
Impact of DNA sequence-data on the taxonomy of anamorphic fungi

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Fungal systematics is an essential part of biological research especially in the context of its ecological and economic implications. The classification of pleomorphic and non-pleomorphic anamorphs, however, is unsettled, which can be attributed to the historical practice of the dual nomenclature/classification system. This paper reviews the historical establishment and limitations of the dual system of classification, and narrates the possible utilities of DNA sequence-data in developing a system of classification based on evolutionary relationships. The dual classification system is a failed hypothesis. DNA sequence-data are now routinely used to link anamorphs with a holomorph and to provide phylogenetic placement for anamorphs with unknown teleomorphs. Emerging phylogenetic and nomenclatural scenarios in the *Botryosphaeriales*, *Chaetosphaeriales*, *Fusarium graminearum*, pestalotiopsis-like anamorphs, and the *Mycosphaerella* complex are illustrated to indicate potential nomenclatural and taxonomic complexities associated with the dual nomenclature/classification system. The mycological community has a daunting task of developing a system of classification that fulfils the needs of diverse taxonomic users. Molecular characters and tools are, undoubtedly, an indispensable part of fungal systematics.

Key words: barcoding, coelomycetes, deuteromycetes, hyphomycetes, molecular phylogeny, PhyloCode, systematics

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1. Introduction

Fungi represent a major clade in the tree of life (Maddison and Schulz, 2006) and their traditional circumscription included all eukaryotic, heterotrophic, absorptive organisms that develop diffused, branched, tubular bodies and reproduce by means of spores (Kendrick, 2000). Their important characteristics are listed in the *Dictionary of the Fungi* (Kirk *et al.*, 2001) under “Fungi”. Unlike most organisms, fungi can reproduce sexually and asexually (Alexopoulos *et al.*, 1996). Manifestation of more than one type of reproductive morphology by a single entity has been a major challenge for taxonomists in naming and classifying them naturally. This paper addresses the

historical burden of the dual system of classification, and narrates the prospective utilities of DNA sequence-data in developing a classification system based on evolutionary relationships.

2. Classification of fungi

Traditional classification of fungi and fungi-like eukaryotes

Fungi and fungi-like eukaryotes were traditionally classified as a subkingdom in the Kingdom *Plantae* with divisions Myxomycota (for plasmodial forms) and Eumycota (for nonplasmodial, frequently mycelial form) ((Bessey, 1950; Ainsworth *et al.*, 1973), (Fig. 1)). The Eumycota included subdivisions Mastigomycotina (Chytridiomycetes, Hyphochytridiomycetes, Oomycetes), Zygomycotina (Zygomycetes, Trichomycetes), Ascomycotina, Basidiomycotina, and Deuteromycotina. The Deuteromycotina included “asexual” members of the Ascomycotina and Basidiomycotina and was used for convenience.

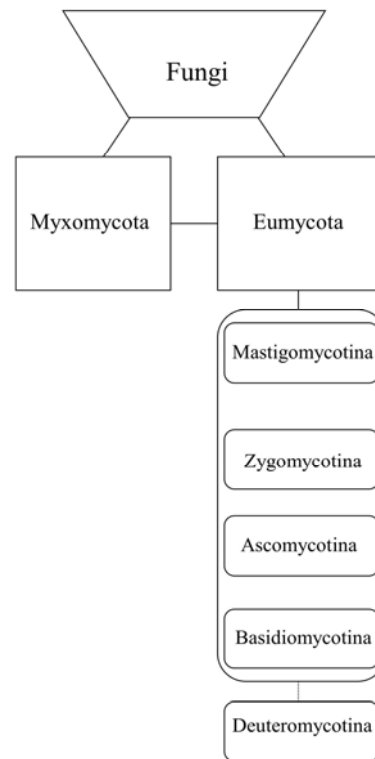


Fig. 1. Traditional classification of fungi (Ainsworth *et al.*, 1973).

The Fungal Tree of Life

Recent advances in DNA sequence technologies and analytical methods have revolutionised fungal systematics (Table 1, Section III). Fungi are now recognised as entirely distinct from the Kingdom *Plantae* and classified in a separate Kingdom, *Fungi* (Whittaker, 1969; Carlile and Watkinson, 1994; Cavalier-Smith, 1998, 2001; Hibbett *et al.*, 2007). Fungi are more closely related to animals than plants (Wainright *et al.*, 1993; Baldauf and Palmer, 1993; Berbee and Taylor, 2001; Lang *et al.*, 2002; Lutzoni *et al.*, 2004; James *et al.*, 2006a). Kirk *et al.* (2001) accepted phyla *Ascomycota*, *Basidiomycota*, *Chytridiomycota*, and *Zygomycota* within the Kingdom *Fungi*, while *Myxomycota* (plasmodial molds), *Dictyosteliomycota* (cellular slime molds), and *Oomycota* (water molds) were excluded from the Kingdom (Bruns *et al.*, 1991; Barr, 1992; Bruns *et al.*, 1992; Berbee and Taylor, 1993, 1995). Some unicellular eukaryotes, such as *Pneumocystis carinii* and Microsporidia are phylogenetically related to the *Fungi* (Edman *et al.*, 1998; Keeling, 2003; Lutzoni *et al.*, 2004; James *et al.*, 2006a).

Recently, a comprehensive phylogenetic classification of the *Fungi* has been proposed (Hibbett *et al.*, 2007). The *Ascomycota* and *Basidiomycota* are classified in a subkingdom, *Dikarya* (Fig. 2). The traditional *Chytridiomycota* and *Zygomycota* are polyphyletic (Lutzoni *et al.*, 2004; James *et al.*, 2006a) and their classification has now undergone major changes (Hibbett *et al.*, 2007). The *Chytridiomycota* is retained in a restricted sense, while the taxa traditionally placed in the *Zygomycota* are distributed between *Glomeromycota* and several subphyla *incertae sedis* (Schüßler *et al.*, 2001; Lutzoni *et al.*, 2004; Hibbett *et al.*, 2007). With respect to the placement of microsporidia (Phylum *Microsporidia*), it is now hypothesised that microsporidia is derived from an endoparasitic chytrid ancestor similar to *Rozella allomycis*, on the earliest diverging branch of the fungal phylogenetic tree (James *et al.*, 2006a; Hibbett *et al.*, 2007).

3. Sexuality and life cycle patterns in fungi

Types of fungal reproduction

Reproduction is one of the six characteristics of life and it refers to formation of new individuals of a species. Through reproduction, an organism passes on genes to their offspring. Reproduction in fungi can take place by clonal propagation or mating and recombination (Taylor *et al.*, 1999). Recombination can occur either by meiosis or by mitosis recombination via parasexuality, while clonal propagation can be affected by mitosis or also by

meiotic division associated with spore production in homothallic fungi (Taylor *et al.*, 1999). Reproduction that involves union of two nuclei (karyogamy) followed by meiosis is referred to as sexual reproduction, while that lacks karyogamy as asexual reproduction (Alexopoulos *et al.*, 1996). Sexual reproduction results in high incidence of recombination and formation of new genotypes and is important in elimination of deleterious mutations (Alexopoulos *et al.*, 1996).

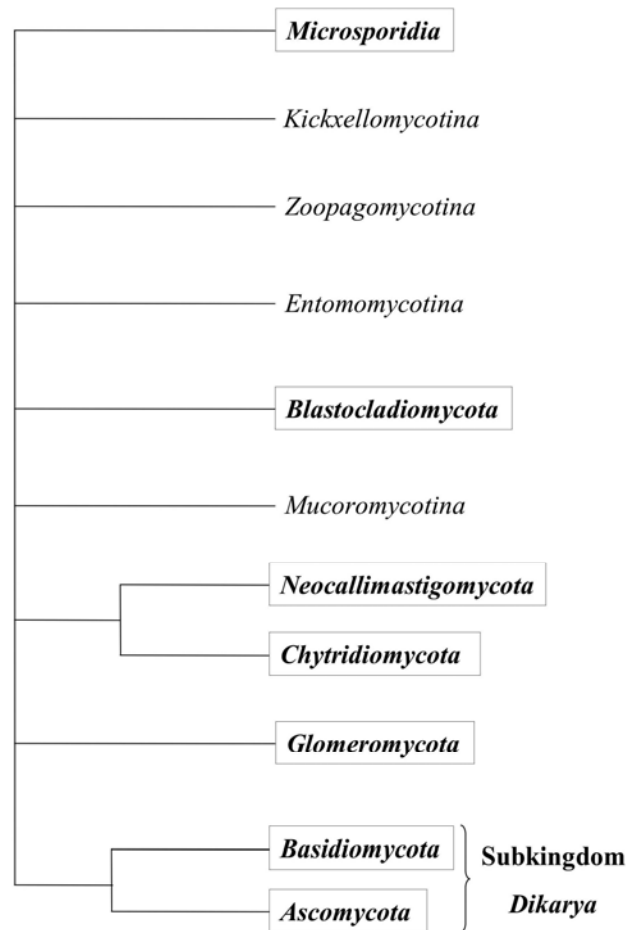


Fig. 2. Phylogenetic classification of the Kingdom *Fungi* (Hibbett *et al.*, 2007).

Life history patterns in fungi

Diversity of life cycles in fungi is complex. Based on life-cycle patterns,

seven major groups of fungi are described in Slot and Hibbett (2007). They are: 1) unicellular “asexual” fungi (e.g. *Candida albicans*), 2) unicellular sexual fungi (e.g. *Chytriumyces hyalinus*), 3) filamentous “asexual” fungi (e.g. *Fusarium oxysporum*), 4) filamentous fungi with sexual and asexual reproduction, but no multicellular fruiting bodies (e.g. *Rhizopus stolonifer*), 5) filamentous fungi with sexual reproduction and multicellular fruiting bodies (e.g. *Agaricus bisporus*), 6) filamentous fungi with sexual reproduction and asexual reproduction (e.g. *Peziza vesiculosa*), and 7) Plant pathogens with sexual and asexual reproduction on multiple hosts (e.g. *Puccinia graminis*). In the subkingdom *Dikarya*, the morphological structures associated with the production of ascospores and basidiospores are referred to as sexual structures, whereas those associated with the production of conidia, sclerotia, stromata, bulbils and chlamydospores are asexual structures (Alexopoulos *et al.*, 1996).

Lack of sex or absence of sexual morphology?

One-fifth of the reported fungi, mainly from the *Dikarya*, are known by their asexual structures. It is unlikely that all of them lack sex. In fact, it is widely believed that truly asexual species are likely to be very rare (Judson and Normark, 1996; Normark *et al.*, 2003). For example, arbuscular mycorrhizal fungi were believed to have lived without sex for 400 million years, i.e. clonal (Sanders *et al.*, 2003). There is a potential existence of genetic and phenotypic variation in this group (Sanders *et al.*, 1995, 1996; Bever and Morton, 1999; Sanders *et al.*, 2003). There have also been recent reports on sexuality in so-called asexual species (e.g. *Aspergillus fumigatus*, *Candida albicans*, *Coccidioides immitis*) (Burt *et al.*, 1996; Lucas *et al.*, 2000; Tzung *et al.*, 2001; Miller and Johnson, 2002; Dyer *et al.*, 2003; Magee and Magee, 2004; Tavanti *et al.*, 2004; Paoletti *et al.*, 2005; Pringle *et al.*, 2005). Absence of sexual morphology, therefore, does not necessarily imply absence of sex.

It is believed that the ability to reproduce both sexually and asexually (i.e. pleomorphism) is a primitive condition in the *Dikarya* that offers more options to a fungus in dispersal and survival, especially in less-favourable environmental conditions (Alexopoulos *et al.*, 1996). Based on their ecological functions, asexual morphologies in fungi are divided into eight main categories: mycelial, mononematous, conidiomatal, germination, survival, yeast-like, spermatial, and vegetative anamorphs (Seifert and Samuels, 2000). The ecological and economic importance of fungi with no known sexual morphologies has been reviewed and detailed in various papers (Cole and Kendrick, 1981; Subramanian, 1983; Seifert and Samuels, 2000; Seifert and Gams, 2001) and will not be elaborated here.

4. A brief history of the dual classification and nomenclature system

Classification of fungi is problematic and has been controversial, especially when every pleomorphic fungus can potentially propagate through different modes of reproduction at different geographical locations and at different times (Sutton, 1973; Kendrick, 1979; Weresub and Hennebert, 1979; Sutton, 1980; Subramanian, 1983; Sugiyama, 1987; Hennebert, 1991; Reynolds and Taylor, 1993; Hawksworth, 1994; Guarro *et al.*, 1999; Seifert *et al.*, 2000a, b; Seifert and Gams, 2001). The documented history of nomenclature and classification of fungi with no known sexual structures goes back to the 18th century. Various authors have reviewed this topic (e.g. Sutton, 1973, 1980; Kendrick, 1979; Subramanian, 1983; Seifert and Gams, 2001). Important historical developments in the taxonomy of the fungi in the context of pleomorphism are listed in Table 1 and summarised in the following sections.

Prior to the 20th century

Common molds such as *Aspergillus* and *Botrytis* with no known sexual morphologies were given generic names by Micheli (1679-1737), followed by H.J. Tode, C.H. Persoon, F. Link, G. Kunze, A.C.J. Corda, and others (Table 1). The developments such as discovery of sexual process in *Syzygites* (C.G. Ehrenberg), studies on life cycle of *Aspergillus glaucus* (J. Schilling), and discontent over giving generic names to asexual morphologies (E. Fries) were followed by seminal works on fungal pleomorphism by C. Tulasne, E.L. Tulasne, H.A. De Bary and O. Brefeld (Table 1). The natural classification of pleomorphic fungi, however, was not encouraged as there were more fungi that lacking sexual morphologies than those known with a complete life history. Concurrently, K.W.G.L. Fuckel's *Fungi Imperfecti* concept and later the Saccardoan system of classification (Deuteromycetes) (Fig. 3) based on conidial and conidiophore morphology resulted in a comprehensive yet practical solution for classifying "asexual" fungi. The system was designed for convenience rather than for phylogenetic inference.

The 20th century

In the early 20th century, inspired by J. Constantin's ontogeny-centric view on classification, J.P. Vuillemin favoured conidial ontogeny as the basis of classification. Vuillemin's ideas, however, were only taken seriously later when Hughes (1953) demonstrated different modes of conidial development.

Table 1. Important historical developments in fungal taxonomy in the context of pleomorphism (Sutton, 1973; Kendrick, 1979; Subramanian, 1983; Tubaki, 1981; Seifert and Gams, 2001).

| I. Prior to the 20th Century |
|---|
| Application of generic names to “asexual” fungi (e.g. <i>Aspergillus</i> , <i>Botrytis</i>) by P.A. Micheli (1679-1737) |
| Description and classification of “asexual” fungi by various mycologists - H.J. Tode, C.H. Persoon, F. Link, C.G.N. von Esenbeck, G. Kunze, J.K. Schmidt, C.F. Ph. von Martius, C.G. Ehrenberg; Schweinitz, K.F.H. Wallroth, A.C.J. Corda, M.J. Berkeley, C.G.T. Preuss, H.F. Bonorden, J.B.G.W. Fresenius, T. Hartig etc. |
| The use of the term “Hyphomycetes” by C.F. Ph. von Martius (1794-1868) |
| Discovery of sexual process in <i>Syngites</i> (<i>Mucorales</i>) by C.G. Ehrenberg (1795-1876) |
| The first attempt to follow the life history of <i>Aspergillus glaucus</i> from spore to spore method in 1827 by J. Schilling |
| The conidial forms are degenerates of the sexual fungi – E.M. Fries (1794-1878) |
| The connection between <i>Aspergillus glaucus</i> and <i>Eurotium herbariorum</i> based on pure culture-method in 1854 by H.A. de Bary (1831-1888) |
| Microscopic observation of the common mycelium connecting sexual and asexual morphologies of fungi by E.L. Tulasne and C. Tulasne. (Published many papers on life histories of fungi in <i>Selecta Fungorum Carpologia</i> (1861-1865)). |
| Improvement of culture methods, elucidation of life histories many (pathogenic) fungi using pure cultures – by O. Brefeld (1839-1925). |
| Proposal of the form-class <i>Fungi Imperfecti</i> for fungi with no known sexual morphologies by K.W.G.L. Fuckel (1821-1876) |
| Establishment of the Saccardoan system of classification of the <i>Fungi Imperfecti</i> (<i>Deuteromycotina</i>) (Fig. 3) based on conidial and conidiophore morphology by P.A. Saccardo (1845-1920). |
| Proposal of a classification based on the mode of insertion of the spores on conidiophores and on the presence and absence of mucilage around the conidia in 1888 by J. Costantin |
| II. The 20th Century |
| Development of Costantin’s idea by J.P. Vuillemin (1861-1932) (More stress on conidial ontogeny in classification). |
| Introduction of the Coelomycetes (1919) and recognition of classes, Hyphomycetes and Coelomycetes in the Deuteromycetes (1935) by W.P. Grove. |
| Importance to mode of dispersal of spores in hyphomycetes classification by E.W. Mason, E.M. Wakefield and G.R. Bisby |
| Proposal to use conidial ontogeny as a primary character in classifying of fungi with no known sexual morphologies by Hughes (1953) |
| Development of Hughes’ idea by Tubaki (1958), Subramanian (1962), Nilsson (1964), Barron (1968), Subramanian (1971, 1983) |
| Analysis on pleomorphic nature of fungi, connections between different morphs of a fungal species and the Holomorph Concept- Hennebert and Weresub (1977), Kendrick (1979), Weresub and Hennebert (1979), Subramanian (1983), Sugiyama (1987), Reynolds and Taylor (1993). |

Table 1 continued. Important historical developments in fungal taxonomy in the context of pleomorphism (Sutton, 1973; Kendrick, 1979; Subramanian, 1983; Tubaki, 1981; Seifert and Gams, 2001).

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| How natural should anamorph genera be? (Gams, 1995): “The taxonomy of anamorphic fungi has always been artificial, and classification of anamorph genera cannot aim at genera that adequately reflect natural relationships and the most convenient generic delimitation must be considered for individual cases” |
| The genus for genus concept (Seifert <i>et al.</i> , 2000a, b): a single teleomorph genus corresponds to a comparable anamorph genus. |
| The generic names of anamorphic fungi as unitalicized nouns or descriptive nouns when they are known to be paraphyletic or polyphyletic (Seifert <i>et al.</i> , 2000a, b) |
| III. Some recent molecular work on Fungal Systematics |
| White <i>et al.</i> , 1990; Bruns <i>et al.</i> , 1991; Barr, 1992; Bruns <i>et al.</i> , 1992; Baldauf and Palmer, 1993; Berbee and Taylor, 1993; Wainright <i>et al.</i> , 1993; Berbee and Taylor, 1995, 2001; O’Donnell <i>et al.</i> , 2001; Lang <i>et al.</i> , 2002; Lutzoni <i>et al.</i> , 2004; Cai <i>et al.</i> , 2005; Aime <i>et al.</i> , 2006; Alves <i>et al.</i> , 2006; Ayala-Escobar <i>et al.</i> , 2006; Begerow <i>et al.</i> , 2006; Binder and Hibbett, 2006; Blackwell <i>et al.</i> , 2006; Celio <i>et al.</i> , 2006; Den Breeÿen <i>et al.</i> , 2006; Geiser <i>et al.</i> , 2006; Hansen and Pfister, 2006; Hibbett, 2006; Hosaka <i>et al.</i> , 2006; Hunter <i>et al.</i> , 2006a, b; James <i>et al.</i> , 2006a, b; Kodsueb <i>et al.</i> , 2006a; Larsson <i>et al.</i> , 2006; Matheny <i>et al.</i> , 2006; Miadlikowska <i>et al.</i> , 2006; Miller <i>et al.</i> , 2006; Moncalvo <i>et al.</i> , 2006; Phillips <i>et al.</i> , 2006; Photita <i>et al.</i> , 2005; Redecker and Raab, 2006; Schoch <i>et al.</i> , 2006; Spatafora <i>et al.</i> , 2006; Sugiyama <i>et al.</i> , 2006; Suh <i>et al.</i> , 2006; Summerell <i>et al.</i> , 2006; Taylor and Berbee, 2006; Tsui <i>et al.</i> , 2006a; Van Wyk <i>et al.</i> , 2006; Wang <i>et al.</i> , 2006; White <i>et al.</i> , 2006; Vijaykrishna <i>et al.</i> , 2006; Zhang <i>et al.</i> , 2006; Arenal <i>et al.</i> , 2007; Burgess <i>et al.</i> , 2007; Hibbett <i>et al.</i> , 2007; Phillips <i>et al.</i> , 2007. |

Many authors followed Hughes’ ideas on conidial ontogeny (Table 1). There was, however, an equal interest in the pleomorphic nature of fungi and its implications on classification and nomenclature (Table 1). The development and popularity of the Holomorph concept (Hennebert and Weresub, 1977; Weresub and Hennebert, 1979; Reynolds and Taylor, 1993) and the recent progress in DNA sequencing and analytical methods (Table 1), now, offer an opportunity to refine the artificial classification of anamorphic fungi. The amalgamation of two classification systems and development of a phylogeny-based fungal classification system, however, suffer from the heritage of the dual classification system.

5. The Holomorph concept

The idea of a holomorph

A typical fungal life cycle involves two phases - teleomorphosis and anamorphosis (Hennebert, 1987). Teleomorphosis is the sexual phase of the

fungal life cycle and involved in the production of *meiotic diaspores*. The associated morphological, sexual reproductive structures referred to as the teleomorph, which is the sole constituent of teleomorphosis. Anamorphosis is the asexual phase of the fungus and involved in the development of *mitotic diaspores* (conidia) or other propagules (Hennebert, 1987). The asexual, morphological reproductive structures are referred to as the anamorph. Anamorphosis, unlike teleomorphosis, can result in more than one morphologically distinct anamorphs, which are known as synanamorphs

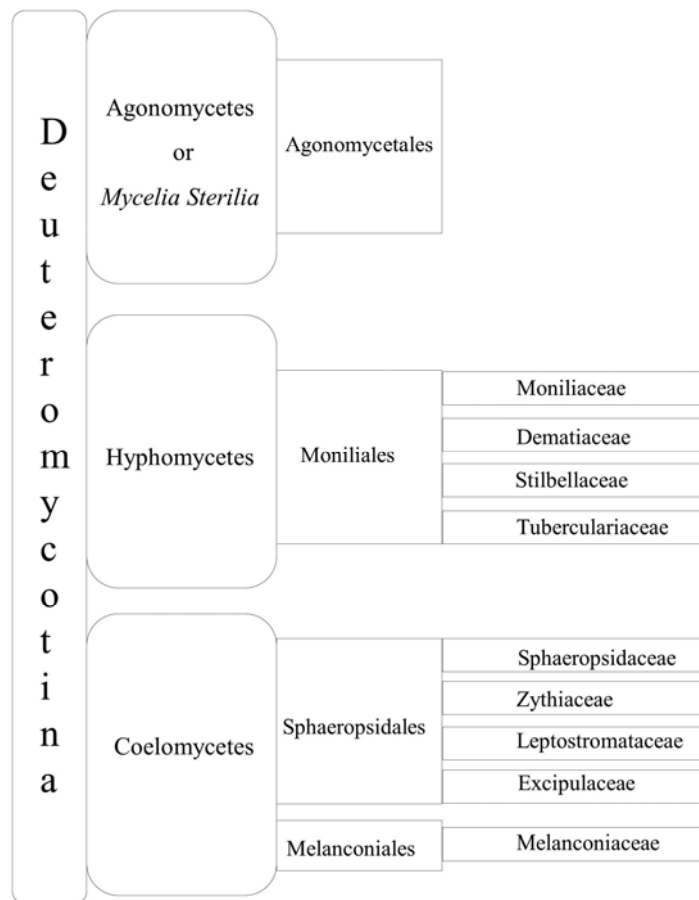


Fig. 3. Saccardo's classification of Deuteromycotina (Talbot, 1971).

(Hughes, 1979). Pleomorphism in fungi results in the occurrence of morphologically distinct, visibly unconnected asexual and sexual phases of the same fungal species at different times or in different habitats (Burnett, 2003). The whole fungus concept or the holomorph concept (Hennebert and Weresub, 1977; Weresub and Hennebert, 1979; Hennebert, 1987; Reynolds and Taylor,

1993) brings together different phases of a fungal life cycle under one fungal entity, the holomorph.

The whole fungus or the holomorph is defined as “*a fungus in its all meiotic (teleomorphosis) or mitotic (anamorphosis), sexual and asexual potential expressions of morphological nature and covers the unknown and known morphs of the fungus*” (Hennebert, 1987). The teleomorph of a whole fungus has been traditionally classified and named separately from their anamorphs. Each of the morphs of anamorphosis was also given different binomials as if they were different species. As a result, a whole fungus finds itself in two classification and nomenclature systems against the principle of natural classification (Hennebert and Weresub, 1977; Kendrick, 1979; Weresub and Hennebert, 1979; Hennebert, 1987; Sugiyama, 1987; Reynolds and Taylor, 1993; Seifert *et al.*, 2000a. b; Kirk *et al.*, 2001).

The whole fungus: e.g. *Orbilia auricolor*

The whole fungus concept assumes that all the fungi produce sexual morphologies. Pleomorphism in fungi, however, can attain different levels of complexity, depending on our understanding of life cycle of a fungus (Hennebert, 1987). Pleomorphism in *Orbilia auricolor* is interesting, with different levels and forms of pleomorphism. *Orbilia* is an ascomycete genus in the *Orbiliaceae* (*Orbiliales*, *Orbiliomycetes*). *Orbilia auricolor* is connected to four morphologically distinct anamorphs (Table 2) (Mo *et al.*, 2005). Mathematically, there can be 29 and 31 different kinds of possible pleomorphisms and holomorphisms, respectively. There are 15 different possible ways of reproductive duality i.e. existence of a sexual and an asexual phase (Hennebert, 1987) (Table 2). In the absence of the teleomorph, there are 14 different possible forms of pleomorphism in anamorphosis (Table 2).

Thus, the holomorph or whole fungus concept in *Orbilia auricolor* includes both teleomorphosis and anamorphosis, and covers known sexual (teleomorphic *Orbilia auricolor*) and asexual (*Arthrotrrys cladodes* var. *macroides*, *A. oligospora*, *A. yunnanensis*, and *Monacrosporium psychrophilum*) morphological reproductive expressions. However, it is noted that *Orbilia auricolor* is a species-complex (Mo *et al.*, 2005) and the genetic structure of the teleomorph and its culturally connected anamorphs is not well understood. At the same time, possible phenotypic plasticity in *Arthrotrrys cladodes* var. *macroides*, *A. oligospora*, *A. yunnanensis*, and *Monacrosporium psychrophilum* should be considered. There is an indication of a significant phenotypic variation influenced by salinity-gradient in some of the members of *Arthrotrrys* (Aung Swe, pers.)

Table 2. Pleomorphism in *Orbilia auricolor* (The area with grey background represents teleomorphosis and resultant teleomorph, while the area with white background represents anamorphosis and resultant four anamorphs).

| | <i>Orbilia auricolor</i> | <i>Arthrobotrys cladodes</i> var. <i>macroides</i> | <i>A. oligospora</i> | <i>A. yunnanensis</i> | <i>Monacrosporium psychrophilum</i> |
|----|--------------------------|--|----------------------|-----------------------|-------------------------------------|
| 1 | P | | | | |
| 2 | | P | | | |
| 3 | | | P | | |
| 4 | | | | P | |
| 5 | | | | | P=PRESENT |
| 6 | | P | P | | |
| 7 | | P | | P | |
| 8 | | P | | | P |
| 9 | | P | P | P | |
| 10 | | P | | P | P |
| 11 | | P | P | P | |
| 12 | | | P | P | |
| 13 | | | P | | P |
| 14 | | | P | P | P |
| 15 | | | | P | P |
| 16 | | P | | P | P |
| 17 | | P | | | |
| 18 | | | P | | |
| 19 | | | | P | |
| 20 | | | | | P |
| 21 | | P | P | | |
| 22 | | P | | P | |
| 23 | | P | | | P |
| 24 | | P | P | P | |
| 24 | | P | | P | P |
| 26 | | P | P | P | |
| 27 | | | P | P | |
| 28 | | | P | | P |
| 29 | | | P | P | P |
| 30 | | | | P | P |
| 31 | | P | | P | P |

Nature of pleomorphism in the *Ascomycota*

Pleomorphism in the *Ascomycota* is uneven and diverse. A group of fungi classified under one form-genus have shown to have sexual states in different teleomorphic genera, e.g. *Acremonium*, *Chalara*, *Cladobotryum*, *Cryptococcus*, *Cylindrotrichum*, *Dendrotrichum*, *Fusarium*, *Gliocladium*, *Graphium*,

Myrothecium, *Papulospora* (Seifert *et al.*, 2000 a, b), *Penicillium* (Samson and Frisvad, 2004), *Phialophora*, *Selenosporella*, *Seuicillium*, *Sporothrix*, *Stigmina*, *Stilbella* and *Verticillium* (Seifert *et al.*, 2000 a, b). Conversely, some of the teleomorph groups are anamorph rich, e.g. *Hypocreales* (Rossman, 2000), *Mycosphaerella* (Crous *et al.*, 2000; Verkley and Priest, 2000; Crous *et al.*, 2006d), *Botryosphaeriales* (Denman *et al.*, 2000; Crous *et al.*, 2006c), and *Chaetosphaeriales* (Réblová, 2000; Réblová and Winka, 2001; Fernández and Huhndorf, 2005; Fernández *et al.*, 2006; Shenoy *et al.*, 2006). A group of form-genera that have been delineated based on shared conidial or conidial ontogenic characters share teleomorphs in different taxonomic classes, e.g. sporidesmium-like anamorphs (Wu and Zhuang, 2005; Shenoy *et al.*, 2006); *Diplococcium-Spadicoides* (Goh and Hyde, 1996, 1998), form-genera of helicosporous fungi (Tsui and Berbee, 2006; Tsui *et al.*, 2006b) and the Ingoldian fungi (Belliveau and Bärlocher, 2005; Campbell *et al.*, 2006). Some of the speciose genera such as *Aspergillus* (Balajee and Marr, 2006), *Colletotrichum* (Sutton, 1992; Armstrong-Cho and Banniza, 2006), and *Penicillium* (Pitt and Samson, 1993; Cannon and Kirk, 2000) include more members without teleomorphs than those with sexual morphologies.

Anamorph-teleomorph connections

Anamorph-teleomorph connections are important in amalgamation of the two classification systems and various papers and resources list the connections (Ellis, 1971a, 1976; Kendrick and Dicosmo, 1979; Carmichael *et al.*, 1980; Tubaki, 1981; Subramanian, 1983; Sivanesan, 1984; Sugiyama, 1987; Sutton and Hennebert, 1994; Kirk *et al.*, 2001; Index Fungorum, 2007; The Anamorph-Teleomorph Database, 2007; Shearer *et al.* 2007). One fifth of the known fungi lack sexual morphologies and are yet to be connected to their teleomorphs. The morphological determination of affiliation between anamorph and teleomorph has either been based on circumstantial or experimental criteria (Kendrick, 1979; Reynolds, 1993). The circumstantial criteria such as observation of co-habitation are unreliable, while experimental observation of pleomorphic holomorph by single-spore or mated culture of another morph is the most preferred morphological evidence. Conversely, many of the teleomorphs are known solely by their sexual structures. For example, more than 65 species have been described in teleomorph genus *Oxydothis* (Hyde 1993, 1994; Shenoy *et al.*, 2005; Hidayat *et al.*, 2006). However, there is only one anamorph-teleomorph connection i.e. *Selenosporella* known for the genus (Hyde, 1994).

6. Fungal systematics and molecular characters

Classification as a hypothesis

Classification and identification are the main activities of systematics, which fundamentally aims to: 1) discover all branches of the evolutionary tree of life, 2) document all the changes that occurred during the evolution, and 3) to describe all species (Judd *et al.*, 2002). Fungal systematics (Fig. 4) starts with identification, a process by which an unknown fungus is compared with known and named groups of fungi. The identification process is followed by determination, in which relationships of the identified fungus with known fungi are inferred. Identification and determination steps are followed by naming and classification of the fungus (Talbot, 1971). A classification includes three main activities: describing and grouping, storage of information, and prediction of phylogenetic relationships of organisms (Judd *et al.*, 2002). Classification is a hypothesis; every proposed grouping in a classification is a hypothesis (Wheeler, 2004).

Fungal species concepts

Species is one of the basic units of biological classification. Species is a hypothesis, which is to be tested when new data are available. It is, however, not easy to define a fungal species. There are four major categories in the fungal species concepts, which are summarised by Moncalvo (2005): 1) **The Morphological Species Concepts** based on overall morphological similarity among fungi; 2) **Ecological and Physiological Species Concepts** (*A species is a lineage that occupies an adaptive zone minimally different from that of any other lineage in its range and evolves separately from all lineages outside its range*) (Agapow *et al.*, 2004; Moncalvo, 2005); 3) **The Biological Species Concept (BSC)** (*Species are interbreeding populations that are reproductively isolated from other populations*) (Mayr, 1942); and 4) **Evolutionary and Phylogenetic Species Concepts** (*A species should represent a monophyletic group of organisms that share at least one uniquely derived character that descends from a common ancestor*) (Moncalvo, 2005).

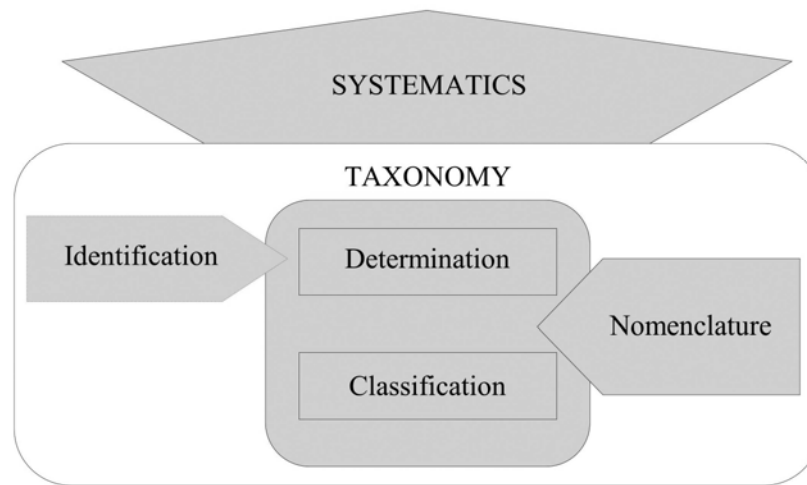


Fig. 4. Relationships between identification, determination, classification, nomenclature taxonomy, and systematics (Talbot, 1971).

Molecular characters in fungal systematics

Phylogeny-centred fungal systematics is mainly based on recognition and naming monophyletic groups. It is believed that classification based on monophyletic groups is *more predictive and of greater heuristic value than those based on overall similarity or weighting of particular characters* (Judd *et al.*, 2002). Morphological characters have been used for the last 300 years to identify, classify, and infer phylogenies of fungi. They are relatively easy to observe and record and they assist in the differentiation process (Talbot, 1971). Morphological characters significantly assist in identification of fungi as evident from a plethora of identification keys and morphological descriptions. Morphological characters, however, may not reflect phylogenetic relationships as many of them are subject to plasticity, parallelism, and reversal (homoplasy) (Judd *et al.*, 2002). Phylogenetic Species Concepts and molecular characters, combined together, can overcome most of the limitations associated with Biological Species Concept and the other species concepts. It is, however, unreasonable to claim that molecular data are superior to morphological data in phylogenetic inference. Nevertheless, molecular characters are also known to be subject to convergence and parallelism (Judd *et al.*, 2002). Molecular characters such as DNA sequence-data are essentially advantageous as they offer a greater number of discrete characters, which can be analysed statistically to infer phylogenetic relationships. Molecular data, especially DNA sequence-data have been widely used to: 1) establish anamorph-

teleomorph connections, 2) infer phylogenetic relationships of form-genera, of anamorph-rich clades, and of anamorphic generic-complexes, and 3) in species delineation of monophyletic groups of anamorphic taxa. More importantly, newly generated DNA sequence-data aid to test taxonomic hypotheses at different strata of classification.

7. Recent advances in the taxonomy of anamorphic fungi

Anamorph-teleomorph connections

Determination of anamorph-teleomorph connections can, sometimes, be complicated when one or both the morphs cannot be cultured or induced to sporulate on artificial media. The circumstantial evidence such as observation of two morphs on the same substrate is an insufficient proof of anamorph-teleomorph connections. The type of evidence, however, can have certain predictive significance, which can be tested using DNA sequence-data. There have been some interesting studies on anamorph-teleomorph connections using DNA sequence-data and cultures. Table 3 lists selected anamorph-teleomorph connections proven by DNA sequence-data or cultural studies.

Brachysporium* anamorphs of *Cryptadelphia

The phylogenetic connection of *Brachysporium* species with their sexual states (Réblová and Seifert, 2004) is interesting. *Brachysporium* anamorphs are not easy to culture and very rarely produce teleomorphs on agar media. Réblová and Seifert (2004) frequently observed some perithecia on fresh/herbarium collections of *B. abientinum*, *B. brevius*, *B. obovatum*, *B. nigrum*, *B. pendulisporium* and *B. polyseptatum*. None of the ascospore-cultures of the associated perithecia sporulated on agar media, while only *B. nigrum* produced conidia, but no teleomorph on agar media. The LSU nu-rDNA of *Brachysporium nigrum* (the conidial isolate) and the associated perithecia (the single-ascospore culture) were sequenced. The two sequences, interestingly, differed by only 1/1200 bp, which is reasonable proof for the anamorph-teleomorph connection. Molecular phylogenetic analyses of LSU nu-rDNA sequence-data also suggested that *Brachysporium nigrum*, its teleomorph, and the presumed teleomorph of *B. polyseptatum* present on substrate are monophyletic in the *Trichosphaeriales* (*Sordariomycetes*). All the six sexual structures present on *Brachysporium* specimens were morphologically similar, therefore, described as a holomorphic genus *Cryptadelphia* with *Brachysporium* as presumed anamorphs.

Table 3. Recent selected anamorph-teleomorph connections mainly based on DNA sequence and culture-based studies.

| Anamorph | Teleomorph | Reference |
|--|---------------------------------|--|
| <i>Aschersonia incrassata</i> | <i>Hypocrella zhongdongii</i> | Liu and Hodge (2005) |
| <i>Ascochyta fabae</i> | <i>Didymella fabae</i> | Peever <i>et al.</i> (2007) |
| <i>Ascochyta lentis</i> | <i>Didymella lentis</i> | Kaiser <i>et al.</i> (1997) |
| <i>Ascochyta pinodes</i> | <i>Didymella pinodes</i> | Peever <i>et al.</i> (2007) |
| <i>Ascochyta rabiei</i> | <i>Didymella rabiei</i> | Peever <i>et al.</i> (2007) |
| <i>Aspergillus flavipes</i> | <i>Fennellia flavipes</i> | In Wheeler <i>et al.</i> (2000) |
| <i>Aspergillus nidulans</i> | <i>Emericella nidulans</i> | Hinrikson <i>et al.</i> (2005) |
| <i>Candida fermentati</i> | <i>Pichia caribbica</i> | Vaughan-Martini <i>et al.</i> (2005) |
| <i>Cladosporium herbarum</i> | <i>Davidiella tassiana</i> | Braun <i>et al.</i> (2003) |
| <i>Colletogloeopsis</i> , <i>Pseudocercospora</i> , <i>Stenella</i> , <i>Trimmatostroma</i> spp. | <i>Mycosphaerella</i> spp. | Crous <i>et al.</i> (2006d) |
| <i>Colletotrichum acutatum</i> | <i>Glomerella acutata</i> | Guerber and Correll (2001) |
| <i>Colletotrichum truncatum</i> | <i>Glomerella truncata</i> | Armstrong-Cho and Banniza, (2006) |
| <i>Cylindrocarpon macrodidymum</i> | <i>Neonectria macrodidymum</i> | Halleen <i>et al.</i> (2004) |
| <i>Cylindrocarpon liriodendri</i> | <i>Neonectria liriodendri</i> | Halleen <i>et al.</i> (2006) |
| <i>Cylindrocladium</i> spp. | <i>Calonectria</i> spp. | Crous <i>et al.</i> (2006b) |
| <i>Cytospora</i> spp. | <i>Valsa</i> spp. | Adams <i>et al.</i> (2005) |
| <i>Dactylellina quercu</i> | <i>Orbilbia quercu</i> | Liu <i>et al.</i> (2005) |
| <i>Discula betulina</i> | <i>Gnomonia intermedia</i> | Green and Castlebury (2007) |
| <i>Dissoconium dekkeri</i> | <i>Mycosphaerella lateralis</i> | Braun <i>et al.</i> (2003) |
| <i>Dothiorella viticola</i> | <i>Botryosphaeria viticola</i> | Luque <i>et al.</i> (2005) |
| <i>Grosmannia radiaticola</i> | <i>Pesotum pini</i> | Kim <i>et al.</i> (2005) |
| <i>Hirsutella sinensis</i> | <i>Cordyceps sinensis</i> | Liu <i>et al.</i> (2001) |
| <i>Hyalorhinoclaidiella</i> spp. | <i>Ceratocystiopsis</i> spp. | Zipfel <i>et al.</i> (2006) |
| <i>Lecanicillium</i> sp. | <i>Torrubiella piperis</i> | Bischoff and White (2004) |
| <i>Leptographium</i> spp. | <i>Grosmannia</i> spp. | Zipfel <i>et al.</i> (2006) |
| <i>Menispora tortuosa</i> | <i>Chaetosphaeria tortuosa</i> | Réblová <i>et al.</i> (2006) |
| <i>Pestalotiopsis microspora</i> | <i>Pestalosphaeria hanseni</i> | Metz <i>et al.</i> (2000) |
| <i>Phaeoacremonium</i> spp. | <i>Togninia</i> spp. | Mostert <i>et al.</i> (2003, 2006) |
| <i>Phomopsis</i> spp. | <i>Diaporthe</i> spp. | Van Rensburg <i>et al.</i> (2006) |
| <i>Pleurostomophora ootheca</i> | <i>Pleurostoma ootheca</i> | Vijaykrishna <i>et al.</i> (2004) |
| <i>Sorocybe resiniae</i> | <i>Amorphotheca resiniae</i> | Braun <i>et al.</i> (2003) |
| sphaeria-like | <i>Regiocrella camerunensis</i> | Chaverri <i>et al.</i> (2005) |
| <i>Sporothrix/ Pesotum</i> spp. | <i>Ophiostoma</i> spp. | Roets <i>et al.</i> (2006), Zhou <i>et al.</i> (2006), Zipfel <i>et al.</i> (2006) |
| <i>Trichoderma atroviride</i> | <i>Hypocrea atroviridis</i> | Dodd <i>et al.</i> (2003) |
| <i>Trichoderma crystalligenum</i> | <i>Hypocrea crystalligena</i> | Jaklitsch <i>et al.</i> (2006) |

***Septoria passerinii* and its *Mycosphaerella* functional teleomorph**

The anamorphic taxon *Septoria passerinii*, the causative agent of Septoria Speckled Leaf Blotch (SSLB) was considered to be asexual (Cunfer and Ueng, 1999). This anamorphic fungus is morphologically similar to *Septoria tritici*, the anamorph of the wheat pathogen *Mycosphaerella graminicola* (Goodwin *et al.*, 2001). The sequence comparison and phylogenetic analysis of internal transcribed spacer (ITS) region rDNA of *Septoria passerinii* and *Mycosphaerella graminicola* (Goodwin *et al.*, 2001) revealed the phylogenetic affiliation of *S. passerinii* with *M. graminicola*. Based on their phylogenetic analyses, Goodwin *et al.* (2001) predicted that the teleomorph of *S. passerinii*, if existed, would be a *Mycosphaerella*! Ware *et al.* (2007) tested this prediction by co-inoculating isolates with opposite mating types onto susceptible barley cultivars and characterised putative hybrid progeny by AFLP, RAPD, mating type, and ITS sequencing and phenotypic analyses. These analyses, interestingly, have led to the discovery of *Mycosphaerella* teleomorph after approximately 125 years of the description of *S. passerinii*.

The above examples illustrate the limitations associated with the culture-based anamorph-teleomorph connections and also demonstrate the utility of DNA sequence-data and other molecular tools in integrating different morphs of a holomorph and other implications in plant pathology, e.g. the discovery of a functional teleomorph *S. passerinii* is important for resistance breeding efforts in barley (Ware *et al.*, 2007).

Multiple phylogenetic species in a morphological species

Fusarium graminearum is the primary causal agent of Fusarium Head Blight (FHB) in wheat and barley. It was thought to be a single potentially panmictic species spanning six continents (O'Donnell *et al.*, 2004). O'Donnell *et al.* (2004) investigated species limits within the *Fusarium graminearum* clade using multi-gene sequences and identified nine phylogenetic species within the morphological species. As the nine phylogenetic species could not be diagnosed by a combination of conidial characters, they formally recognised those phylogenetic species using fixed nucleotide differences. The formal recognition of the phylogenetic species will facilitate communication among plant pathologists, mycotoxicologists, and quarantine specialists, and help plant breeders in resistant plant breeding efforts (O'Donnell *et al.*, 2004). This study narrates the inadequacy of morphological characters in defining species boundary and the potential use of DNA sequence-data in phylogenetic species-

delimitation, which is very useful in case of economically important fungi.

Polyphyly of form-genera

Recent molecular phylogenetic studies have confirmed polyphyly/paraphyly of many of well-recognised anamorphic genera and species, whose classification is subject to further refinement. Prominent examples include: *Acremonium* (Glenn *et al.*, 1996); *Chalara* (Paulin and Harrington, 2000; Paulin *et al.*, 2002; Fernández *et al.*, 2006), *Cryptococcus* (Fell *et al.*, 2000; Scorzetti *et al.*, 2002), *Dendrotrichum* (Schroers, 2000), *Fusarium* (Rossman *et al.*, 1999; Rossman, 2000), *Geosmithia* (Kolarik *et al.*, 2005), *Gliocladium* (Seifert *et al.*, 2000b), *Graphium* (Okada *et al.*, 1998, 2000), *Myrothecium*, *Papulospora*, *Penicillium*, *Phialophora*, *Selenosporella*, *Sequicillium*, *Sporothrix*, *Stigmina*, *Stilbella* and *Verticillium* (Seifert *et al.*, 2000a, b). The generic names of paraphyletic or polyphyletic anamorphs have been used as unitalicized, descriptive nouns and in a monomorphic, form-sense (Seifert *et al.*, 2000a, b).

***Chalara*:** *Chalara* is characterised by deep-seated phialides and conidia produced by ring wall building (Nag Raj and Kendrick, 1975; Minter, 1982, 1983). Members of *Chalara* are associated with teleomorphs from different taxonomic classes. Paulin and Harrington (2000) listed teleomorphic affiliations of *Chalara* species with the *Dothideales*, *Laboulbeniales*, *Leotiales*, *Microascales*, *Sordariales*, and the *Trichosphaeriales*. Many of the *Chalara* anamorphs lack sexual morphology (Paulin and Harrington, 2000) and DNA sequence-data have been used to integrate them with Ascomycete Systematics. Initial molecular studies by Paulin and Harrington (2000) also reported their affinities with the *Dothideomycetes* and *Leotiomyces*. Recent molecular work demonstrates phylogenetic affinities of *Chalara* with the *Chaetosphaeriales* (Fernández *et al.*, 2006). Interestingly, a few *Chalara* species appeared to be phylogenetically related to the *Xylariales* (Cai Lei pers.).

***Phialophora*:** *Phialophora* has a conserved morphology and is known to have teleomorphs in the *Caliciales*, *Chaetothyriales*, *Diaporthales*, *Dothideales*, *Hypocreales*, *Leotiales*, *Ophiostomatales*, *Sordariales*, and *Spathulosporales* (Gams *et al.*, 2000). Réblová and Seifert (2007) have summarised recent studies on phylogeny of *Phialophora*.

***Diplococcium-Spadicoides*:** *Diplococcium* and *Spadicoides* are dematiaceous, hyphomycetous genera, which had been primarily delineated with varying emphasis on branching of conidiophores and catenation of conidia (e.g. Ellis, 1963, 1971b, 1972; Wang, 1976; Wang and Sutton, 1982). Earlier authors considered branching of conidiophores to be taxonomically more important than catenation of conidia, while Sinclair *et al.* (1985) stressed on catenation of conidia. The re-circumscription of *Spadicoides* to include species that produce solitary conidia from branched or unbranched conidiophores has resulted in the generic delineation relying solely on catenation of conidia (Goh and Hyde, 1996, 1998). Morphological data on anamorph-teleomorph associations suggest affiliations of *Diplococcium* with *Helminthosphaeria* (*Sordariomycetes*) and the *Pleosporaceae* (*Dothideomycetes*) (Ellis, 1971b; Subramanian, 1983; Subramanian and Sekar, 1989; Samuels *et al.*, 1997; Goh and Hyde, 1998; Réblová 1999b). However, only the *Diplococcium pulneyens* - *Othia pulneyensis* connection is based on single-spore isolation (Subramanian and Sekar, 1989). One *Spadicoides* species is associated with *Tengiomyes indicus* (*Helminthosphaeriaceae*, *Sordariomycetes*) (Réblová, 1999b). Recent data from multi-gene phylogenetic studies (Wang *et al.* unpubl.), however, suggest that both *Diplococcium* and *Spadicoides* are polyphyletic. *Diplococcium* species have phylogenetic affinities with the *Helotiales* (*Leotiomycetes*) and *Pleosporales* (*Dothideomycetes*), while *Spadicoides* species are phylogenetically linked with the *Pleosporaceae* (*Dothideomycetes*), and the *Sordariomycetidae* (*Sordariomycetes*) (Wang *et al.* unpubl.). The morpho-centric taxonomy of *Diplococcium-Spadicoides* is artificial and is only informative as taxon names and groupings for diagnostic keys.

***Sporidesmium sensu lato*:** *Sporidesmium* and morphologically similar genera include several dematiaceous, hyphomycetous genera taxonomically segregated from *Sporidesmium sensu lato* (Ellis, 1958, 1971a, 1976; Kirk, 1982; Subramanian, 1992; Hernández-Gutiérrez and Sutton, 1997; Shoemaker and Hambleton, 2001; Wu and Zhuang, 2005). These anamorphic fungi were grouped based on asexual characters such as presence or absence of conidiophores, type of conidiophore proliferation and conidial septation. Morphological data, either based on cultural studies or association of two morphs on the same substrate, however, suggested their association with teleomorphic fungi in five ascomycete families within the *Dothideomycetes* and *Sordariomycetes* (Shenoy *et al.*, 2006). Based on phylogenetic analyses of the LSU nu-rDNA sequences, Réblová and Winka (2001) reported that two species of *Sporidesmium sensu lato* are phylogenetically linked to the *Chaetosphaeriales* (*Sordariomycetes*). Shenoy *et al.* (2006) incorporated a

phylogenetic investigation based on multi-gene sequences to assess the possible familial placement of *Ellisemia*, *Linkosia*, *Repetophragma*, *Sporidesmiella*, *Sporidesmium*, and *Stanjehughesia*. Their studies indicate *Sporidesmium* and morphologically similar anamorphs are polyphyletic, having affiliations with the *Dothideomycetes* and *Sordariomycetes*. Further studies on this group are required in order to refine their classification as inadequate taxon sampling may have influenced the results of the molecular studies.

Anamorphs of the *Botryosphaerales*, *Chaetosphaerales*, *Mycosphaerella* and others

***Botryosphaerales*:** *Botryosphaeria* (*Botryosphaeriaceae*, *Botryosphaerales*, *Dothideomycetes*) is a species-rich genus (Denman *et al.*, 2000; Schoch *et al.*, 2006). The teleomorph genus was believed to have eighteen associated coelomycetous genera, i.e. *Botryodiplodia*, *Chaetodiplodia*, *Colletotrichella*, *Diplodia*, *Diplodiella*, *Dothiorella*, *Fusicoccum*, *Kabatia*, *Lasiodiplodia*, *Macrophoma*, *Pelionella*, *Placosphaeria*, *Phyllosticta*, *Rhynchodiplodia*, *Selenophoma*, *Sphaeriopsis*, *Striodiplodia* and *Strionemadiplodia* (Sutton, 1980; Sivanesan, 1984; Pennycook and Samuels, 1985; Samuels and Singh, 1986; Barr, 1987; Morgan-Jones and White, 1987; von Arx, 1987; Jacob and Rehner, 1998; Denman *et al.*, 2000). Based on morphological observations and phylogenetic analyses of ITS nu-rDNA sequence-data, Denman *et al.*, (2000) recognised two phylogenetic groupings in *Botryosphaeria*: one correlated with diplodia-like anamorphs (conidia mostly ovoid, pigmented, thick-walled) and the other with fusicoccum-like anamorphs (conidia mostly fusoid, hyaline, thin-walled) (Jacob and Rehner, 1998; Denman *et al.*, 2000). This hypothesis was initially supported by other molecular studies (Zhou and Stanosz, 2001; Alves *et al.*, 2004; Slippers *et al.*, 2004).

Morphological observations and phylogenetic analyses of the LSU nu-rDNA with magnified sampling have identified ten clades within the *Botryosphaerales* (Crous *et al.*, 2006c). The clades were correlated with distinct morphological characters (Fig. 5). Some groups such as *Stenocarpella* (i.e. diplodia-like anamorphs) occurring on maize were found to be phylogenetically unrelated to the *Botryosphaerales* and are now accommodated in the *Diaporthales* (*Sordariomycetes*). Likewise, one dothiorella-like anamorph and an atypical *Phyllosticta* species clustered outside the *Botryosphaerales* (Crous *et al.*, 2006c). *Phyllosticta* is a speciose group (Aa and Vanev, 2002) and has also been connected to *Guignardia*, which also known to have anamorphs in *Kabatia*, *Placosphaeria*, *Sarcophoma* and *Selenophoma*, (Muller, 1957; Hoog and Hermanides-Nijhof, 1977; Hoog,

1979; Sutton, 1980). Recent multi-gene phylogenetic studies indicate that *Phyllosticta* is the only anamorphic genus linked to *Guignardia* (Crous *et al.*, 2006c; Duong *et al.*, 2007) and both the anamorph and teleomorph genera are monophyletic in the *Botryosphaeriaceae*, *Botryosphaeriales* (Crous *et al.*, 2006c; Schoch *et al.*, 2006; Duong *et al.*, 2007). The species-delineation in *Phyllosticta*, however, is still problematic and requires future studies.

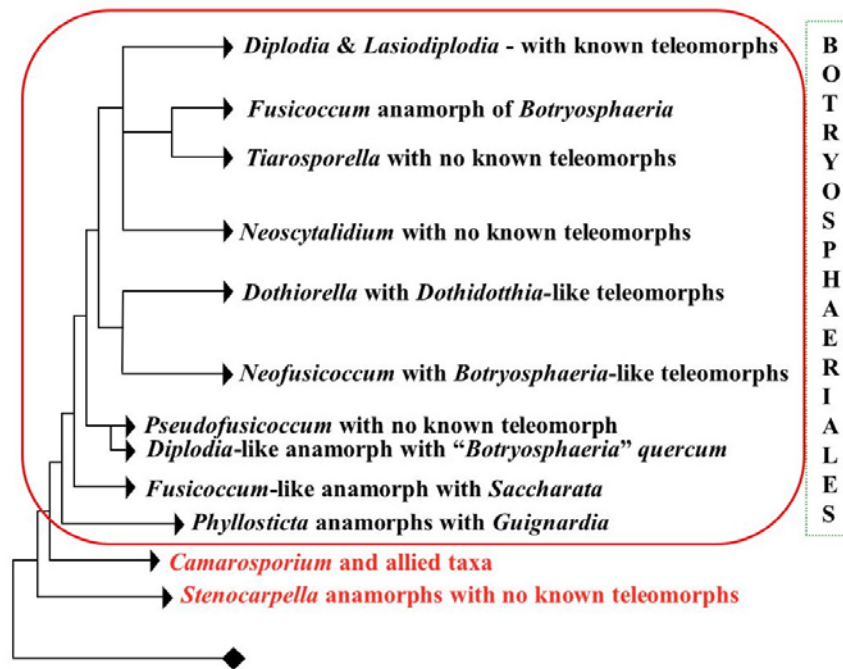


Fig. 5. Phylogenetic affiliations of anamorphic fungi in the *Botryosphaeriales* (Crous *et al.*, 2006c).

Chaetosphaeriales: *Chaetosphaeria* (*Chaetosphaeriaceae*, *Chaetosphaeriales*, *Sordariomycetes*) includes morphologically less-differentiated teleomorphs. They have been connected to more than eleven morphologically distinct form-genera (Réblová, 2000; Réblová and Winka, 2000; Fernández and Huhndorf, 2005; Fernández *et al.*, 2006). The teleomorphs offer inadequate taxonomic characters; therefore, anamorphic characters have primarily been used to segregate new teleomorph species (Réblová, 2000). Based on molecular, cultural, and morphological analyses, Réblová (2000) defined *Chaetosphaeria sensu stricto* that included four ‘natural’ groups, i.e., the *Chloridium*, *Gongromerzia*, *Kylindria*, and *Menispora* groups. Phylogenetic studies based on the nuclear rDNA and β -tubulin gene sequence-data (Fernández *et al.*,

2006), however, demonstrated varying degrees of overlap in the teleomorph and anamorph characters. Apparently, anamorphic developmental patterns in the *Chaetosphaeriaceae* do not reflect phylogenetic relationships (Fernández *et al.*, 2006).

In this review, the phylogenetic relationships of members of the *Chaetosphaeriaceae* were analysed based on a magnified nuclear LSU nrDNA dataset, that included two unpublished new sequences of an anamorphic fungus, *Paliphora intermedia* (CBS 896.97, the type strain from Australia; CBS199.95 from Cuba). In distance-based analysis, there were two extra noticeable phylogenetic groupings in the *Chaetosphaeriaceae* (Fig. 6). The first one was represented by *Sporidesmium sensu lato* and *Lecythothecium duriligni*. The second interesting grouping included *Paliphora intermedia*, an anamorph with tetric conidiogenous cells, and *C. minuta*. The phylogenetic affiliations of *Sporidesmium sensu lato* within the *Chaetosphaeriaceae* were discussed in Réblová and Winka (2001) and Shenoy *et al.* (2006), while that of *Paliphora intermedia* will be detailed in a separate paper (Wang *et al.*, unpubl.). It is, however, noted that more genetic data, especially from anamorphic fungi, will be needed as previous molecular studies on the *Chaetosphaeriaceae* (Réblová and Winka, 2000, 2001; Fernández *et al.*, 2006; Shenoy *et al.*, 2006) and the NJ tree presented here were based on inadequate taxon sampling.

***Mycosphaerella* and its anamorphs:** *Mycosphaerella* (*Mycosphaerellaceae*, *Capnodiales*, *Dothideomycetes*) (Schoch *et al.*, 2006) is one of the largest and most important groups of fungi, with 2000 described species (Crous *et al.*, 2000). They have been mainly distinguished based on the host (Aptroot, 2006). *Mycosphaerella* species have been associated with more than twenty-seven anamorph genera (Kendrick and DiCosmo, 1979), while Sutton and Hennebert (1994) accepted only twenty-three anamorph genera. *Mycosphaerella* species produce inconspicuous fruiting bodies with highly conserved morphology, and grow poorly in culture (Hunter *et al.*, 2006b). Therefore, morphology-based species delimitation in *Mycosphaerella* included both the teleomorphic and anamorphic characters (Crous, 1998). Based on molecular studies, Crous *et al.* (1999) indicated a possible convergent evolution in the *Mycosphaerella* complex and accepted a monophyletic group of *Mycosphaerella* and its anamorphs in twenty-three form-genera (Crous *et al.*, 2000, 2001). Hunter *et al.* (2006b), based on phylogenetic analyses of multi-gene sequence-data, suggested that *Mycosphaerella* constitutes heterogeneous groups. They also observed that only a few of the groups are closely linked to certain anamorph genera and suggested the extensive polyphyly within many anamorph genera associated with *Mycosphaerella*, including *Passalora*, *Phaeophleospora*,

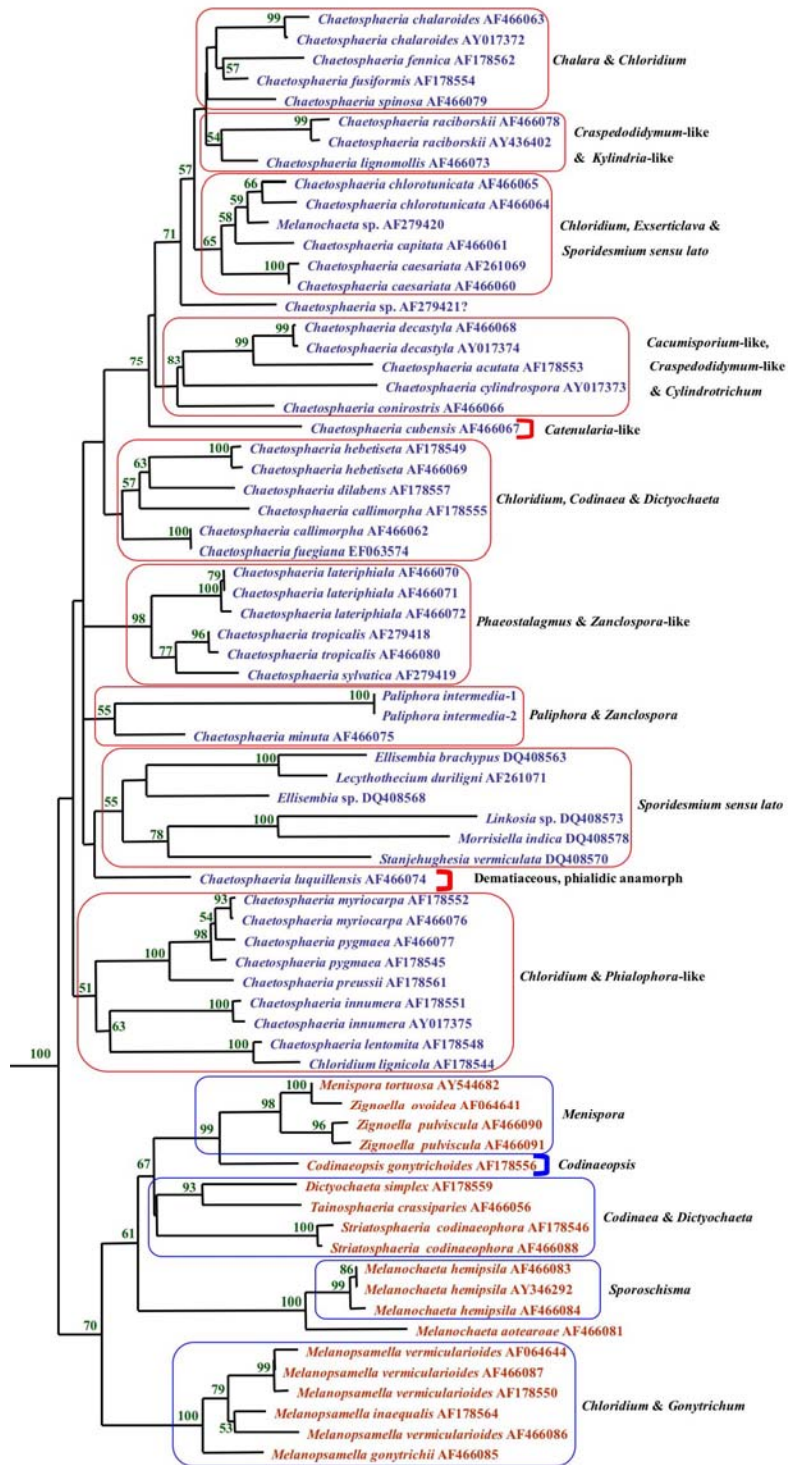


Fig. 6. Phylogenetic affinities of *Sporidesmium sensu lato* and *Paliphora intermedia* within the *Chaetosphaeriaceae* based on neighbour joining analysis of nuclear LSU rDNA dataset.

Stenella, and *Pseudocercospora* (Crous *et al.*, 2006d). Interestingly, Hunter *et al.* (2006b) also observed that *Mycosphaerella* species from *Eucalyptus* clustered in two distinct groups, which indicate that there are possibly two phylogenetic genera within *Mycosphaerella*.

The helicosporous fungi: Helicosporous fungi are defined by their asexual spores that have an axis curved through a minimum of 180° (Kirk *et al.*, 2001). There are more than 200 species of helicosporous fungi in 45 form-genera and 90% of them are yet to be connected to their teleomorphs (Goos, 1987). Therefore, the form-genera were delimited mainly based on conidial morphology and conidiogenesis (Goos, 1987). Morphological data, however, indicate their affiliations with multiple families in different classes of the *Ascomycota* (Goos, 1987; Zhao *et al.*, 2007). Tsui and Berbee (2006b) identified six convergent lineages of helicosporous fungi in the *Ascomycota*, most of them were in the *Tubeufiaceae* (*Dothideomycetes*). They also confirmed the polyphyly of the form-genera. It was speculated that the spore forms are convergent and represent adaptation to dispersal in aquatic environments rather than reliable taxonomic characters (Tsui and Berbee, 2006b).

Aquatic hyphomycetes: Belliveau and Bärlocher (2005) reassessed the phylogenetic significance of conidial morphology and development in aquatic hyphomycetes. Classification of aquatic hyphomycetes, which are also known as freshwater or amphibious hyphomycetes or Ingoldian fungi, have been based on anamorphic characters as 90 % of the aquatic hyphomycetes are yet to be connected to their teleomorphs (Webster, 1992; Cai *et al.*, 2003; Sivichai and Jones, 2003; Belliveau and Bärlocher, 2005). Belliveau and Bärlocher (2005) reported aquatic hyphomycetes are phylogenetically affiliated to the *Dothideomycetes*, *Leotiomycetes*, *Orbiliomycetes*, and *Sordariomycetes* and provided molecular evidence for the multiple origins of aquatic hyphomycetes.

Recently, Campbell *et al.* (2006) tested the hypothesis that similar conidial morphologies in aquatic hyphomycetes are a result of convergent evolution. Their analyses included form-genera *Goniopila*, *Lemonniera* and *Margaritispora*, and the results showed that morphological groupings were entirely incongruent with molecular derived phylogeny. Their study further supports the hypothesis that anamorphic characters such as conidial shape are not reliable indicators of phylogeny. The study suggested that conidial shape is

probably a result of convergent evolution in response to the aquatic environment (Campbell *et al.*, 2006).

Other interesting studies: Other recent work on the taxonomy of anamorphic fungi using DNA sequence-data are listed in Table 4.

***Phylogroups* concept in the taxonomy of anamorphic fungi**

The *Phylogroup* concept is an informal but more precise way of communication of new information concerning phylogenetic classification of a group of fungi, especially when taxonomic decisions involve many name changes based on insufficient phylogenetic information. The *Phylogroup* concept recognises each of the major clades in a phylogenetic tree as a *Phylogroup*, an evolutionary entity. The most popular taxon or a group of taxa with the highest representation in the *Phylogroup* can be chosen as the type-member/s of the *Phylogroup*. The *Phylogroups* can be treated as new informal but potential taxonomic categories within a family or an order. In many examples provided above, we have dealt with asexual fungi that are polyphyletic. Application of the *Phylogroup* concept would be very difficult in these cases. There are, however, a few anamorphic-groups, which are found to be monophyletic. *Pestalotiopsis* and allied genera are an excellent example to illustrate how the *Phylogroup* concept can be integrated.

Pestalotiopsis is a heterogeneous group of coelomycetous fungi and the inter-specific delineation of the genus has been based on conidial morphology (Guba, 1961; Nag Raj, 1993), conidiogenesis (Sutton, 1980) and teleomorph associations, which has been described for only a few species (Barr, 1975, 1990; Zhu *et al.*, 1991; Metz *et al.*, 2000). *Pestalotiopsis* shares overlapping morphological characters with similar anamorphs such as *Bartalinia*, *Discosia*, *Monochaetia*, *Pestalotia*, *Seimatosporium*, *Seiridium*, and *Truncatella*. There has been considerable ambiguity and confusions in inter-generic classification, which has been dealt differently by various authors (Guba, 1961; Sutton, 1980; Nag Raj, 1993). Initial molecular studies (Jeewon *et al.*, 2002, 2003a, b) indicated monophyly of pestalotiopsis-like anamorphs; however, their inter-generic relationships are still unclear. Phylogenetic analyses of magnified datasets from four gene-loci (Jeewon *et al.*, unpubl.) support the monophyly of the pestalotiopsis-like anamorphs (Fig. 7). Most of the sub-clades were represented by more than one type of form-genera with overlapping morphological characters. In such a scenario, we may recognise the sub-clades as *Phylogroups*, i.e. evolutionary entities. In this example, five *Phylogroups*

can be seen: *Monochaetia*, *Pestalotiopsis*, *Seimatosporium/ Sarcostroma*, *Seiridium* and *Truncatella/Bartalinia* (Fig. 7).

Table 4. A list of selected studies related to the taxonomy of anamorphic fungi

| Taxonomic group | Reference |
|---|--|
| <i>Agaricales</i> | Walther <i>et al.</i> (2005) |
| <i>Alternaria</i> | Chou and Wu (2002); Peever <i>et al.</i> (2004, 2005) |
| <i>Beauveria-Cordyceps</i> | Rehner and Buckley (2005) |
| <i>Bionectra</i> | Schroers <i>et al.</i> (2000); Rossman <i>et al.</i> (2001); Schroers (2001) |
| <i>Calonectria</i> | Schoch <i>et al.</i> (2000, 2001); Crous (2002); Crous <i>et al.</i> (2004, 2006b) |
| <i>Carpoligna-Pleurothecium</i> | Fernandez <i>et al.</i> (1999) |
| <i>Cercospora</i> | Crous <i>et al.</i> (2006a) |
| <i>Colletogloeopsis</i> | Cortinas <i>et al.</i> (2006) |
| <i>Colletotrichum</i> | Sreenivasaprasad <i>et al.</i> (1996); Du <i>et al.</i> (2005) |
| <i>Conioscyphascus-Conioscypha</i> | Réblová and Seifert (2005) |
| <i>Cytospora</i> | Adams <i>et al.</i> (2005) |
| <i>Embellisia-Nimbya</i> | Pryor and Bigelow (2003) |
| <i>Geotrichum</i> | Hoog and Smith (2005) |
| <i>Harknessia-Wuestmeia</i> | Lee <i>et al.</i> (2004) |
| <i>Helicomysa</i> | Kirschner and Chen (2004) |
| <i>Leohumicola</i> | Hambleton <i>et al.</i> (2005) |
| <i>Melinomyces</i> | Hambleton and Sigler, (2005). |
| <i>Oidiodendron</i> | Rice and Currah (2005a, b). |
| <i>Ophiostoma-Sporothrix</i> | Wingfield <i>et al.</i> (1999); Harrington <i>et al.</i> (2001); De Beer <i>et al.</i> (2003); Zhou <i>et al.</i> (2004); Aghayeva <i>et al.</i> (2005); Zipfel <i>et al.</i> (2006) |
| Pestalotoid fungi | Lee <i>et al.</i> (2006) |
| <i>Pezicula</i> and its anamorphs | Verkley (1999) |
| <i>Phaeoacremonium-Togninia</i> | Mostert <i>et al.</i> (2006) |
| <i>Pleosporaceae</i> | Kodsueb <i>et al.</i> (2006b) |
| <i>Pseudocercospora</i> | Crous <i>et al.</i> (2006a) |
| <i>Quambulariaceae</i> | De Beer <i>et al.</i> (2006) |
| <i>Trichoderma</i> and other hypocrealean members | Dodd <i>et al.</i> (2000); Lieckfeldt and Seifert (2000); Kuhling-Gradiner <i>et al.</i> (2002); Chaverri <i>et al.</i> (2003); Chaverri and Samuels (2003); Druzhinina <i>et al.</i> (2006); Overton <i>et al.</i> (2006); Samuels (2006) |

9. Identification and Nomenclature

DNA barcoding

Taxonomy is not primarily concerned with identification (Talbot, 1971), which mainly deals with recognition of the identity or essential characters of an

organism. Identification of an organism or a species, however, is an important part of systematics. Seifert *et al.* (2007) have rightly stated that the correct identification of a species leads to its correct biology (viz. ecological roles, physiological and biochemical properties) and its societal risks or benefits. Morphology-centric identification systems, like any other components of systematics, have limitations. Hebert *et al.* (2002) listed four of the limitations: 1) incorrect identification due to the phenotypic plasticity and genetic variability in the morphological identification characters, 2) ineffectiveness in discriminating morphologically cryptic taxa, 3) imperfect identification of pleomorphic organisms based on their poorly known life-cycle, and 4) dependence on a high level of identification expertise. Interestingly, it has also been stated in Hebert *et al.* (2002) that few taxonomists can critically identify more than 0.01% of the estimated 10-15 million species (Hammond, 1992; Hawksworth and Kalin-Arroyo, 1995).

There have been several attempts to incorporate molecular data into identification systems. Hebert *et al.* (2002) proposed a novel and interesting system of identification for animals based on diversity of the mitochondrial gene Cytochrome Oxidase I (COI). They chose a 648-bp region of COI gene because of its lack of introns, limited exposure to recombination, and haploid mode of inheritance of the gene (Saccone *et al.*, 1999; Hebert *et al.*, 2002). DNA barcoding is an ambitious system that essentially attempts to provide rapid, accurate and automatable species identifications by using short, standardized gene regions as internal species tags (Hebert and Gregory, 2005). It fundamentally seeks to assist in *delimiting* species, which according to Hebert and Gregory (2005) denotes to *highlight genetically distinct groups exhibiting levels of sequence of divergence suggestive of species status*. This, in the words of Talbot (1971) means *recognising that two individuals are identical within bounds of normal variation*. DNA barcoding aims to function complementary to Linnean classification as Hebert and Gregory (2005) specifically cautioned that DNA barcodes alone are never sufficient to *describe* new species, which is the core focus of taxonomy, not identification *per se*.

The efficacy of DNA barcoding has been evaluated in some major groups such as birds (Hebert *et al.*, 2004b), fishes (Ward *et al.*, 2005), and Lepidopteron insects (Hebert *et al.*, 2004a; Hajibabaei *et al.*, 2006), marine algae (Saunders, 2005). Data retrieved from the Taxonomy browser of the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert, 2007) suggest that so far 37378 species belonging to animals, fungi [Basidiomycota (539), Eumycota (599), Glomeromycota (11), Myxomycota (1)], plants and protists have been bar-coded.

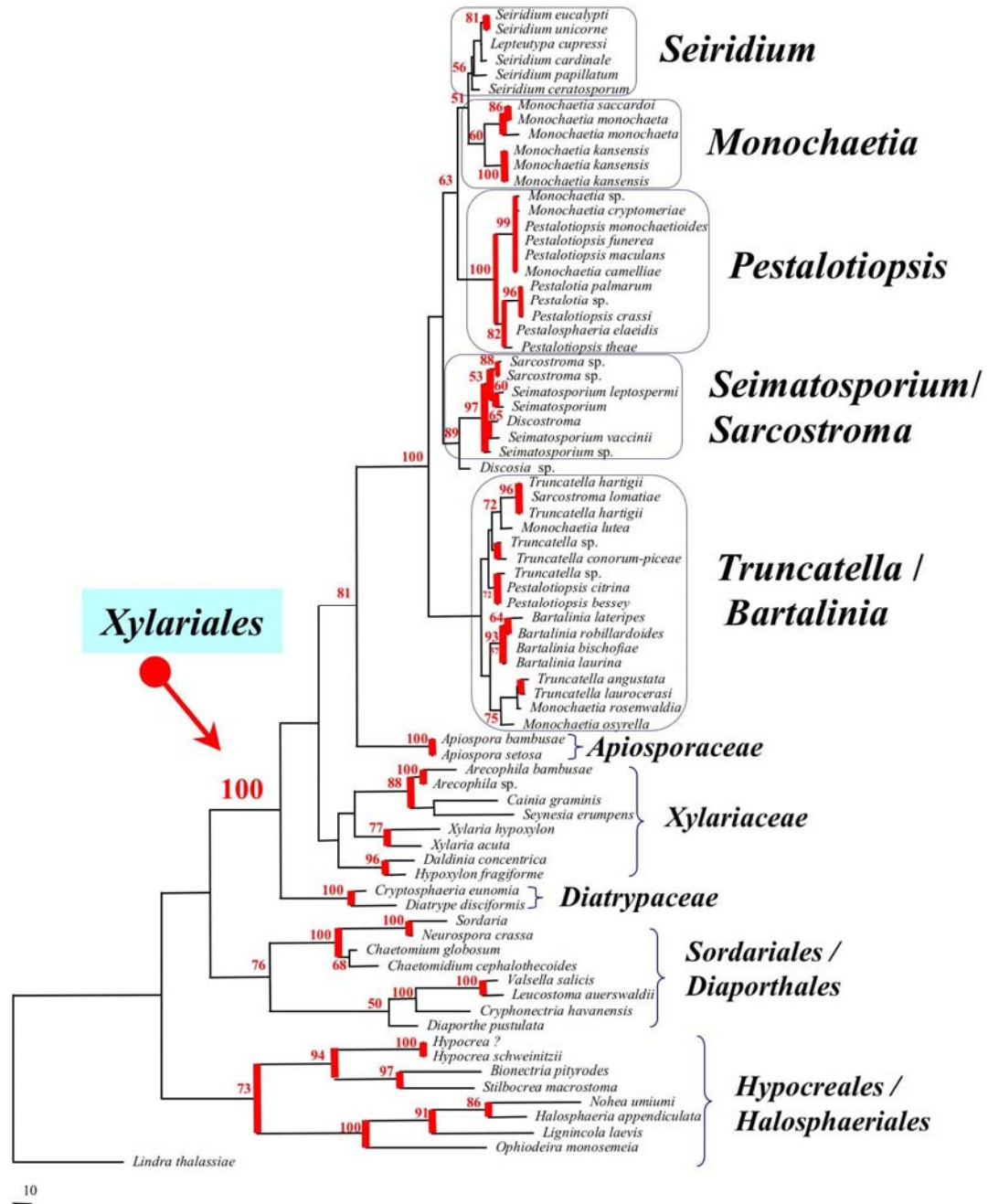


Fig. 7. The LSU nu-rDNA phylogeny and *Pestalotiopsis* and allied anamorphic fungi (Jeewon *et al.*, unpubl.)

The barcoding results from animal lineages have been encouraging as evident from the results where more than 95% species-level resolution was provided in most cases (Ward *et al.*, 2005; Smith *et al.*, 2005; Hajibabaei *et al.*, 2006), and while in a few cases the incomplete resolution revealed existence of new species (e.g. Hebert *et al.*, 2004a, b). In flowering plants, use of the COI gene in DNA barcoding was suggested to be inappropriate as the gene evolves at a much slower rate in higher plants than in animals (Kress *et al.*, 2005). Consequently, instead of the COI gene, the nuclear internal transcribed spacer regions (ITS) and the plastid trnH-psbA intergenic spacer have been proposed for potential DNA barcoding in flowering plants (Kress *et al.*, 2005), while COI gene appears to be promising in marine algae (Saunders *et al.*, 2005).

In Kingdom *Fungi*, the morphology-based identification of a species is not always easy and, in many instances, incorrect. This can be attributed to the lack of distinctive morphological characters and predominance of microscopic species in the Kingdom (Seifert *et al.*, 2007). Various gene regions have been employed such as nuclear large ribosomal subunit (Kurtzman and Robbnet, 1998), internal transcribed spacer (ITS) (Berch *et al.*, 2002; Schmidt and Moreth, 2002; Cunnington *et al.*, 2003; Druzhinina *et al.*, 2005; Koljalg *et al.*, 2005), partial β -tubulin gene sequences (Samson *et al.*, 2004) and partial elongation factor 1-alpha (EF-1 α) sequences (Geiser *et al.*, 2004) to identify fungi to the species level. Recently, Seifert *et al.* (2007) examined patterns of sequence divergences in the full COI gene for 38 taxa in the Kingdom *Fungi* and fungus-like Oomycota. They reported that COI gene varied from 1,584 to 22,006 bp with varying number and length of introns, and the coding region varied from 1,584 to 1,905 bp. Their sequence analysis suggested that divergences in COI gene in fungi are considerable, unlike in plants (Kress *et al.*, 2005).

Seifert *et al.* (2007) also investigated COI variation in the genus *Penicillium* subgenus *Penicillium* and closely related species. Their study reported that COI gene has lower sequence divergence than to β -tubulin gene, however the latter provided a higher degree of taxonomic resolution. Seifert *et al.* (2007), at the same time, supported the use of the COI gene as a fungal barcode marker as: 1) COI sequences can be aligned across all fungal lineages easily, where as aligning the ITS and β -tubulin is problematic (e.g. Our studies on genus *Colletotrichum* indicate that aligning ITS and β -tubulin sequences is unachievable and impossible (Data not shown)); 2) the broader exploration of COI diversity across major fungal lineages will positively affect the development of a barcoding system for fungi that shares a common gene target with animals and protists.

Recently, the mycological community has preferred the ITS nu-rDNA to CO1 as the most appropriate gene for DNA barcoding in fungi (Unpublished Report of the All Fungi Barcode of Life Planning Workshop, 2007). The former has been chosen as there are significant, potential problems associated with CO1 gene such as difficulty with amplification, presence of multiple/mobile introns of differing lengths, presence of multiple copies of the gene and poor resolution in some taxa. It is also noted that the mitochondrial genome evolves differently in *Fungi* and may not work well for the highly variable and relatively recently evolved true Fungi. Though the ITS nu-rDNA also has problems such as poor resolution and presence of paralogs, this gene region has been chosen as *the best of several imperfect choices*. Balajee and Marr (2006), however, favoured the use of RPB2, along with other genes, to identify the *Aspergillus* spp. It is noted that RPB2 is a single-copy gene, is highly conserved (Liu *et al.*, 1999) and has been used to resolve phylogenetic relationships in numerous taxa such as *Ascheronia* and *Sporidesmium* (Liu *et al.*, 1999; Liu and Hall, 2004; Matheny 2005; Liu *et al.*, 2006; Shenoy *et al.*, 2006).

The DNA barcoding approach, however, has come under some criticism, which has been discussed by Hebert and Gregory (2005). One of the potential drawbacks of DNA barcoding is its reliance on the reference databases for comparison. Nilsson *et al.* (2006) conducted a study based on a large set of fungal DNA sequences from the inclusive International Nucleotide Sequence Database and showed that: the taxon sampling of fungi is far from complete, about 20-30% of the entries may be incorrectly identified to species level, and the majority of entries lack descriptive and up-to-date annotations. They have also shown that more than 10% of all publicly available fungal ITS sequences have compromised taxonomic annotations. These results, undoubtedly, emphasise on closer collaboration of DNA barcoding efforts with alpha-taxonomy. DNA barcodes appear less suitable for inferring phylogenetic relationships as evident from recent studies by Hajibabaei *et al.* (2006), who reported low statistical support at many internal nodes of a phylogenetic tree based on short barcode sequences. Recently, Min and Hickey (2007) studied the effect of sequence length of fungal mitochondrial sequences on the utility of the data for species identification and phylogenetic reconstruction. Their study also suggested that the standard short barcode sequences (approximately 600 bp) are not suitable for inferring accurate phylogenetic relationships.

Nomenclature and PhyloCode

Talbot (1971) stated that nomenclature is primarily concerned with laws and principles related to the correct application of scientific names to taxa, and

with grouping into consecutive categories of definite rank. The nomenclature of fungi is governed by the International Code of Botanical Nomenclature (ICBN) (Kirk *et al.*, 2001). According to L.K. Weresub, “...the rules of nomenclature exist simply to give you some direction on how to express your taxonomic opinion. But they must allow you to express whatever kind of taxonomic opinion you hold, no matter how idiotic that opinion may be. The rules govern nomenclature, not taxonomy” (Kendrick, 1979). The name of a species essentially is for reference and it is *a nomenclatural entity, a part of language* (Talbot, 1971). Kirk *et al.* (2001, p. 356-358) have summarised the current trends in nomenclature of fungi.

The current methods of fungal nomenclature are type-based (Moore *et al.*, 1998; Kirk *et al.*, 2001). The type-based nomenclature was devised to aid taxonomists in *simplifying the variability in nature, to establish relationships, and to assist in identification* (Moore *et al.*, 1998). There are two kinds of types: **conceptual type** and **nomenclatural type**. A conceptual type is tied to the name of a taxon in the form of a description or circumscription and this kind of typification, however, is known to create frequent nomenclatural instability (Moore *et al.*, 1998). A nomenclatural type is represented by a type specimen, to which a name is permanently attached. The nomenclatural types are of two kinds: 1) a **classification type** – is the type of name of a subordinate taxon, which helps to typify the name of higher taxon; 2) a **collection type** – is a specimen that is permanently attached to a name (Moore *et al.*, 1998).

In fungal nomenclature, Article 59 of the ICBN permits the use of one or several anamorph names in addition to the teleomorph name in pleomorphic *Ascomycota* and *Basidiomycota*, excluding the lichen forming-taxa. The typification of anamorphic fungi without a known teleomorph follows anatomical typification, in which anamorphic material can only serve to typify the name of a taxon with restricted anamorphic application. The teleomorph type can typify the name of a teleomorph with holomorphic application (Hennebert, 2003). Naming of pleomorphic and non-pleomorphic anamorphs has been controversial and has been discussed by various authors (e.g. Kendrick 1979; Sugiyama, 1987; Seifert *et al.*, 2000b; Reynolds and Taylor, 1993; Gams *et al.*, 2003). With the help of molecular phylogenetic tools, all anamorphs – both pleomorphic and non-pleomorphic – can potentially be integrated within the holomorphic classification system. It is desirable that a holomorphic name should symbolise the phylogenetic characters, not merely the reproductive structures of the taxa.

There has been a strong disagreement over naming of organisms as evident from the development of the PhyloCode (Cantino and de Queiroz, 2007). The PhyloCode represents a novel set of rules of naming organisms

based on the principle of common descent, i.e. the Phylogenetic Nomenclature System (de Queiroz and Gauthier, 1990, 1992, 1994; Bryant and Cantino, 2002; de Queiroz, 2006; Cantino and de Queiroz, 2007). The Phylogenetic Nomenclature System has been criticised regarding: instability in the content of taxa, the utilitarian role of classification, nomenclatural types and specifiers, the legislative control in the PhyloCode, the role of characters in phylogenetic nomenclature, ranks and species names, theoretical basis for phylogenetic nomenclature, and Crown clades. These issues are discussed and refuted in Bryant and Cantino (2002). The PhyloCode is a set novel and revolutionary ideas, which have to compete against well-established Botanical and other Biological Nomenclature systems. More details on the PhyloCode can be found on Internet website, <http://www.ohiou.edu/phylocode> and in various papers (e.g. Monsch, 2006; Rieppel, 2006; Dubois, 2007; Hills, 2007).

10. Future directions and conclusions

Fungal systematics is an essential part of biological research especially in the context of the ecological and economic importance attached to it. Phylogeny-centric fungal systematics is an ideal approach for discovering unknown branches of the fungal tree of life and better understanding evolutionary changes in the known fungal lineages. The taxonomy of known fungi is in a transitional stage. It is evident that recent advances in molecular tools and analytical methods have revolutionised fungal systematics (e.g. James *et al.*, 2006a; Hibbett *et al.*, 2007). Classification of pleomorphic and non-pleomorphic anamorphs, however, is unsettled and still problematic. This is attributed to the historical practice of the dual nomenclature/classification system, which was a historical necessity, but presently a burden. It is widely accepted that the Deuteromycotina is a failed taxonomic hypothesis (Kendrick, 1979; Sugiyama, 1987; Reynolds and Taylor, 1993; Seifert *et al.*, 2000b; Gams *et al.*, 2003). The traditional anamorphic classification system positively assists in identification of a plethora of asexual morphologies, but is less suited for phylogenetic inference (e.g. Shenoy *et al.*, 2006).

It is rightly stated that proper identification reveals the correct biology of a fungus. Consequently, incorrect identification can potentially cause some problems, especially in plant quarantine and identification of plant pathogens. Therefore, further studies on the efficacy of various genetic markers (e.g. ITS nu-rDNA, RPB2) as DNA barcodes are needed. Morphological species concepts, in many instances, have over-estimated or underestimated the speciation-events (Jeewon *et al.*, 2004). In the case of *Fusarium graminearum*, the number of species appears to have been under-estimated (O'Donnell *et al.*, 2004). DNA sequence-data are routinely being used to test morphological

species concepts and other taxonomic hypotheses and interesting results have been reported (e.g. two possible phylogenetic genera within *Mycosphaerella* (Hunter *et al.*, 2006b)). New phylogenetic species are also being described based on nucleotide-differences (O'Donnell *et al.*, 2004).

The classification of anamorphic fungi based on incomplete life histories or on one type of reproductive morphology has resulted in more than one name for a single species. DNA sequence-data are being successfully used to link the morphs of a holomorph and provide a better proof for anamorph-teleomorph connections in association with culture-based studies. The pleomorphic anamorphs are increasingly being classified as holomorphic taxa based on taxonomic analysis of DNA, morphological and other available data (e.g. *Brachysporium* anamorphs in holomorphic genus *Cryptadelphia* (Réblová and Seifert, 2004)). The phylogenetic placement of non-pleomorphic anamorphs or orphan anamorphs is also increasingly being predicted using DNA sequence-data (e.g. *Sporidesmium sensu lato* in the *Chaetosphaeriales*, (Shenoy *et al.*, 2006) (Fig. 6)). The present nomenclature of pleomorphic fungi is, however, controversial (Gams *et al.*, 2003). The Genus for Genus concept (Seifert *et al.*, 2000a,b; Rossman, 2000) favours a single teleomorph genus to be matched with a comparable anamorph genus. It is, however, stated that the anamorph generic name provides no additional information when anamorphic characters become part of the definition of the holomorph (Réblová and Seifert, 2007).

Molecular phylogenetic analysis in the Kingdom *Fungi* has a brief history of 15-25 years. As further and diverse groups of anamorphic fungi are sequenced, scenarios such as a monophyletic clade that includes a mosaic of pleomorphic and non-pleomorphic fungi, sharing few similar reproductive, morphological characters will be more common. The emerging phylogenetic and nomenclatural scenarios in the *Botryosphaeriales* (Crous *et al.*, 2006c; Fig. 5), *Chaetosphaeriales* (Fernández *et al.*, 2006; Fig. 6), *Fusarium graminearum* clade (O'Donnell *et al.*, 2004), pestalotiopsis-like anamorphs (Jeewon *et al.*, unpubl.; Fig. 7), and the *Mycosphaerella* complex (Hunter *et al.*, 2006b) also indicate at the potential nomenclatural complexities associated with type-based and the dual nomenclature system. Fungal taxonomy will be slow to accept another set of revolutionary changes such as Phylogenetic Nomenclature System against a well-established Botanical Nomenclature System. The clade-based nomenclature as prescribed by the PhyloCode primarily relies on fungal DNA sequences. Fungal taxonomists, therefore, would need to generate more sequences from many representative groups across the Kingdom before they could accept the PhyloCode.

Changes are an integral part of nature and also in the taxonomic process. These changes can be accepted and followed by 1) development of fast and

reliable identification systems, 2) designing supportive nomenclatural rules, and 3) incorporation of refined taxonomic principles. The mycological community has a daunting task of developing a system of classification that fulfils the needs of diverse taxonomic users in biological research, industry, agriculture, etc. Molecular characters and tools, unquestionably, are an indispensable part of fungal systematics.

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