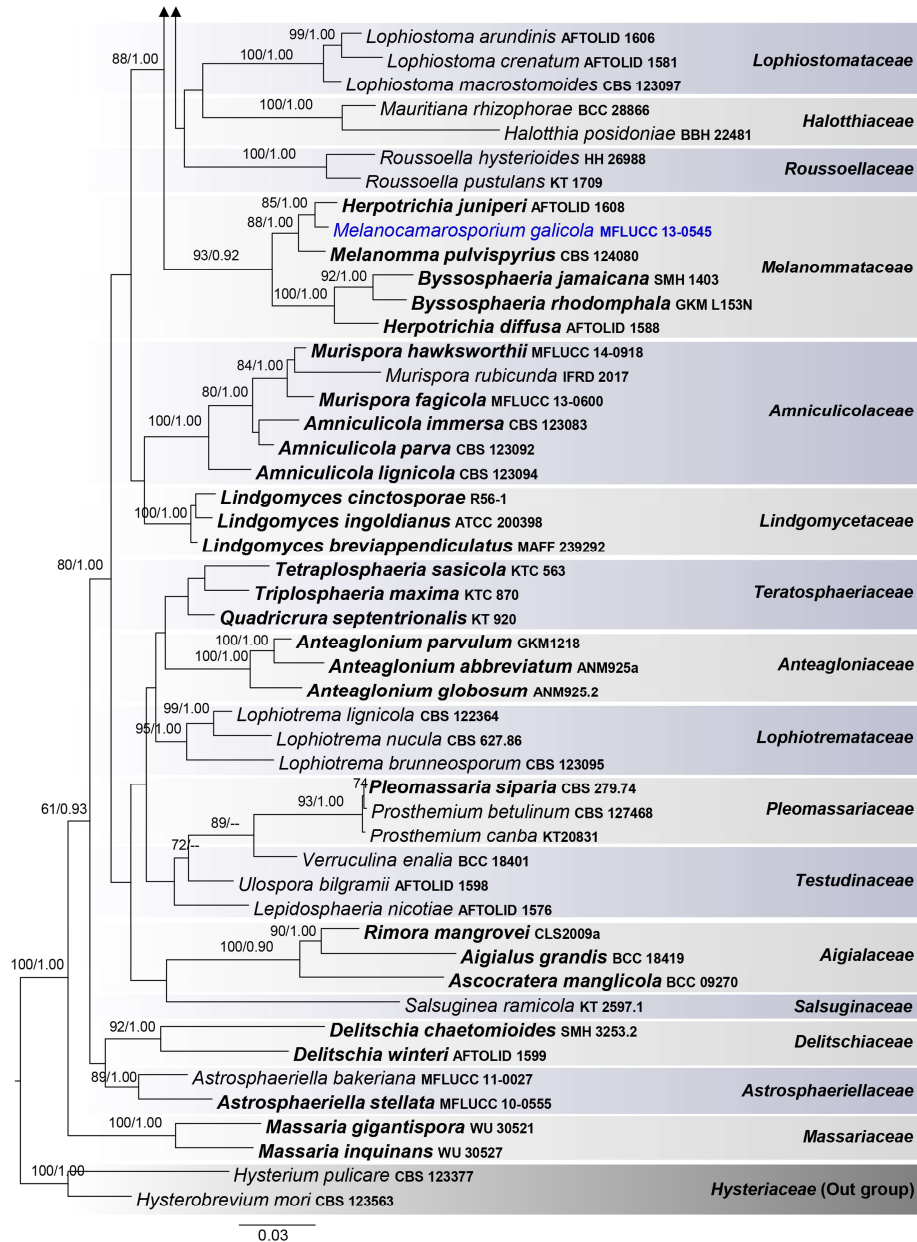


Fig. 1– Continued

However, several phoma-like taxa cluster in different families of *Pleosporineae* and thus several genera have been introduced (de Gruyter et al. 2010, 2013) to accommodate these variants. Table 2 summarizes the recently introduced phoma-like genera in *Pleosporales*. Fig. 2 shows the placements of phoma-like taxa in *Pleosporales*.

Coniothyrium-like taxa

Conidial characters of coniothyrium-like taxa are inadequate to distinguish genera merely based on morphology and, therefore, recent taxonomic studies have relied totally on sequence data analyses (Wijayawardene et al. 2016). Sutton (1980) mentioned that *Coniothyrium sensu stricto* comprises species that produce 0–1-septate conidia but added that ‘the majority of species described in *Coniothyrium* were not congeneric with the type species’. Sutton (1980) defined *Microsphaeropsis* for the taxa with phialidic conidiogenesis and retained species with annellidic conidiogenesis in *Coniothyrium*. Verkley et al. (2004) showed that coniothyrium-like taxa are not monophyletic and several taxa resided in *Didymosphaeriaceae*.

Table 2 Phoma-like genera introduced since Kirk et al. (2008)

Genus	Family	Reference
<i>Allophoma</i>	<i>Didymellaceae</i>	Chen et al. 2015
<i>Boeremia</i>	<i>Didymellaceae</i>	Aveskamp et al. 2010
<i>Calophoma</i>	<i>Didymellaceae</i>	Chen et al. 2015
<i>Heterophoma</i>	<i>Didymellaceae</i>	Chen et al. 2015
<i>Heterospora</i>	<i>Leptosphaeriaceae</i>	de Gruyter et al. 2013
<i>Neascochyta</i>	<i>Didymellaceae</i>	Chen et al. 2015
<i>Neodidymelliopsis</i>	<i>Didymellaceae</i>	Chen et al. 2015
<i>Nothophoma</i>	<i>Didymellaceae</i>	Chen et al. 2015
<i>Paraboeremia</i>	<i>Didymellaceae</i>	Chen et al. 2015
<i>Paraleptosphaeria</i>	<i>Leptosphaeriaceae</i>	de Gruyter et al. 2013
<i>Phomatodes</i>	<i>Didymellaceae</i>	Chen et al. 2015
<i>Pyrenochaetopsis</i>	<i>Cucurbitariaceae</i>	de Gruyter et al. 2009
<i>Subplenodomus</i>	<i>Leptosphaeriaceae</i>	de Gruyter et al. 2013
<i>Xenodidymella</i>	<i>Didymellaceae</i>	Chen et al. 2015

Since Verkley et al. (2004), (Table 3), several coniothyrium-like taxa have been introduced and the generic concept is totally based on DNA sequence analyses. In recent years, new taxa have been introduced that are morphologically very similar (Phukhamsakda et al. 2016a, Wijayawardene et al. 2016).

The introductions are based on phylogenetic data, however in many cases the coelomycete morph is described first and then the sexual morph is found and introduced later (E.g. *Pseudocamarosporium* fide Wanasinghe et al. in prep.). This is likely to happen more and more in the future.

Genera with many species epithets and host based species delimitation

In the past, species in several genera were introduced based on host association, and this caused a proliferation of names (e.g. in *Ascochyta*, *Camarosporium*, *Diplodia*). Slippers et al. (2004) stated that the host is not an important factor in *Botryosphaeriaceae* species differentiation and, thus, Phillips et al. (2012) predicted that ‘many of the names in *Diplodia* are likely to be synonyms’. However, Phillips et al. (2012) did provide several examples of *Diplodia* species that show some host specificity. Thus, it cannot be assumed that genera with many species epithets, but lacking sequence data, can be either consolidated into fewer species or remain in a ‘host-based’ system of classification. Several recent studies introduced new species based on host association and discussed the limitation of occurrence of some species on certain host plants (Chen et al. 2015).

Therefore, re-collecting species that were introduced based on host association and epitypification is an essential step towards resolving their taxonomic status. Besides, this could also affect two other aspects.

1. Some species may not be host-specific, and occur on a range of host plants. Hence one species may have many synonymous epithets since the species occurs on different hosts. DNA sequence analyses are needed to determine whether different species epithets belong to the one species or to different species.

2. Even though morphologically similar, some taxa differ in phylogeny, thus belonging to different genera. In earlier taxonomic works, certain taxa were named based on morphology and host association. Hence, particular species could be named under an incorrect generic name. As Ariyawansa et al. (2014) suggests, re-collecting taxa is essential to clarify the phylogenetic species/generic boundaries and epitypification of certain species. e.g. *Pseudocamarosporium propinquum* fide Wijayawardene et al. (2014c).

Dayarathne et al. (2017) further discussed the necessity of utilization of old names in current classification and nomenclature.

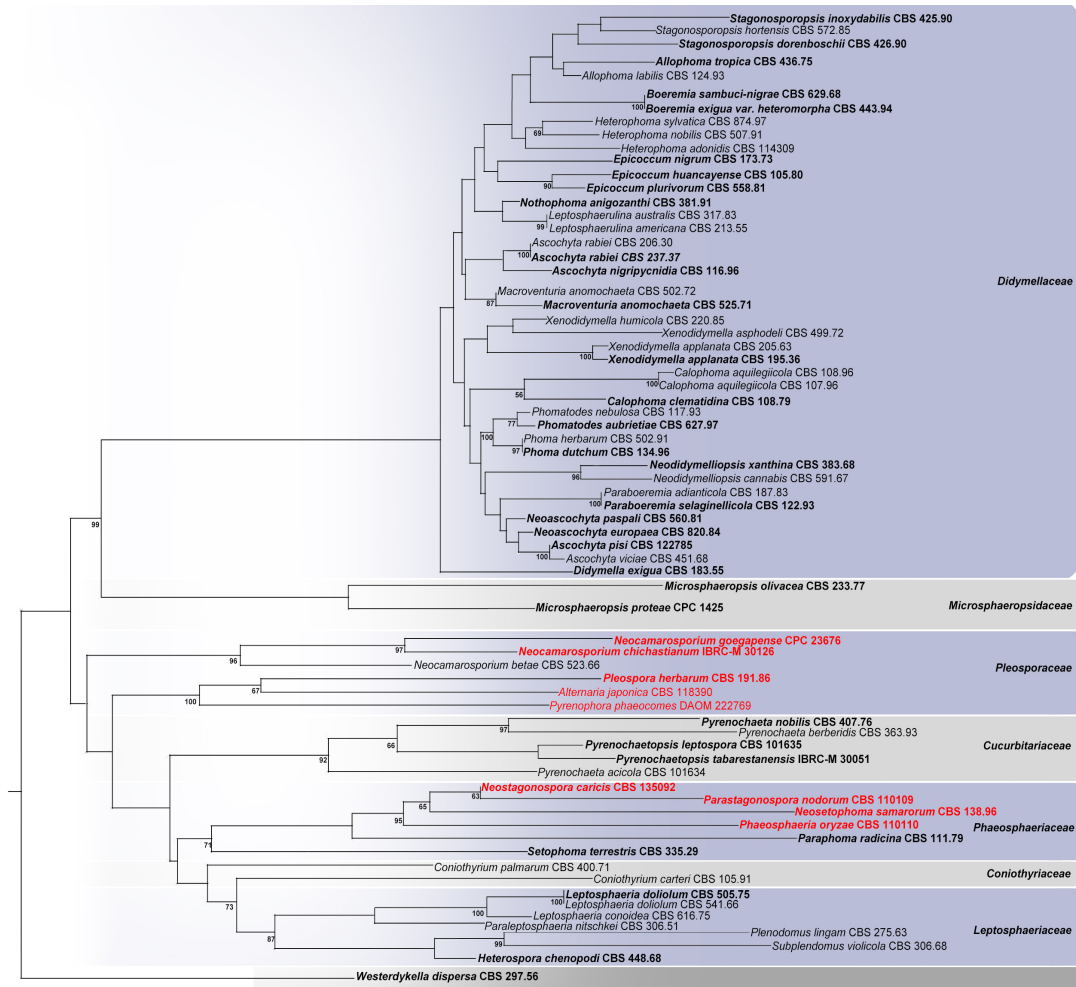


Fig. 2 – The best scoring ML tree of distribution of phoma-like taxa generated from analyses of combined dataset of LSU, ITS, RPB2 and β -tubulin sequences. Bootstrap values of ML analyses (>50 %) resulting from 1000 bootstrap replicates are given at the nodes. The original strain numbers are given after the species names. Families are differentiated with alternative colours in the right justified column. The tree is rooted to *Westerdykella dispersa* (CBS 297.56). Non-phoma-like taxa are shown in red. Ex-type strains are shown in bold.

However, recent study of Ascomycota by Wijayawardene et al. (2017) recognised that naming newly collected taxa based on old name is much more complicated as some genera have not been re-visited for decades.

Need to re-visit poorly known taxa

Approximately 600 genera of coelomycetous fungi lack sequence data and, in general, have not been linked to a sexual morph or placed in a natural taxonomic position (Wijayawardene et al. 2012). Many ‘historic genera and species were previously studied on the basis of morphology alone and without any cultures. It is essential to obtain and maintain cultures of fungi since DNA-based identification is based largely on cultures (Abd-Elsalam et al. 2010). Many genera have not been re-visited since they were first described and it may be difficult to gather detailed illustrations and descriptions of these genera (Wijayawardene et al. 2016).

In some cases, species lack a type specimen or the specimens are in poor condition and therefore re-visiting such species is difficult. For example, Sutton (1975) stated that the type material

of *Coryneum nigrellum* Lacroix is unavailable in Paris herbarium and he thus treated it as a doubtful species.

Table 3 Coniothyrium-like genera introduced since Verkley et al. (2004)

Taxon	Taxonomic placement	Reference
<i>Alloconiothyrium</i>	<i>Didymosphaeriaceae</i>	Verkley et al. 2014
<i>Forliomyces</i>	<i>Sporormiaceae</i>	Phukhamsakda et al. 2016a
<i>Paulkirkia</i>	<i>Floricolaceae</i>	Wijayawardene et al. 2016
<i>Verrucoconiothyrium</i>	<i>Didymosphaeriaceae</i>	Crous et al. 2015b
<i>Xenoconiothyrium</i>	<i>Teratosphaeriaceae</i>	Crous et al. 2011

As the type material of *Coryneum nigrellum* is unavailable, Wijayawardene et al. (2016) described a new species, *C. pruni* Wijayaw. et al. on *Prunus* sp., the same host from which *C. nigrellum* was recorded. Such a move brings up the question of ‘why do we retain names of doubtful species or genera?’

Sutton & Dyko (1989) treated *Diplodia pinea* (Desm.) Kickx., a pine pathogen, as a synonym of *Sphaeropsis sapinea* (Fr.) Dyko & Sutton. However, Phillips et al. (2013) re-examined *Sphaeria pinea* Desm. (Desmazières No 1277 in PC, basionym of *D. pinea*) and concluded that the smaller conidia of this species differentiate it from *Sphaeria sapinea*, the basionym of *Diplodia sapinea*. Furthermore, Saccardo (1880) introduced *Sphaeropsis* for *Diplodia* species with brown, aseptate conidia and Phillips et al. (2013) showed that *Sphaeropsis sensu stricto* (based on *Sphaeropsis visci*) is phylogenetically distinct from *Diplodia sensu stricto*. Thus, it is important to re-visit genera with a large number of species and compare the findings with sequence data analyses.

Recent studies by Crous et al. (2015a, b, c) and Wijayawardene et al. (2016) discussed the taxonomic status of several coelomycetous taxa including historic genera. Re-visiting genera is important to clarify the validity of some genera such as *Microdiplodia* and *Pestalotia* (Wijayawardene et al. 2016).

Genera sharing close morphologies with hyphomycetous taxa

Traditional taxonomy, based largely on morphology, distinguished coelomycetous and hyphomycetous taxa primarily on the sporulating structures or conidiomata (Kendrick & Nag Raj 1979). Kendrick (2000) stated that ‘the production of conidia in enclosed structures or the absence of such enclosure’ is the basic criterion to define a particular fungus as coelomycetous or hyphomycetous. Some genera, such as *Scolicosporium* have been treated as hyphomycetous in some studies (Spooner & Kirk 1982, Seifert et al. 2011).

However, Wijayawardene et al. (2013, 2016) showed that the genus *Scolicosporium* is distinguished by their conidiomata produced beneath the plant integument and thus concluded it is coelomycetous. Confusion among taxonomists on conidiomatal structure (specially qualifying acervuli and sporodochia) has an effect on morphology-based identification and causes further misidentifications. Wijayawardene et al. (2016) pointed out the importance of following basic criteria in Kendrick & Nag Raj (1979) to determine whether a conidiomata is an acervulus or a sporodochium. Thus, acervulus can be recognized as,

1. The hymenium develops beneath an integument entirely of host origin
2. Conidiogenous cells are restricted to the floor of the cavity
3. At maturity, there is usually a split of the host integument, and considerable exposure of the relatively flat hymenium
4. The hymenium layer arises from a more or less well developed pseudoparenchymatous stroma that forms at some level within the tissue of the host (Adopted from Kendrick & Nag Raj 1979)

Wijayawardene et al. (2016) suggested observing a series of vertical sections of immature and mature conidiomata before they can be regarded as sporodochia or acervuli.

Table 4 Summary of adopted names and suppressed names of pleomorphic coelomycetous genera (Agreeing to Article 59.1) (Modified table from Wijayawardene et al. 2016)

Adopted names	Suppressed name(s) (sexual, asexual or synasexual)	References
<i>Apiognomonina</i> Höhn. 1917 <i>Arthriniium</i> Kunze [†]	<i>Discula</i> Sacc. 1884 <i>Apiospora</i> Sacc.	Rossmann et al. 2015a Senanayake et al. 2015, Réblová et al. 2016
<i>Camarosporula</i> Petr. <i>Ascodichaena</i> Butin <i>Blumeriella</i> Arx	<i>Anthracostroma</i> Petr. <i>Polymorphum</i> Chevall. <i>Microgloeum</i> Petr., <i>Phloeosporella</i> Höhn.	Rossmann et al. 2015b Johnston et al. 2014 Johnston et al. 2014
<i>Botryohyphoxylon</i> Samuels & J.D. Rogers <i>Botryosphaeria</i> Ces. & De Not.	<i>Iledon</i> Samuels & J.D. Rogers <i>Fusicoccum</i> Corda	Wijayawardene et al. 2014b, Rossmann et al. 2015b Phillips et al. 2013, Wijayawardene et al. 2014b
<i>Capnodium</i> Mont.	<i>Polychaeton</i> (Pers.) Lév.	Chomnunti et al. 2011, Rossmann et al. 2015b
<i>Chaetomella</i> Fuckel (= <i>Volutellospora</i> Thirum. & P.N. Mathur = <i>Harikrishnaella</i> D.V. Singh & A.K. Sarbhoy) <i>Chlorociboria</i> Seaver ex C.S. Ramamurthi et al. <i>Coma</i> Nag Raj & W.B. Kendr. <i>Coniella</i> Höhn.	<i>Zoellneria</i> Velen. <i>Dothiorina</i> Höhn <i>Ascocoma</i> H.J. Swart <i>Pilidiella</i> Petr. & Syd., <i>Schizoparme</i> Shear <i>Pseudovalsa</i> Ces. & De Not. <i>Digitosporium</i> Gremmen <i>Cyclopetella</i> Petr.	Johnston et al. 2014 Johnston et al. 2014 Alvarez et al. 2016 Rossmann et al. 2015a Johnston et al. 2014 Wijayawardene et al. 2014b, Rossmann et al. 2015b Rossmann et al. 2015a
<i>Cryptosporella</i> <i>Cytospora</i> Ehrenb.	<i>Disculina</i> Höhn. <i>Valsa</i> Fr., <i>Valsella</i> Fuckel, <i>Leucostoma</i> (Nitschke) Höhn., <i>Valseutypella</i> Höhn., <i>Entomosporium</i> Lév., <i>Bostrichonema</i> Ces. <i>Phomopsis</i> (Sacc.) Bubák	Rossmann et al. 2015a Rossmann et al. 2015a Rossmann et al. 2015a Johnston et al. 2014
<i>Diplocarpon</i> F.A. Wolf (= <i>Entomopeziza</i> Kleb.) <i>Diaporthe</i> Nitschke	<i>Adisciso</i> Kaz. Tanaka et al. <i>Sphaceloma</i> de Bary <i>Endothiella</i> Sacc. 1906 <i>Sphaeronaema</i> Fr., <i>Topospora</i> Fr., (= <i>Mastomyces</i> Mont. = <i>Clinterium</i> Fr.), <i>Fuckelia</i> Bonord., <i>Chondropodiella</i> Höhn.	Udayanga et al. 2011, Rossmann et al. 2015a Wijayawardene et al. 2016 Hyde et al. 2013 Rossmann et al. 2015a Johnston et al. 2014
<i>Discosia</i> Lib.* <i>Elsinoë</i> Racib. <i>Cryphonectria</i> Sacc. & D. Sacc. <i>Godronia</i> Moug. & Lév.	<i>Brunchorstia</i> Erikss. <i>Heteropatella</i> Fuckel <i>Ellurema</i> Nag Raj & W.B. Kendr.	Johnston et al. 2014 Johnston et al. 2014 Wijayawardene et al. 2016; Réblová et al. 2016
<i>Gremmeniella</i> M. Morelet <i>Heterosphaeria</i> Grev. <i>Hyalotiopsis</i> Punith.	<i>Leptostroma</i> Fr. <i>Planistromella</i> A.W. Ramaley <i>Eruptio</i> M.E. Barr	Johnston et al. 2014 Hyde et al. 2013 Crous et al. 2009, Hyde et al. 2013, Wijayawardene et al. 2014b

<i>Leptotrochila</i> P. Karst.	<i>Sporonema</i> Desm.	Johnston et al. 2014
<i>Massariovalsia</i> Sacc.	<i>Melanconiopsis</i> Ellis & Everh.	Rossman et al. 2015a
<i>Mastigospora</i> Höhn.	<i>Wuestneiopsis</i> J. Reid & Dowsett	Rossman et al. 2015a
<i>Mazzantia</i> Mont.	<i>Mazzantiella</i> Höhn.	Rossman et al. 2015a
<i>Melanconis</i> Tul. & C. Tul.	<i>Melanconium</i> Link	Rossman et al. 2015a
<i>Micraspis</i> Darker	<i>Periperidium</i> Darker	Johnston et al. 2014
<i>Monochaetiellopsis</i> B. Sutton & DiCosmo	<i>Hypnotheca</i> Tommerup	Johnston et al. 2014
<i>Neofabraea</i> H.S. Jacks.	<i>Phlyctema</i> Desm. (= <i>Allantozythia</i> Höhn)	Johnston et al. 2014
<i>Ocotomyces</i> H.C. Evans & Minter	<i>Uyucamyces</i> H.C. Evans & Minter	Johnston et al. 2014
<i>Pezicula</i> Tul. & C. Tul.	<i>Cryptosporiopsis</i> Bubák & Kabát (= <i>Lagynodella</i> Petr.)	Johnston et al. 2014
<i>Phacidiopycnis</i> Potebnia (= <i>Potebniamyces</i> Smerlis)		Johnston et al. 2014
<i>Discosporiopsis</i> Petr.)		
<i>Phacidium</i> Fr.	<i>Ceuthospora</i> Grev.	Johnston et al. 2014
<i>Phaeosphaeria</i> I. Miyake	<i>Phaeoseptoria</i> Speg.	Wijayawardene et al. 2014b
<i>Phyllosticta</i> Pers.	<i>Guignardia</i> Viala & Ravaz	Wikee et al. 2011
<i>Pilidium</i> Kunze (= <i>Sclerotiopsis</i> Speg.)	<i>Discohainesia</i> Nannf., <i>Hainesia</i> Ellis & Sacc.	Johnston et al. 2014
<i>Plagiostoma</i> Fuckel	<i>Diplodina</i> Westend.	Rossman et al. 2015b
<i>Ploioderma</i> Darker.	<i>Cryocaligula</i> Minter	Johnston et al. 2014
<i>Pragnopora</i> A. Massal	<i>Pragnopycnis</i> B. Sutton & A. Funk	Johnston et al. 2014
<i>Prillieuxina</i> G. Arnaud	<i>Leprieurina</i> G. Arnaud	Hongsanan et al. 2014
<i>Prosthemia</i> Kunze	<i>Pleomassaria</i> Speg.	Wijayawardene et al. 2014b
<i>Pycnopeziza</i> W.L. White & Whetzel	<i>Acarosporium</i> Bubák & Vleugel ex Bubák (= <i>Chaetalysis</i> Peyrone, <i>Ciliosira</i> Syd.)	Johnston et al. 2014
<i>Pyrenopeziza</i> Fuckel	<i>Cylindrosporium</i> Grev.	Johnston et al. 2014
<i>Rhizothyrium</i> Naumov	<i>Rhizocalyx</i> Petr.	Johnston et al. 2014
<i>Rhytisma</i> Fr.	<i>Melasmia</i> Lév.	Johnston et al. 2014
<i>Scleropezicula</i> Verkley	<i>Cryptosymphodula</i> Verkley	Johnston et al. 2014
<i>Seimatosporium</i> Corda	<i>Discostroma</i> clem.	Réblová et al. 2016
<i>Sphaeropsis</i> Sacc.	<i>Phaeobotryosphaeria</i> Speg.	Phillips et al. 2013; Rossman et al. 2015b
<i>Stamnaria</i> Fuckel	<i>Titaeospora</i> Bubák	Johnston et al. 2014
<i>Stilbospora</i> Pers.	<i>Prosthecium</i> Fresen.	Voglmayr & Jaklitsch 2014; Rossman et al. 2015a
<i>Teratosphaeria</i> Syd. & P. Syd.	<i>Colletogloeopsis</i> Crous & M.J. Wingf., <i>Kirramyces</i> J. Walker et al.	Hyde et al. 2013
<i>Tympanis</i> Tode	<i>Sirodothis</i> Clem. (= <i>Pleurophomella</i> Höhn)	Johnston et al. 2014
<i>Unguiculariopsis</i> Rehm	<i>Deltosperma</i> W.Y. Zhuang	Johnston et al. 2014

+Coelomycetous morph is in bold

* Not accepted in Réblová et al. 2016

Morphology, phylogeny and evolutionary relationship; impact on coelomycetes

Unlike sequence-based phylogenetic analyses, morphology does not show evolutionary relationships between genera that have been placed in the one family or higher taxonomic ranks (Sutton 1980). For example, Sutton (1980) placed *Lecanosticta* and *Stilbospora* together with 43 other genera (including several genera with conidia bearing appendages) in the suborder Blastostromatineae (i.e. conidiogenesis holoblastic, conidiomata stromatic). Recent sequence-based

phylogenetic analyses have shown that *Lecanosticta* and *Stilbospora* have distinct lineages, viz. *Mycosphaerellaceae*, *Capnodiales* (Quaedvlieg et al. 2014, Wijayawardene et al. 2016) and *Stilbosporaceae*, *Diaporthales* (Voglmayr & Jaklitsch 2014; Wijayawardene et al. 2016), respectively. No asexual genera were placed in a natural classification system prior to 1990s and instead were treated as a distinct group, i.e. sub kingdom Deuteromycotina (Ainsworth 1966) although Kendrick (1989) objected to this separate, artificial placement.

Recent phylogenetic studies have shown a complicated picture on generic boundaries drawn from earlier morphology-based studies and this is presented as follows.

1. Morphologically similar but phylogenetically distinct genera
 - a. Camarosporium-like taxa including *Neocamarosporium*, *Paracamarosporium*, *Pseudocamarosporium*, *Didymellocamarosporium*.
 - b. Phoma-like taxa
2. Morphologically distinct genera (in conidial morphology) but close in phylogeny
 - a. *Camarosporium sensu stricto* is a well-known genus with dematiaceous, muriform conidia. Recent phylogenetic analyses showed that several phragmosporous taxa group in *Camarosporium sensu stricto* and these will be introduced as *Camarosporium* species (Wanasinghe et al. in prep).
 - b. Swart & Williamson (1983) established *Vermisporium* with hyaline to sub-hyaline, uniformly thin-walled conidia, which are 10–20 times as long as they are wide. Nag Raj (1993) accepted *Vermisporium* as a distinct genus and recognised ten species. However, Barber et al. (2011) showed that the type species of *Vermisporium*, *V. walkeri* H.J. Swart & M.A. Will. and several other species clusters with *Seimatosporium sensu stricto* (which has 2–4 septate, brown conidia) and thus were treated as a synonym of *Seimatosporium*. Therefore, it is essential to rely largely on phylogenetic analyses in the introduction of species or genera.

One fungus, one name

The dual nomenclature system (Saccardo 1904) of allowing a valid name for both the sexual and asexual morph of a species, ended on 30 July 2011 when the ‘one fungus, one name’ concept was implemented (Hawksworth 2012, Wingfield et al. 2012). Future usage of pleomorphic genera including coelomycetous asexual morphs have been proposed in Johnston et al. (2014), Wijayawardene et al. (2014b), Maharachchikumbura et al. (2015, 2016), Réblová et al. (2016), Rossman et al. (2015a, b). In Table 4, we summarize the adopted names of pleomorphic coelomycetous genera.

Future challenges

In traditional fungal taxonomy, based on morphology, culture-based studies were not common and most historic genera or species lack cultures. Thus, molecular sequences are unavailable for most of these taxa. Hence, re-collecting of historic species and epitypification is a significant challenge for future DNA-based studies. The lack of type specimens or specimens in poor condition also complicates advancement and thus, neotypification and epitypification are essential (Ariyawansa et al. 2015).

There are many habitats where the asexual coelomycetous fungi have been poorly studied due to the previous difficulties in identifying taxa. Coelomycetes are common in freshwater habitats (Wijayawardene et al. 2016), but are rarely identified beyond genus (e.g. *Phoma* sp.). There are also many marine coelomycetes (Jones et al. 2015), but very little is known concerning their taxonomic affinities and they are often only identified to genus level. For example, *Phomopsis mangrovei* needs re-collecting as it is probably not a *Diaporthe* species. Even the coelomycetes on leaf litter are rarely named beyond genus in ecological studies (e.g. *Neocamarosporium*) and this need revisiting.

Some genera, such as lichenicolous taxa, cannot be grown on artificial media and these provide a huge challenge. Hence, direct sequencing methods need to be devised and carried out.

Another area that need to be studied is the evolution of coelomycetous genera and species related with their hosts. In a recent special issue of Mycosphere on evolution and ranking, three papers dealt with evolution of *Dothideomycetes* families with coelomycete morphs (Hongnanan et al. 2016, Mapook et al. 2016, Phukhamsakda et al. 2016b). However, the evolution of phytopathogenic genera, such as *Colletotrichum*, *Diaporthe* and others with their hosts, now that we have ample molecular data (Udayanga et al. 2012, Damm et al. 2014) could be an interesting topic for future research.

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