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Perspectives into the value of genera, families and orders in classification

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Abstract

This paper briefly discusses the history of fungal taxonomy and contributes to the concepts and the importance of ranking genera, families and orders. We propose recommendations for introducing species into appropriate ranks such as genera, families and orders, as well as the rationale to maintain species in one genus or segregate one genus into several genera. Various ways to rank fungi have commonly been based on morphological and phylogenetic species concepts. More recently, the use of molecular clocks, coupled with estimates of divergence times, has provided insights into how to assign species and support their establishment at different taxonomic hierarchical levels. Case studies are given from the order Botryosphaeriales and Pleosporales, and the genera *Camarosporium*, *Colletotrichum*, *Diaporthe*, *Pestalotiopsis*, *Lophiostoma* and *Agaricus* to demonstrate taxonomic ambiguities and the subjectivity in classification of fungi.

Key words – Divergence time – Hierarchy – Ranks – Recommendation – Taxonomic Concepts

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Introduction

Taxonomy is an artificial process, which uses pigeonholes to place similar taxa, so that they are organized into manageable groups. Our artificial scheme of classification of grouping organisms have always led to taxonomic controversies, and this is true of most organisms, including fungi. In the past, fungi were classified based only on similarities in morphology as there was not any development of specific molecular techniques/tools that could strengthen traditional species concepts and classification (Guarro et al. 1999). However, with the advent of molecular methods in fungal taxonomy and by combining both morphology and molecular data, it has been possible to develop a more reliable and natural system of classification that reflects true phylogenetic relationships (Jeewon et al. 2002, 2003a, b, Hyde et al. 2013, Maharachchikumbura et al. 2015, 2016, Wijayawardene et al. 2016). While our current morphological based classification system has stood the test of time for instance in classifying bitunicate versus unitunicate fungi at a higher taxonomic level, there is still much discordance at lower taxonomic levels. More recently some researchers have proposed the use of divergence times as universally standardized criteria for ranking organisms (Avise & Johns 1999, Avise & Mitchell 2007, Zhao et al. 2016) and this has been carried out with some groups of fungi (Pang et al. 2013, Zhao et al. 2016). We recommend that this approach should be applied in all studies that provide or rearrange new ranks of fungi, as this will provide further evidence to the subjective ranking arrangements. In this paper we discuss the concept of genus, family and order. We provide definitions for each of these terms and briefly discuss their histories. We discuss various ways in which each of the ranks has been applied in fungal classification schemes using selected examples from ascomycetes and basidiomycetes. These examples illustrate the different ways mycologists rank fungi and how this differs considerably across groups. Evolutionary divergence times may be one way in which we can standardize ranks. However, when we use morphology, phylogeny or divergence times in the delineation of genera, there will always be disagreements as the science of classification is subjective and in a constant transition. All mycologists should strive towards stable classification schemes, as the public that use such schemes do not want them to continually change. Therefore, we urge mycologists to aim for consensus and not division.

What are genera, families and orders?

Taxonomy is the science of defining groups of biological organisms on the basis of shared characteristics and giving names to those groups (Judd et al. 2007, Simpson & Michael 2010). Organisms are converged together into taxa (singular: taxon) and given a classification level (e.g. species), which can be placed within hierarchical groups of a given rank (e.g. genus). They can be aggregated to form a super group of higher rank (e.g. family, order) and form a taxonomic hierarchy (Judd et al. 2007, Simpson & Michael 2010). Regarded as the Father of Taxonomy, the Swedish naturalist Carl Linnaeus developed two well-known systems referred to as the i) hierarchical classification system, ii) system of binomial nomenclature, to categorize and name species respectively.

The Linnaean system recently has progressed to a system of modern biological classification, based on systematics (phylogenetics and cladistics). Thus, molecular systematics has provided the basis for classification schemes of Fungi at various ranks (Hibbett et al. 2007, Zhang et al. 2012, Hyde et al. 2013, 2014, Wijayawardene et al. 2014b, 2016, Maharachchikumbura et al. 2015, 2016). These phylogenetic schemes based on sequence data are more qualitative, reliable, natural and informative and are able to link asexual and sexual morphs. This is unlike the majority of earlier taxonomic studies on fungi, which were subjective, because most were predominantly based on morphological characters (Ariyawansa et al. 2014). For example, Barr (1987, 1990) placed Mytilinidiaceae in the order Melanommatales because of the thin-walled peridium of scleroparenchymatous cells, enclosing a hamathecium of narrow trabeculate pseudoparaphyses. Barr & Huhndorf (2001) however, noted that the family was somewhat atypical of Melanommatales. Recent multi-gene phylogenetic analyses do not support the separation of Melanommatales from Pleosporales (Liew et al. 2000), thus Melanommataceae was reinstated in

the order Pleosporales (Mugambi & Huhndorf 2009, Zhang et al. 2012). Furthermore, Liew et al. (2000) reported that narrow trabeculate pseudoparaphyses were not significant morphological characters to delineate these orders. Molecular data has since given support for the introduction of the order Mytilinidiales to which the Mytilinidiaceae belongs (Boehm et al. 2009).

The order as a distinct rank of biological classification was first introduced by the German botanist Augustus Quirinus Rivinus in his classification of plants. Later, Carl Linnaeus (1735) applied it consistently to the division of all three kingdoms of nature (minerals, plants, and animals) in his *Systema Naturae* (1735, 1st. ed.). Generally, the suffix "-ales" is used to denote that the rank is an order in vascular plants and Fungi (McNeill et al. 2012).

In biological classification, the family (Latin: familia, plural familiae) is one of the eight major taxonomic ranks that classified between order and genus. A family may be divided into subfamilies as intermediate ranks, above the rank of genus (McNeill et al. 2012). The rules for naming families are given by various international codes. In fungal, algal, and botanical nomenclature, the suffix "-aceae" is generally added to in a family name to denote its rank. There are some exceptions where historic and widely used names are treated validly, such as Gramineae and Palmae (McNeill et al. 2012).

The genus (pl. genera) is one of the eight taxonomic ranks used in the biological classification of living and fossil organisms. It is a compilation of species and is below family in the hierarchy. In binomial nomenclature, the genus name forms the first part of the binomial species name for each species within the genus. Vellinga et al. (2015) proposed several guidelines for introducing new genera and in particular emphasizing monophyletic status with appropriate support of the genera concerned, adequate taxon sampling in phylogenies and analyses of more than one gene. Although this has not been the case years ago, with fungi, now incorporation of molecular data and adhering to these guidelines has become commonplace. The boundaries of genera, families and orders are determined by taxonomists and are subjective (Ariyawansa et al. 2014). Very often there is no major consensus and different taxonomists hold on to different viewpoints (Ariyawansa et al. 2014). There are no strict rules that a taxonomist needs to follow in describing or recognizing an order, a family or a genus. Some taxa are accepted almost universally, while others are recognized only rarely. Apart from genus, family and order, other higher ranks (kingdom, phylum and class) have been developed, but these are not discussed herein as taxonomic issues at higher hierarchical level have been rather less subjected to controversies.

Why are genera, families and orders important?

Taxonomists sum up the relationships among species at different levels to facilitate the development of a universal system so that people can readily communicate with one another and this is particularly important when discussing the causes of diseases of animals and plants. Scientists group animal and plant pathogens into genera, families and orders and develop universal ways to properly identify pathogens of interest for better disease management strategies. For example, *Erysiphe* causes powdery mildew of numerous plants (Cole 1966, Xu et al. 2003, Curto et al. 2006). This can be controlled by spraying mildew infected crops with sulphur (Bush et al. 2006). Another use is in the correct identification of fungal pathogens to monitor their introduction into the country by quarantine services (Than et al. 2008, Hyde et al. 2010, Cai et al. 2011a). In novel compound screening, the more diverse the fungi are, the more likely they are to produce diverse products (Harvey 2008). Novel bioactive chemicals, such as antibiotics and vitamins are derived from fungal metabolic products. If we find species belonging to a family that produce novel chemicals, then this can allow better screening of fungi with bioprospecting potential, as well as looking for closely related species with similar properties (Karwehl & Stadler 2016).

How to decide on ranking of genera, families and orders

Morphological characters have been used over the last 300 years to identify and classify fungi (Talbot 1971). The order Peronosporales contains a number of important plant pathogens from the Albuginaceae, Peronophythoraceae, Peronosporaceae and Pythiaceae and familial delineation is mainly based on sporangiophore characters. For example, Pythiaceae and

Peronophythoraceae mainly differ in the growth of sporangiophores (Xu et al. 2003). Undeniably, it is difficult and highly subjective to rank organisms based on morphology, especially for asexual and non sporulating fungi (Jeewon et al. 2002, 2003a, Promputtha et al. 2005, 2007). For example, the classification of many genera within ascomycetes has been very subjective at the family and order levels given the divergence or heterogeneity of morphological characters (Shenoy et al. 2006, Jayasiri et al. 2015). Among fungi it is very unlikely that each family can be categorised and delineated based on one or a few morphs. This has led to many fungi, even though properly described, being treated as 'orphans' that could not be assigned to specific ranks. Within Dothideomycetes, six families Ascoporiaceae, Coccoideaceae, Cookellaceae, Perisporiopsidaceae, Protoscyphaceae and Pseudoperisporiaceae are included under families *incertae sedis* (Hyde et al. 2013), because molecular data is not available to assign them in an appropriate order. Historically, morphological structures have been the basis to segregate species in different orders. For example, the family Diaporthaceae (Sordariomycetes) was placed in the Sphaeriales based on sphaerical or flask-shaped fruiting bodies (Müller & von Arx, 1962). However, Diaporthales was later recognized as a separate order based on the characteristic stromatic tissue (Chadefaud 1960). Recent molecular data has also confirmed Diaporthales as a distinct order (Zhang & Blackwell 2001). Further taxonomic revisions based on a combined morphological and molecular approach have also clarified relationships at the familial level. In particular, six major lineages (Gnomoniaceae *sensu stricto*, Melanconidaceae *sensu stricto*, *Schizoparme* complex, *Cryphonectria-Endothia* complex, Valsaceae *sensu stricto* and Diaporthaceae *sensu stricto*) were established (Castlebury et al. 2002), but this has been revised by Lumbsch and Huhndorf (2010).

Traditional morphological approaches to classify fungi are problematic and continually fail to provide a reliable evolutionary framework, especially at the species level (Cai et al. 2011b). The application of DNA sequence data in systematics has proven to be more objective and indispensable in providing a more natural classification to the Kingdom Fungi. Molecular data has also allowed mycologists to detect and classify morphologically similar species, such as cryptic species (Stielow et al. 2011). Cryptic fungal species are those which are morphologically similar with unclear boundaries and thus cannot be identified properly. These are known in lichen forming fungi, endophytic, pathogenic and many soil fungi (Grünig et al. 2004, Matute et al. 2006, Gams 2006, Crespo & Lumbsch 2010, Pérez et al. 2012). Many species names of *Colletotrichum* have been recognized as complicated cryptic species, including *C. acutatum* and *C. dematium* (Cai et al. 2009, Shivas & Cai 2012). *Colletotrichum gloeosporioides* recently has been shown to contain several cryptic pathogenic species based on DNA sequence analyses (Hyde et al. 2014).

Yeasts species are different to most fungal groups and are delineated based on morphology, growth rate and fermentation on a range of substrates and sequence data, in particular ITS and D1/D2 regions of the LSU rDNA. The latter leads to their rapid identification (Kurtzman et al. 2011a, b). For example, the nearest taxon to *Candida taylorii* is a *Candida* sp. strain May-089, but the former differs by 18 bases in D1/D2 LSU rDNA and utilizes rhamnose as a substrate (Statzell-Tallman et al. 2010). A good taxon delimitation should be with respect both morphology and molecular evidence. Jeewon & Hyde (2016) discussed about guidelines for estabilishment of new taxa. Distinct morphological characters and distinct well-supported lineages are the universal criteria to delimit taxa. Our recommendations for designating genera, families and orders are provided in Box 1.

The difference in divergence time scales between ranks in genera, families and orders

The relevance between two different ranks is expected to reduce as the result of the cumulative dispersal and local extinction during their divergence time (Hardy & Senterre 2007). Sometimes the subsistent evidence suggests the presence of the original form features, but at other times the ambiguous evidence may lead considerable debate. Although recently some data has become available, the known about evolutionary relationships among fungi remains indistinct, because of the lack of fossil evidence (Guarro et al. 1999). However, new insights into fungal evolution have been provided based on cladistic and molecular approaches. Fungi are known to

Box 1 Recommendations for naming genera, families and orders

Orders
An order is a compilation of families. The order should preferably form a distinct and monophyletic lineage with adequate statistical support (70% bootstrap and 95% posterior probability) based on cladistics analyses of at least two genes (e.g. rDNA and protein coding gene). The families in the order should be morphologically comparable and at least share common characteristics. An order may comprise a single family (e.g. Erysiphales) or numerous families (e.g. Pleosporales), with phylogenetic support.

Families
A family is a compilation of genera with at least one inherent morphological feature that they commonly share or which makes them distinct. The family should preferably form a distinct and monophyletic lineage with adequate statistical support (70% bootstrap and 95% posterior probability) based on cladistics analyses of at least two genes (e.g. rDNA and protein coding gene). The genera in the family should be morphologically comparable and at least share common characteristics. A family may comprise a single genus (e.g. Geosiphonaceae) or numerous genera (e.g. Sordariaceae), with phylogenetic support.

Genus
A genus is a compilation of species and should have all similar basic phenotypic and phylogenetic traits (e.g. as in the genus *Colletotrichum*) and should preferably form a distinct and monophyletic lineage with adequate statistical support (70% bootstrap and 95% posterior probability) based on cladistics analyses of at least two genes (e.g. rDNA and protein coding gene). A genus may comprise a single species (e.g. *Incolasioptera*) or numerous species (e.g. *Agaricus*, more than 400 species). For a genus, it would be quite appropriate to consider at least one morph which is phylogenetically significant that segregates it from other similar genera.

be more closely related to Animalia than to Plantae, although mycology was previously considered a branch of botany (Nikoh et al. 1994). Researchers have analysed amino acid sequences from numerous enzymes showing that plants, animals and fungi had a common ancestor about 1000 MYA (Doolittle et al. 1996). Scientists use the number of base changes to estimate the date of evolutionary radiation (Hawksworth et al. 1995). Supported by fossil evidence, the three main fungal phyla, Ascomycota, Basidiomycota and Zygomycota are considered to have diverged from the Chytridiomycota about 550 MYA (Berbee & Taylor 1993a).

Estimation of fungi divergence times

Morphological characters, molecular data, geographical distribution and fossil traces provide abundant potential information concerning life's evolutionary history on earth (Drummond et al. 2012). Biologists have attempted to calculate divergence among organisms based on a combination of paleontological evidence and molecular data (Taylor & Berbee 2006). Thus, considering fossils as calibration points is important, when estimating the timing of diversification (Wood et al. 2013).

Fungi, possibly the largest and oldest organisms, can be excellent model organisms to reconstruct ancestral lineages, determine evolutionary splits and provide insights into estimates of divergence times (e.g. Li et al. 2005, Vijaykrishna et al. 2006). Current fungal systematic and taxonomic studies mainly focus on organizing and classifying species, genera, and higher ranks using a combination of characters, including molecular, morphological, ecological, and biogeographical data (Hyde et al. 2013, Maharachchikumbura et al. 2015, 2016). Phylogenetic relationships among major groups of the Kingdom Fungi have been the subject of many recent

studies but few have really investigated how morphologies have undergone different evolutionary patterns and estimate divergence rates among different ranks.

The recognitions of taxonomic ranks in the Linnean classification system is considered as universally standardized criteria. However, divergence time has been proposed as a universally standardized criterion by some authors (Avise & Johns 1999, Avise & Mitchell 2007, Zhao et al. 2016). Hennig (1966) suggested that geological age and time of divergence should be inclusive to rank organisms, but it was not until the advent of DNA sequence data analyses and molecular clocks that this idea was further considered. Recently, several studies have been carried out to date the origin and subsequent evolution of the main fungal lineages by molecular clock methods (Vijaykrishna et al. 2006).

One of the first studies that looked at reconciling taxonomic ranks and time divergence estimates is that of Avise and John (1999) who studied evolution of fish, anthropoid primates and fruit flies and then proposed to use approximate dates of nodes as a pervasive ranking criterion in biological taxonomy.

Mycologists were swift to use DNA data variation to date important events in fungal evolutionary history and then those dates were used to compare evolutionary events to those of other organisms. Simon et al. (1993) were the pioneers in this field, and simultaneously nine fungal lineages were revealed which are estimated to have diverged with animals at 600 MYA (Berbee & Taylor 1993b, Taylor & Berbee 2006). Heckman et al. (2001) stated that Fungi occupied terrestrial habitats for at least 1000 MYA. However, these studies ignored the substitution rate variation which Berbee & Taylor (1993b, 2010) expounded as common existence in fungal phylogeny.

Modern phylogenetic studies concerning fossil taxa need precise information, such as, systematic position and dating (Beimforde et al. 2014). Fossilized fungi preserved in amber and chert can be considered as excellent material as they conserve even delicate microstructures (Stankiewicz et al. 1998, Martínez-Delclós et al. 2004). Beimforde et al. (2014) evaluated 13 extraordinarily well-preserved and precisely-dated fossil ascomycetes from amber and chert to demonstrate the utility of fungal organisms in such evolutionary studies.

Vijaykrishna et al. (2006) analysed 18S DNA sequence data combined with a Bayesian relaxed-clock method to show that freshwater and marine ascomycetes evolved from terrestrial ancestors. However, they did not discuss divergence times and ranking which can be used to provide evidence to rank fungi (Drummond et al. 2012). Zhao et al. (2016) analysed 114 taxa of *Agaricus* and proposed to divide it into five subgenera and 20 sections based on divergence time estimation coupled with phylogeny, and then proposed a modified taxonomic system for *Agaricus* using divergence times as a standardized criterion based on phylogenetic relationships and morphology. Slippers et al. (2013) reported that the Botryosphaeriales originated in the Cretaceous period around 103 (45-188) MYA based on estimated mutation rates (molecular clock) of the rDNA SSU locus. In the case study below on Botryosphaeriales, we show how the order probably has too many families based on divergence times and number of genera.

Case studies in ranking fungi

Below we discuss some examples for the classification of fungi in the section, subgenus, genus, family and order levels to show how ranking is both variable and subjective across mycologists dealing with various groups of fungi.

Ranking in Orders

Botryosphaeriales – should we have so many families?

Botryosphaeriales were originally circumscribed based on morphological characters (mostly ascomata, asci and ascospores). More recently, greater emphasis was placed on phylogenetic relationships based on rDNA sequence data, often supplemented with sequences of protein coding genes such as RBP2, *tef1-α* and β-tubulin. Application of molecular clock dating with divergence estimates has also been considered in separating families (Slippers et al. 2013).

In a multigene phylogeny for 96 taxa in Dothideomycetes (Schoch et al. 2006), *Botryosphaeria* and *Guignardia* species formed a clade that could not be associated with any other order. For this reason, they proposed a new order Botryosphaeriales accommodating a single family, Botryosphaeriaceae. Based on phylogenetic data, Minnis et al. (2012) reported that Planistromellaceae also resides within this order and they chose to retain it as a distinct family separate from Botryosphaeriaceae. Wikee et al. (2013) reinstated Phyllostictaceae as a family in Botryosphaeriales to accommodate *Phyllosticta* (= *Guignardia*), while Slippers et al. (2013) introduced new families to accommodate *Saccharata* (Saccharataceae), *Melanops* (*Melanops*aceae) and *Aplosporella* and *Bagnisiella* (Aplosporellaceae). More recently, Wyka & Broders (2016) introduced the new family Septorioideaceae within the Botryosphaeriales to accommodate *Septorioides* species while Yang et al (2016) raised *Pseudofusicoccum* and *Endomelanconiopsis* to family status. Is this too many families?

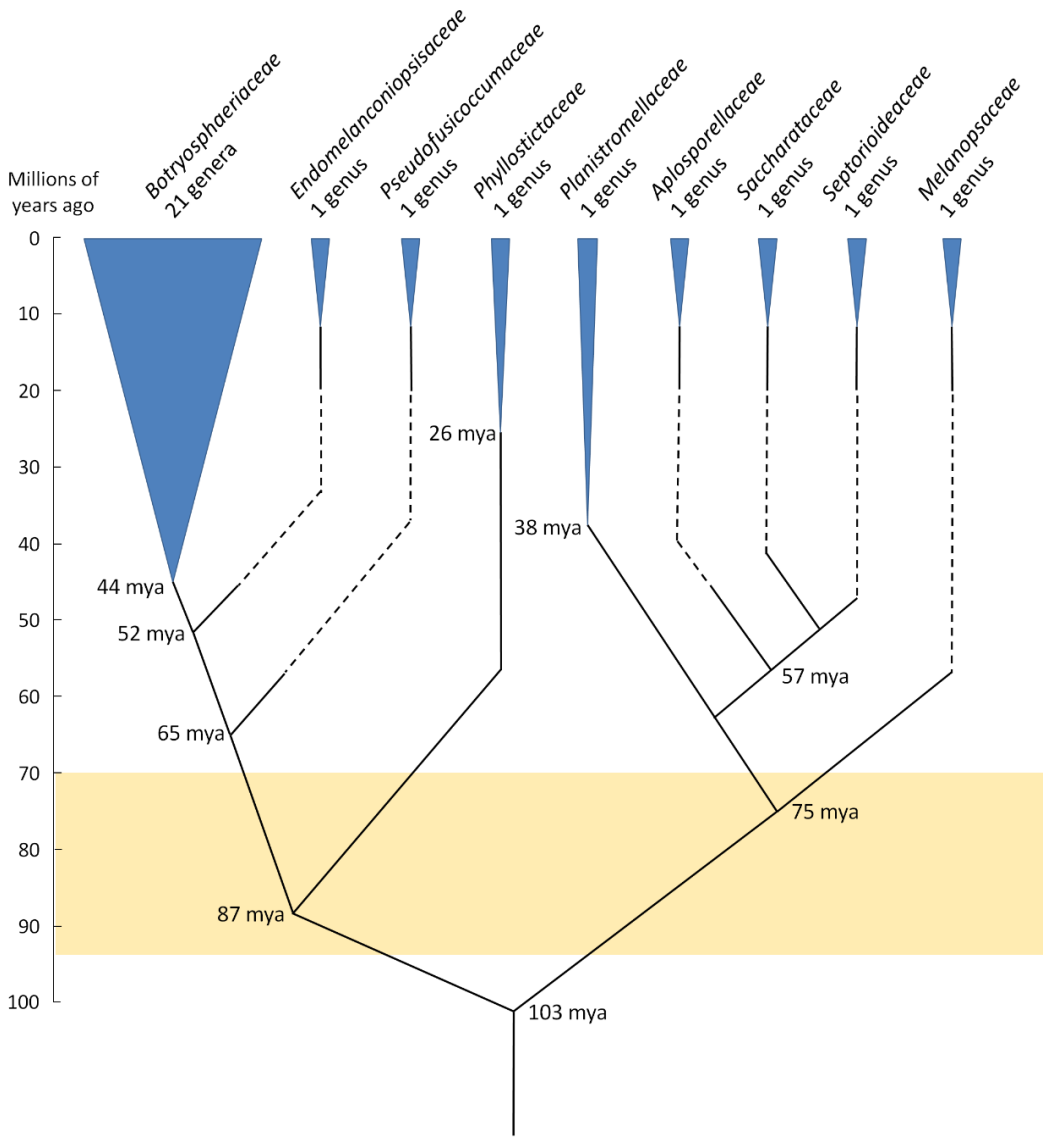

Fig. 1 – Diagram depicting the evolution of families in Botryosphaeriales based on the phylogeny presented by Slippers et al. (2013) and incorporating an estimate of the position of Septorioideaceae from Wyka & Broders (2016). Molecular dating of the emergence of lineages was taken from Slippers et al. (2013) and is given at the branches as millions of years ago (MYA). Vertical axis in millions of years, horizontal axis is dimensionless. Width of the blue triangles is proportional to the number of genera in each family. The yellow box indicates the probable time range for the emergence of families in Botryosphaeriales.

A simplified, diagrammatic representation of families in Botryosphaeriales is provided in Fig. 1. Molecular clock dating based on estimated mutation rates of rDNA sequence data revealed that this order originated around 103 MYA in the Cretaceous period, which coincides with the major periods of radiation and spread of Angiosperms. The Botryosphaeriaceae (together with Pseudofusicoccumaceae and Endomelanconiopsisaceae) and Phyllostictaceae lineages separated around 87 MYA. The other main lineage in Botryosphaeriales split around 75 MYA with one branch leading to Melanopsaceae. The sister lineages of Melanopsaceae are presently considered to comprise four families, namely Aplosporellaceae, Planistromellaceae, Saccharataceae and Septorioideaceae.

Based on ecology and morphology, Botryosphaeriaceae, Phyllostictaceae and Melanopsaceae clearly warrant separate families. Phyllostictaceae are mostly foliar and fruit pathogens, while Botryosphaeriaceae are found mainly in woody tissues of woody hosts. Furthermore, asci and ascospores of Phyllostictaceae are generally smaller than those of Botryosphaeriaceae and their ascospores have gelatinous caps. The large, multilocular fruiting bodies of Melanopsaceae, bearing ascomata and conidiomata distributed at various levels and positions in the stroma (Phillips & Alves 2009) are unique within the Botryosphaeriales. The relatively large ascospores and slow growth rate in culture (Phillips & Alves 2009) further differentiate this family from the other lineages sister to Melanopsaceae. Based on molecular dating analyses these families separated around 70–90 MYA.

It is however, difficult to justify the families Aplosporellaceae, Saccharataceae and Septorioideaceae each represented by a single genus. The range of morphologies in these families corresponds to the range found within Botryosphaeriaceae and it is difficult to find any distinct morphological or ecological features that can separate these lineages from Planistromellaceae. Likewise, the morphologies of Endomelanconiopsisaceae and Pseudofusicuccumaceae fall within the range of morphologies found within Botryosphaeriaceae. Given the argument above, it would seem more appropriate for the time being to treat these so-called families as independent genera within the two families they are mostly closely allied with pending further sampling and phylogenetic support. This would also avoid unnecessary taxonomic confusion and division.

Pleosporales – should we have so many families?

The order Pleosporales was invalidly introduced by Luttrell (1955) and included seven families. This classification was however, not followed by Müller & von Arx (1962) who reused Pseudosphaeriales for Pleosporales and included 12 families. Luttrell (1973) accepted eight families in the order. In their review of bitunicate ascomycetes, von Arx & Müller (1975) accepted only a single order, Dothideales, with two suborders. Barr (1983) included 14 families and six suborders in Pleosporales, giving greater importance to the morphology of pseudoparaphyses at the ordinal level. Pleosporales was formally established by Luttrell & Barr (in Barr 1987) with 18 families. After intensive sampling and multigene phylogenetic studies, 20 families were accepted in Pleosporales (Zhang et al. 2012). Lumbsch & Huhndorf (2010) included 28 families in Pleosporales, while Zhang et al. (2012) accepted only 26 families by excluding Venturiaceae and Phaeotrichaceae.

Molecular studies based on analysis of combined LSU, SSU, RBP1, RBP2 and tef1 sequence data have shown that Pleosporales can be divided into two main suborders (Pleosporineae and Massarineae) and 12 other families *incertae sedis* (Zhang et al. 2012, Ariyawansa et al. 2015a, c, Li et al. 2016). The suborder Massarineae currently contains 15 families and most of the species of this suborder are saprobic in terrestrial or aquatic environments (Ariyawansa et al. 2015a, c, Dai et al. 2015, Li et al. 2016). Pleosporales also contains another 25 families, but their sub-ordinal affinity remains undetermined (Zhang et al. 2012, Ariyawansa et al. 2015a, c). More recently there has been an explosion in the number of families recognised and now it is over 50. Recently introduced families such as Ascocylindricaceae (Ariyawansa et al. 2015b), Dothidotthiaceae (Phillips et al. 2008), and Microsphaeropsidaceae were introduced with emphasis on phylogeny, rather than considering morphological data. Most of these families contain a single genus with

single or several species or strains. In contrast, some genera that form distinct lineages in the order viz. *Asteromassaria, Bactrodesmium, Fuscostagonospora, Inflatispora, Lignosphaeria* and *Pseudoxylomyces,* have been classified under Pleosporales genera *incertae sedis,* thus their familial placement remains unresolved (Ariyawansa et al. 2015a, c). Generally, the main reason that these genera are placed under Pleosporales genera *incertae sedis* and not accommodated in new families, is that they are represented by single species or strain (Ariyawansa et al. 2015a, c, Zhang et al. 2016).

However, are we introducing too many families with each containing just a few species? Some authors would argue that we have too many families, while others would argue that if each family is a distinct lineage supported by molecular data then it is justified. Both arguments have merits and the conclusion is rather subjective. We recommend that if the morphology of taxa in the family is distinct and molecular data support a distinct lineage, then each family should be considered valid. We do not consider that there are too many families in Pleosporales.

Ranking at the generic level

***Camarosporium* – should this comprise several genera?**

The genus *Camarosporium* was introduced by Schulzer (1870) with *C. quaternatum*. as the type species and comprises more than 500 species epithets in Index Fungorum (2016). Sutton (1980) predicted the heterogenic nature of *Camarosporium* based on *C. propinquum*. Moreover, the genus was linked to Botryosphaeriaceae (Liu et al. 2012, Wijayawardene et al. 2012), Leptosphaeriaceae (Schoch et al. 2009) and Cucurbitariaceae (Doilom et al. 2013). *Camarosporium quaternatum* is phylogenetically distinct from Botryosphaeriaceae and Wijayawardene et al. (2014a confirmed that *C. quaternatum* groups in Pleosporineae (Pleosporales), but could not be assigned to any family. Wijayawardene et al. (2014a) who proposed Camarosporiaceae to accommodate *Camarosporium sensu stricto* but it was not formerly introduced.

Since the recent phylogenetic analyses confirmed the heterogenic nature of *Camarosporium*-like taxa, several genera have been introduced in other families, i.e. *Didymellocamerosporium* Wijayaw. et al. (Didymellaceae *fide* Wijayawardene et al. 2016), *Melanocamarosporium* Wijayaw. et al. (Melanommataceae *fide* Wijayawardene et al. 2016), *Neocamarosporium* Crous & M.J. Wingf. (Pleosporaceae), *Paracamarosporium* Wijayaw. et al., *Pseudocamarosporium* Wijayaw. et al. (Didymosphaeriaceae fide Wijayawardene et al. 2014a, 2016), *Suttonomyces* Wijayaw. et al. (Massarinaceae fide Wijayawardene et al. 2016). Clearly, *Camarosporium* warrants its own family and several *Camarosporium*-like genera are warranted and belong in other families. A large number of species lack sequence data and thus it is essential to re-collect and carry out phylogenetic analyses to confirm their placement.

***Colletotrichum* – should this be more than one genus?**

Colletotrichum is an important plant pathogenic genus (Hyde et al. 2009a, b, 2014) and also comprises endophytes and saprobes (Hyde et al. 2014). *Colletotrichum* presently comprises approximately 185 accepted species (Hyde et al. 2014, Liu et al. 2015a, Jayawardena et al. 2016). Phylogenetic analysis has revealed that the genus comprises twelve major clades, as well as a number of singleton species (Yang et al. 2009, Hyde et al. 2014, Liu et al. 2014, Sharma et al. 2015). These clades are referred to by the specific epithet of recognized or historically well-known species. For an example, the gloeosporioides clade comprises *C. gloeosporioides* and its closely related species. However, the species of the graminicola clade are less closely related and have been combined together based on morphological similarities and host-specificity.

There is no universally accepted process for naming the clades, or ways to merge them into traditional taxonomic categories. The draft *Phylocode* (https://www.ohio.edu/phylocode/) represents a major step towards naming the clades. Formal recognition of infra-specific groups within *Colletotrichum* is recommended. The acutatum, gloeosporioides and boninense species complexes have been confirmed as monophyletic (Jayawardena et al. 2016), while the curved-

spored species from herbaceous plants appear to be polyphyletic (Jayawardena et al. 2016). This resulted in the introduction of two new clades, dematium and spaethianum.

Even though the main conidial characters between these species complexes may differ, breaking down the genus into new genera is not considered advantageous, as i) the characters of the acervuli rarely differ and can vary as results of environmental factors, ii) conidial morphology is not a reliable character to distinguish species as it may vary with changes in environmental factors and media conditions. Also, many *Colletotrichum* species produce secondary conidia in culture which may vary from those produced in conidiomata, iii) *Colletotrichum* species have a wide host range (Than et al. 2008). Only the graminicola and caudatum clades appear to be host-specific to genera within the family Poaceae, iv) there are no significant base pair differences between specific gene regions of the species of different clades and v) most of the species are plant pathogens and are well-established in plant pathology and breeder communities. Breaking this genus into different genera would lead to unnecessary confusion. Our main justification for such an advocate stems from the fact that *Colletotrichum* always constitute a strongly supported monophyletic lineage with only *Glomerella* as asexual morphs.

By adopting traditional taxonomic categories and extra-categories, such as sub-genus, or series as defined by International Code of Nomenclature for Algae, Fungi and Plants (ICNAFP) it is possible to assign formal names to these species complexes. However, this is not recommended as they imply an equality of taxa at the same rank, which does not agree with the evolutionary concept of the *Colletotrichum* species (Cai et al. 2009). Therefore, instead of splitting the genus *Colletotrichum* into different genera, use of an informal clade-based nomenclature system is recommended.

***Diaporthe* – should this comprise several genera?**

Diaporthe encompasses endophytes, plant pathogens and saprobes occurring on a wide range of annual and perennial hosts, including economically important crops (Udayanga et al. 2011, 2014, Dissanayake et al. 2015, Liu et al. 2015b), and is typified by *Diaporthe eres* (Wehmeyer 1933, Udayanga et al. 2014). *Phomopsis* is now a synonym of *Diaporthe*, the latter being the older generic name (McNeill et al. 2012). Index Fungorum (2016) lists 973 *Diaporthe* names and 980 *Phomopsis* names. However, the names existing in the literature were frequently introduced based on host association and to a lesser extent morphology. Recent introductions of novel species were based on combined DNA sequence data (Udayanga et al. 2014). Ex-type cultures are available for less than 150 known species despite the huge number of species listed in databases and the literature (Hyde et al. 2014).

The precise use of accepted names of plant pathogenic fungi is necessary for the progress of efficient biosecurity and trade policies (Hyde et al. 2010). Species are presently being redefined based on a polyphasic taxonomic approach including morphological, cultural, phytopathological, mating type and combined DNA sequence data (Mostert et al. 2001, Farr et al. 2002, Santos et al. 2010, Udayanga et al. 2014).

Diaporthe is a species rich genus and accepted species share similar morphological characteristics (Hyde et al. 2014). Almost all *Diaporthe* species show comparable morphology and cluster in a monophyletic clade in the family Diaporthaceae (Maharachchikumbura et al. 2015, 2016), suggesting that all species belong to a single genus. To verify this idea, we compared the morphology and phylogeny of *Diaporthe* in Hyde et al. (2014) and found that most species, despite exhibiting similar morphologies are phylogenetically distinct and hence can be treated as different species within one genus. We assessed the morphological descriptions of *Diaporthe ampelina*, *D. angelicae*, *D. hongkongensis* and *D. schini* from distinct clades of *Diaporthe* in Hyde et al. (2014) and established that there are no morphological distinctions. The existence of both alpha and beta conidia in *Diaporthe* depends on environmental factors and conidial dimensions may vary with environmental dynamics as well as media conditions. Most importantly, there are no significant base pair differences between specific gene regions of *Diaporthe* species of different clades, thus

we conclude that this genus should not be split into several genera. A similar scenario could be applicable to other genera as well (e.g. *Phyllosticta*).

***Pestalotiopsis* – should this be more than one genus?**

One of the great dilemmas in taxonomy/phylogeny is how evolutionary time can give rise to distinct morphological traits that serve as the basis for defining species. It is hard to determine how many genes should have changed for a new taxon to have evolved, or the roles of natural selection and genetic drift in speciation (Coyne 1992). Morphology however, plays a key role in grouping similar taxa into genera.

Pestalotiopsis is an appendage-bearing conidial asexual coelomycetous genus in the family Pestalotiopsidaceae (Hu et al. 2007, Maharachchikumbura et al. 2013, Zhang et al. 2013). Conidial septation appears to be reliable to position taxa in genera of Xylariales (Maharachchikumbura et al. 2014, Senanayake et al. 2015). Sequence data generated to date reveal *Truncatella*, *Pestalotiopsis* and *Seiridium* to represent three distinct genera, which are characterised by 4-celled, 5-celled and 6-celled conidia (Jeewon et al. 2002, Maharachchikumbura et al. 2014, 2016). Many of the phylogenetic analyses resolved *Pestalotiopsis* into three strongly supported clades (Jeewon et al. 2003a, Maharachchikumbura et al. 2011, 2012). These clades corresponded to three conidial types: one with pale brown or olivaceous concolorous median conidial cells, one with versicolorous median conidial cells and the third with dark-coloured concolorous median conidial cells and knobbed apical appendages. Therefore, median cells are considered to be a key character in distinguishing *Pestalotiopsis* taxa.

Jeewon et al. (2003b) and Maharachchikumbura et al. (2014) resolved genera in Amphisphaeriaceae based on analysis of DNA sequence data. Besides accepting *Pestalotiopsis*, they introduced *Neopestalotiopsis* and *Pseudopestalotiopsis*. In *Pestalotiopsis* conidiophores are septate, unbranched and often reduced to conidiogenous cells; conidiogenous cells are ampulliform to lageniform or cylindrical to subcylindrical phialides, and conidia have concolourous median cells. *Neopestalotiopsis* has versicolourous median cells, with indistinct conidiophores, while *Pseudopestalotiopsis* can be distinguished from *Pestalotiopsis* by sequence data and generally dark coloured concolourous median cells with indistinct conidiophores (Maharachchikumbura et al. 2014). The three genera can also be roughly assigned to distinct groups based on the total number of base pairs in the ITS regions (Maharachchikumbura et al. 2014).

Pestalotiopsis shows a high variation in appendage morphology (Jeewon et al. 2002, 2003a, Maharachchikumbura et al. 2012, 2014). These apical appendage characters vary in length number, shape, branched or unbranched nature, presence or absence of knobbed tips and the position of the apical appendage attached to the conidial body (Jeewon et al. 2003a, Maharachchikumbura et al. 2011, 2014). So the question that arises, should *Pestalotiopsis* be segregated into several genera based on these diverse morphological characters. Appendage morphology has been widely used in *Pestalotiopsis* taxonomy to introduce novel taxa (Maharachchikumbura et al. 2016), however conidial appendages alone cannot be used as a useful character for generic separation (Wijayawardene et al. 2016). As an example, *Pestalotiopsis* species possessing similar appendage characters (number, presence or absence of knobbed tips), did not cluster together (Maharachchikumbura et al. 2012, 2014). Therefore, we believe that *Pestalotiopsis*, *Neopestalotiopsis* and *Pseudopestalotiopsis* are supported monophyletic groups.

***Lophiostoma* – should this be more than one genus?**

The family Lophiostomataceae includes a wide range of morphologically diverse taxa which are predominantly saprobic on twigs or bark of various woody plants and herbaceous plants in terrestrial and aquatic environments. Based on morphology, intergeneric arrangements within this family have been treated differently by different authors (Luttrell 1973, von Arx & Müller 1975, Barr 1987, 1992, Holm & Holm 1988, Hawksworth et al. 1995, Zhang et al. 2012). With the availability of DNA sequence data, the number of genera has been reduced and some genera previously assigned to Lophiostomataceae were transferred to different families (Mugambi &

Huhndorf 2009, Zhang et al. 2009, Hirayama & Tanaka 2011). Hyde et al. (2013) and Wijayawardene et al. (2014b) accepted only *Lophiostoma*, *Misturatosphaeria* and *Tumularia* in the family. Thambugala et al. (2015) revised the family Lophiostomataceae based on a multigene phylogenetic analysis and morphological traits of Lophiostomataceous taxa, and recognized 16 genera, including eleven newly introduced genera. Thambugala et al. (2015) reported that *Misturatosphaeria* should be placed in a different family rather than Lophiostomataceae and introduced a new family Floricolaceae to accommodate *Floricola*, *Misturatosphaeria* and seven new genera.

Here we point out a few examples that emphasize that *Lophiostoma* should be more than one genus.

1) *Platystomum* was introduced by Trevisan (1877) and is typified by *Platystomum compressum*. Holm and Holm (1988) treated *Platystomum* as a synonym of *Lophiostoma*, while recent studies treated *Platystomum* as a separate genus in Platystomaceae (Mugambi & Huhndorf 2009, Hyde et al. 2013, Wijayawardene et al. 2014b). Thambugala et al. (2015) accepted *Platystomum* in Lophiostomataceae as a distinct genus based on molecular sequence data and morphological traits of *P. compressum*.
2) Thambugala et al. (2015) introduced the genus *Sigarispora* to accommodate *Lophiostoma ravennicum* and a few other *Lophiostoma* species which are morphologically and phylogenetically distinct from *Lophiostoma.* The distinct characters of *Sigarispora* include immersed to semi-immersed ascomata, a small crest-like ostiole, a peridium of elongate cells of *textura angularis*, and brown cigar-shaped, multi-septate or muriform ascospores (Liu et al. 2015b, Thambugala et al. 2015, Li et al. 2016).

The family Lophiostomataceae presently comprises 16 genera with support from morphology and phylogeny. Given that the Lophiostomataceae is characterised by bitunicate asci that demarcate them from many unitunicate asci, it is now important to apply other analytical tools such as molecular clock methods to provide estimates of divergence times that could provide further insights and evidence towards scientific classification of this group of fungi.

***Agaricus* – ranking within the genus**

The saprotrophic genus *Agaricus*, the type genus of the family Agaricaceae (Agaricales, Agaricomycetes) has a worldwide distribution, and includes economically important species (*A. bisporus* and *A. subrufecens*). The number of recognized species of this genus ranges from 200 (Kirk et al. 2008), 375 (Zhao et al. 2011) to more than 400 due to recent discoveries of new species (Zhao et al. 2012, Chen et al. 2012, Yang et al. 2015, Parra 2013, Lebel 2013, Lebel & Syme 2012).

Historically, this genus has been well-documented mainly from Europe and North America based on morphology, but proposed taxonomic systems are inconsistent in subgenera and sections (Bohus 1995, Cappelli 1984, Heinemann 1978, Kerrigan 1986, Singer 1986, Wasser 1980). Using a combined morphological and molecular approach, some sections have been shown to be monophyletic (*Arvenses*, *Bivelares*, *Xanthodermatei*), while others (*Sanguinolenti* and *Spissicaules*) are polyphyletic (Challen et al. 2003, Geml et al. 2004, Kerrigan et al. 2006, 2008). In recent years, *Agaricus* has been well-studied in Europe and recent morphological and sequence data indicate two subgenera with eight sections (Parra 2008, Parra et al. 2014).

In a more recent and global analysis based on the ITS sequence data from 128 species, especially those specimens from tropical areas, 11 new clades were proposed in the genus (Zhao et al. 2011). Later some of those new clades have been re-recognized as sections *Brunneopicti*, *Nigrobrunnescentes*, *Rarolentes* and *Subrutilescentes* (Chen et al. 2015, Parra et al. 2014, Wang et al. 2015, Kerrigan 2016). Twelve sections are recognized in *Agaricus*, however, most of the new clades (Zhao et al. 2011) are still unresolved because of a lack of phylogenetic statistical support.

Zhao et al. (2016) analyzed more than 700 *Agaricus* specimens of previously recognized subgenera and sections. One-hundred and fourteen representatives were selected in order to infer phylogeny based on combined DNA sequence data with estimates of divergence times. In this

study, the following criteria were set to recognize subgenera and sections i) they must be monophyletic and statistically well-supported in the multi-gene analyses; ii) their respective stem ages should be roughly equivalent, and subgenera stem ages must be older than section stem ages; and iii) they should be identifiable phenotypically, whenever possible. With regard to the second criterion, estimated stem ages for subgenera and sections were ca. 30 MYA and ca. 20 MYA, respectively (Zhao et al. 2016).

Based on these criteria, phylogenetic relationships and morphology, a revised taxonomic system for *Agaricus* was proposed that considered divergence times as a standardized criterion for establishing taxonomic ranks. In this reconstructed *Agaricus* taxonomic system, five subgenera and 20 sections are proposed (Zhao et al. 2016) and evidence points out that *Agaricus* is a single genus that should be further divided into subgenera and sections.

Conclusion

As mycologists discover new species and unravel relationships, more taxonomic confusion and differences in opinion can result. Lumping or splitting taxa among different ranks has always been a contentious issue often leading to unpleasant rhetoric. This paper addresses some pertinent aspects in connection with assigning taxa to different ranks. However, whether using either a lumping or splitting approach, it is recommended that mycologists give due consideration and provide justifications for their decisions. This can include a diversity of characters that justifies generic or familial segregation, differences in sexual or asexual morphs, strongly supported phylogenetic data coupled with estimates of divergence times and ecological features. However, the science of ranking is always likely to be subjective and therefore mycologists should take a conciliatory approach until the evidence is indisputable.

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