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

Belle Damodara Shenoy^{*}, Rajesh Jeewon and Kevin D. Hyde^{*}

Centre for Research in Fungal Diversity, School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong SAR, PR China

Shenoy, B.D., Jeewon, R. and Hyde, K.D. (2007). Impact of DNA sequence-data on the taxonomy of anamorphic fungi. *Fungal Diversity* 26: 1-54.

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

Contents

1. Introduction	2
2. Classification of fungi	3
o Traditional classification of fungi and fungi-like eukaryotes.....	3
o The Fungal Tree of Life	4
3. Sexuality and life cycle patterns in fungi	4
o Types of fungal reproduction	4
o Life history patterns in fungi.....	5
o Lack of sex or absence of sexual morphology?.....	6

^{*}Corresponding authors: B.D. Shenoy; e-mail: bellesheno@gmail.com; K.D. Hyde: e-mail: kdhyde1@gmail.com

4. A brief history of the dual classification and nomenclature system	7
o Prior to the 20 th century	7
o The 20 th century	7
5. The Holomorph concept	9
o The idea of a holomorph	10
o The whole fungus: e.g. <i>Orbilia auricolor</i>	11
o Nature of pleomorphism in the <i>Ascomycota</i>	12
o Anamorph-teleomorph connections	13
6. Fungal systematics and molecular characters	14
o Classification as a hypothesis	14
o Fungal species concepts	14
o Molecular characters in fungal systematics	15
7. Recent advances in the taxonomy of anamorphic fungi	16
o Anamorph-teleomorph connections	16
o <i>Brachysporium</i> anamorphs of <i>Cryptadelphia</i>	16
o <i>Septoria passerinii</i> and its <i>Mycosphaerella</i> functional Teleomorph	18
o Multiple phylogenetic species in a morphological species	18
o Polyphyly of form-genera	19
o <i>Chalara</i>	19
o <i>Phialophora</i>	19
o <i>Diplococcium-Spadicoides</i>	20
o <i>Sporidesmium sensu lato</i>	20
o Anamorphs of <i>Botryosphaerales</i> , <i>Chaetosphaerales</i> , <i>Mycosphaerella</i> , and others ..	21
o <i>Botryosphaerales</i>	21
o <i>Chaetosphaerales</i>	22
o <i>Mycosphaerella</i> and its anamorphs	23
o The helicosporous fungi	25
o Aquatic hyphomycetes	25
o Other interesting studies	26
8. Phylogroups concept in the taxonomy of anamorphic fungi	26
9. Identification and Nomenclature	27
o DNA barcoding	27
o Nomenclature and PhyloCode	31
10. Future directions and conclusions	33

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.

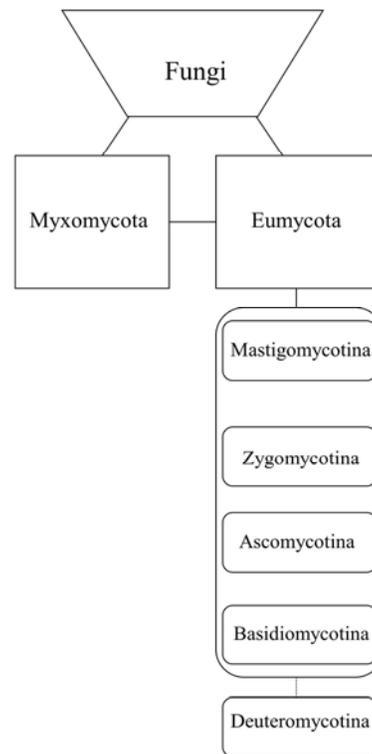


Fig. 1. Traditional classification of fungi (Ainsworth *et al.*, 1973).

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).

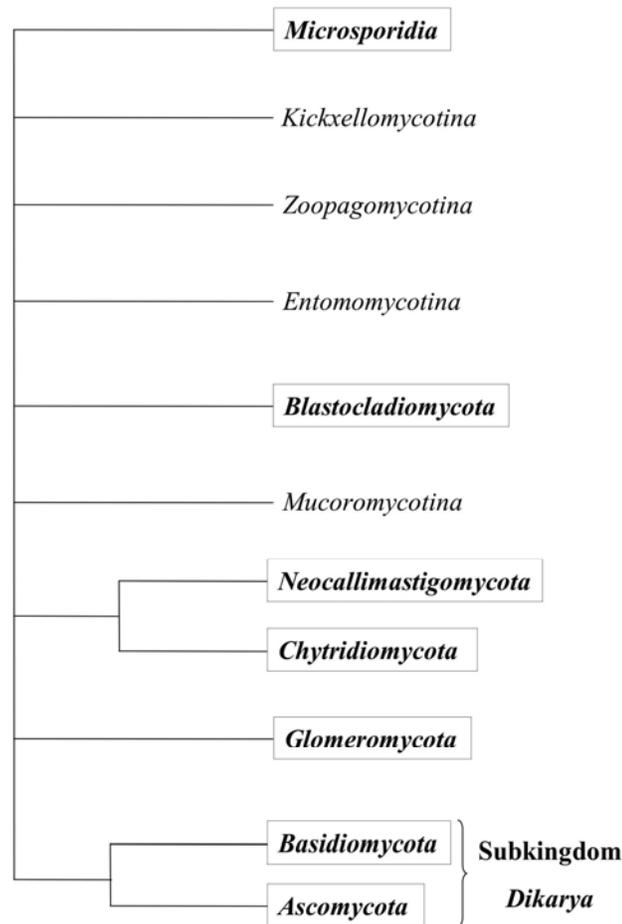


Fig. 2. Phylogenetic classification of the Kingdom *Fungi* (Hibbett *et al.*, 2007).

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. *Chytrium 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).

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

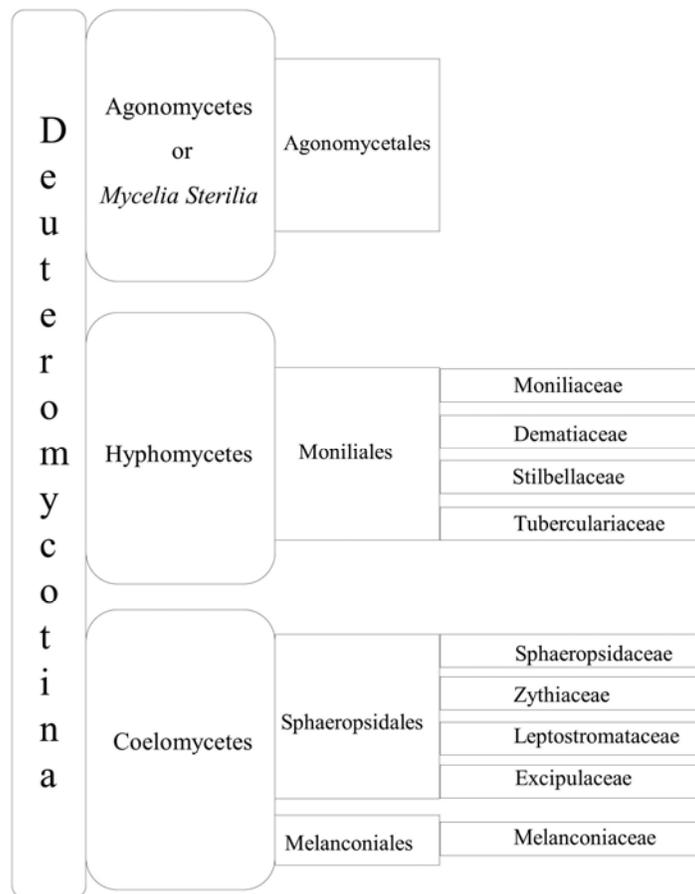


Fig. 3. Saccardo's classification of Deuteromycotina (Talbot, 1971).

(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).

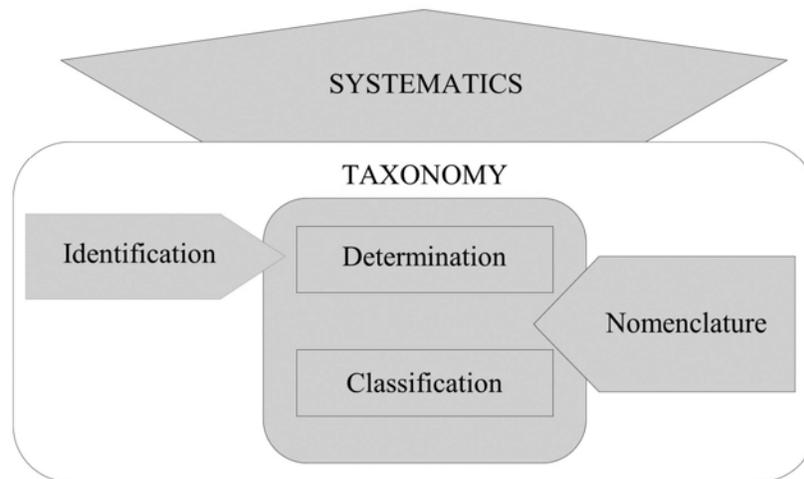


Fig. 4. Relationships between identification, determination, classification, nomenclature taxonomy, and systematics (Talbot, 1971).

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.

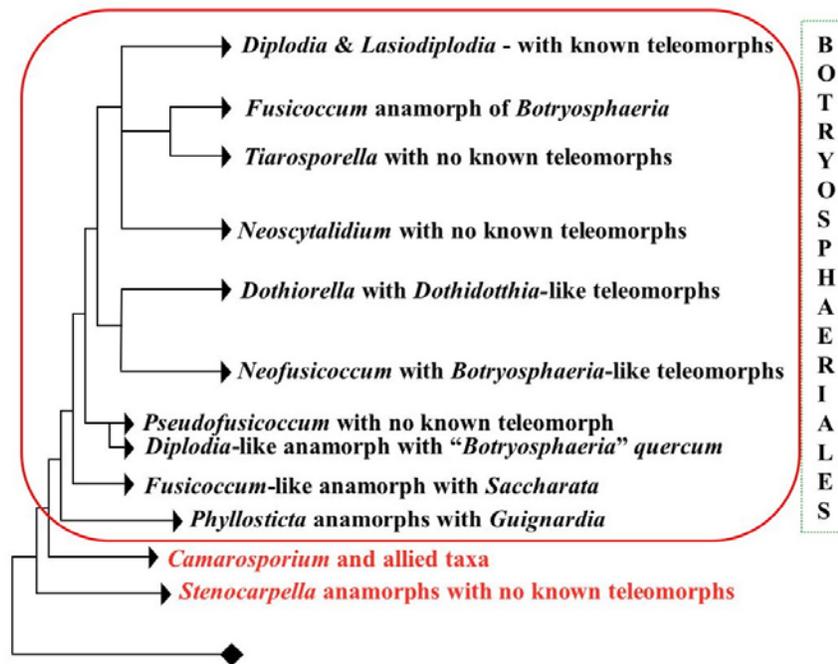


Fig. 5. Phylogenetic affiliations of anamorphic fungi in the *Botryosphaeriales* (Crous *et al.*, 2006c).

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*,

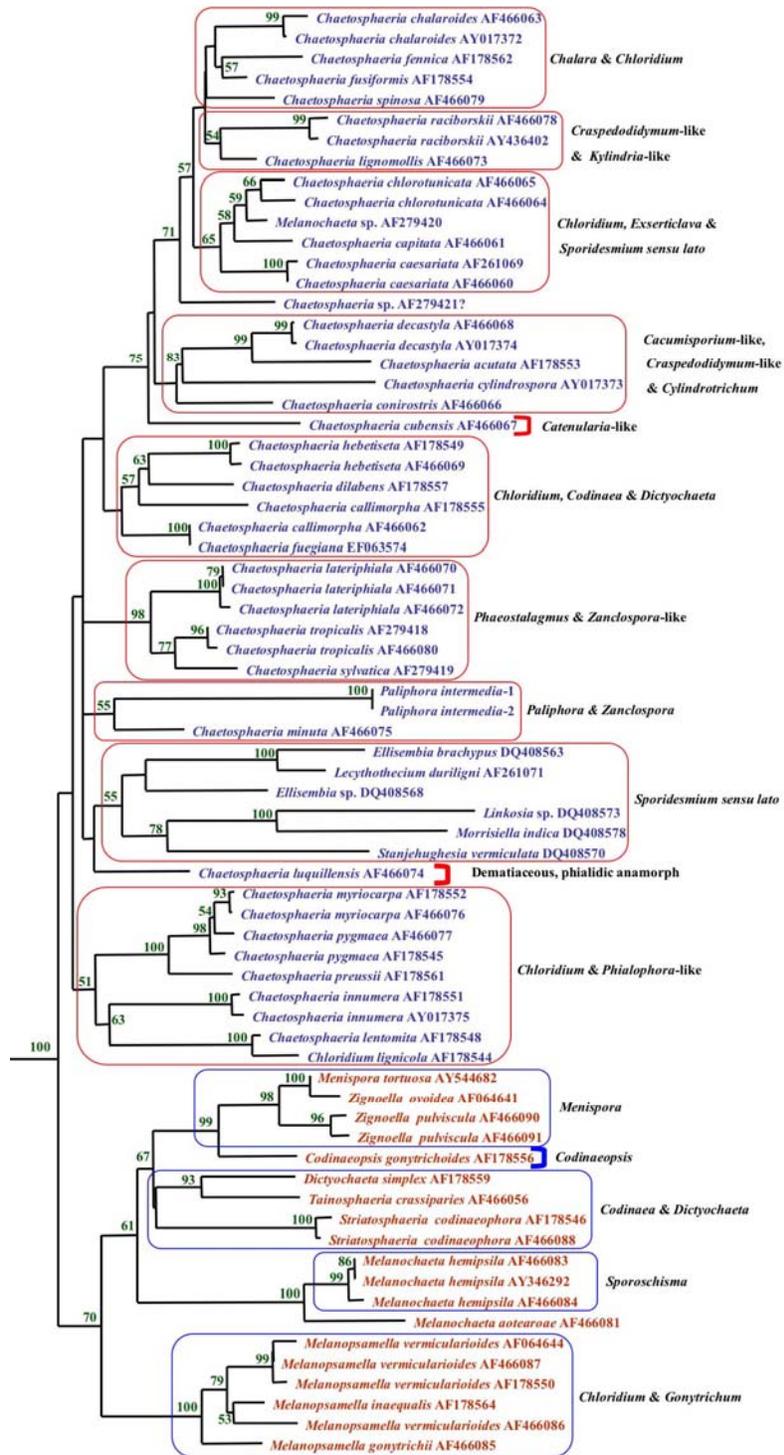


Fig. 6. Phylogenetic affinities of *Sporidesmium sensu lato* and *Paliphora intermedia* within the *Chaetosphaeriaceae* based on neighbour joining analysis of nuclear LSU rDNA dataset.

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>Meliniomyces</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.

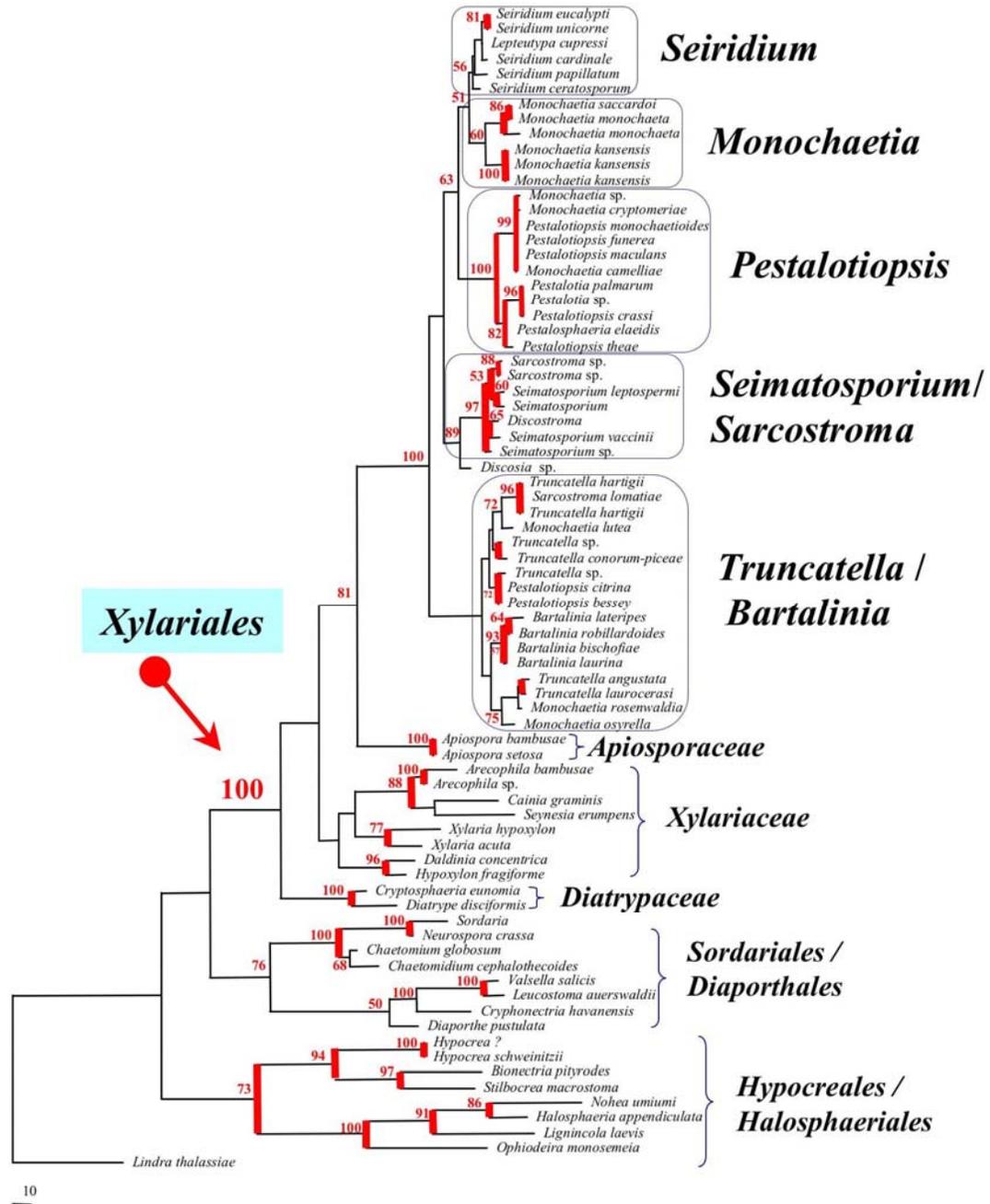


Fig. 7. The LSU nu-rDNA phylogeny and *Pestalotiopsis* and allied anamorphic fungi (Jeewon *et al.*, unpubl.)

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.

Acknowledgments

BDS thanks the University of Hong Kong for a post-graduate studentship. Drs. D. Jayarama Bhat, Pedro Crous, Keith Seifert, Amy Rossman, David Hawksworth, John W. Taylor, Ove Eriksson, Eric McKenzie, Lei Cai, D. Vijaykrishna, Justin Bahl, H. Wang, Aung Swe, R. Kodsueb, and Hu Hongli are thanked for their help in the form of discussion or access to their unpublished data. Helen Leung is thanked for her technical support.

References

- Aa, H.A. van der and Vanev, S. (2002). A revision of the species described in *Phyllosticta*. Centraalbureau voor Schimmelcultures (CBS), Utrecht: 1-510.
- Adams, G.C., Wingfield, M.J., Common, R. and Roux, J. (2005). Phylogenetic relationships and morphology of *Cytospora* species and related teleomorphs (*Ascomycota*, *Diaporthales*, *Valsaceae*) from *Eucalyptus*. *Studies in Mycology* 52: 1-146.
- Agapow, P.M., Bininda-Emonds, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C. and Purvis, A. (2004). The impact of species concept on biodiversity studies. *Quarterly Review of Biology* 79: 161-179.
- Aghayeva, D.N., Wingfield, M.J., Kirisits, T. and Wingfield, B.D. (2005). *Ophiostoma dentifundum* sp. nov. from oak in Europe, characterized using molecular phylogenetic data and morphology. *Mycological Research* 109: 1127-1136.
- Aime, M.C., Matheny, P.B., Henk, D.A., Frieders, E.M., Nilsson, R.H., Piepenbring, M., McLaughlin, D.J., Szabo, L.J., Begerow, D., Sampaio, J.P., Bauer, R., Weiß, M., Oberwinkler, F. and Hibbett, D. S. (2006). An overview of the higher-level classification of *Pucciniomycotina* based on combined analyses of nuclear large and small subunit rDNA sequences. *Mycologia* 98: 896-905.
- Ainsworth, G.C., Sparrow, F.K. and Sussman, A.S. (Eds.) (1973). *The Fungi: An Advanced Treatise*, Volume IVA – A Taxonomic Review with Keys: *Ascomycetes and Fungi Imperfecti*. Academic Press, London: 1-7.
- Alexopoulos, C.J., Mims, C.W. and Blackwell, M. (1996). *Introductory Mycology*, IV edition. John Wiley & Sons, New York: 1-868.
- Alves, A., Correia, A., Luque, J. and Phillips, A. (2004). *Botryosphaeria corticola*, sp. nov. on *Quercus* species, with notes and description of *Botryosphaeria stevensii* and its anamorph, *Diplodia mutila*. *Mycologia* 96: 598-613.
- Alves, A., Correia, A. and Phillips, A.J.L. (2006). Multi-gene genealogies and morphological data support *Diplodia cupressi* sp. nov., previously recognized as *D. pinea* f. sp. *cupressi*, as a distinct species. *Fungal Diversity* 23: 1-15.
- Aptroot, A. (2006). *Mycosphaerella* and its anamorphs: 2. Conspectus of *Mycosphaerella*. CBS Biodiversity Series 5: 1-231.

- Arenal, F., Platas, G. and Peláez, F. (2007). A new endophytic species of *Preussia* (*Sporormiaceae*) inferred from morphological observations and molecular phylogenetic analysis. *Fungal Diversity* 25: 1-17.
- Armstrong-Cho, C.L. and Banniza, S. (2006). *Glomerella truncata* sp. nov., the teleomorph of *Colletotrichum truncatum*. *Mycological Research* 110: 951-956.
- Arx, J.A. von (1987). *Plant-pathogenic Fungi*. J. Cramer, Berlin, Germany.
- Ayala-Escobar, V., Yáñez-Morales, M.J., Braun, U., Groenewald, J.Z. and Crous, P.W. (2006). *Pseudocercospora opuntiae* sp. nov., the causal organism of cactus leaf spot in Mexico. *Fungal Diversity* 21: 1-9.
- Balajee, S.A. and Marr, K.A. (2006). Phenotypic and genotypic identification of human pathogenic aspergilli. *Future Microbiology* 1: 435-445.
- Baldauf, S.L. and Palmer, J.D. (1993). Animals and fungi are each other's closest relatives: Congruent evidence from multiple proteins. *Proceedings of the National Academy of Sciences of the United States of America* 90: 11558-11562.
- Barr, D.J.S. (1992). Evolution and kingdoms of organisms from the perspective of a mycologist. *Mycologia* 84: 1-11.
- Barr, M.E. (1975). *Pestalospaeria*, a new genus in the *Amphisphaeriaceae*. *Mycologia* 67: 187-194.
- Barr, M.E. (1987). *Prodromus to Class Loculoascomycetes*. Newell Inc., Massachusetts, Amherst.
- Barr, M.E. (1990). *Prodromus to nonlichenized, pyrenomycetous members of class Hymenoascomycetes*. *Mycotaxon* 39: 43-184.
- Barron, G.L. (1968). *The Genera of Hyphomycetes from Soil*. Williams and Wilkins, Baltimore, Maryland: 1-364.
- Begerow, D., Stoll, M. and Bauer, R. (2006). A phylogenetic hypothesis of *Ustilaginomycotina* based on multiple gene analyses and morphological data. *Mycologia* 98: 906-916.
- Belliveau, M.J.R. and Bärlocher, F. (2005). Molecular evidence confirms multiple origins of aquatic hyphomycetes. *Mycological Research* 109: 1407-1417.
- Berbee, M.L. and Taylor, J.W. (1993). Ascomycete Relationships: Dating the origin of asexual lineages with 18S ribosomal RNA gene sequence data. In: *The Fungal Holomorph: Mitotic, Meiotic, and Pleomorphic Speciation in Fungal Systematics* (eds. D.R. Reynolds and J.W. Taylor). CAB International, Wallingford, UK: 68-77.
- Berbee, M.L. and Taylor, J.W. (1995). From 18S ribosomal sequence data to evolution of morphology among the fungi. *Canadian Journal of Botany* 73: S677-S683.
- Berbee, M.L. and Taylor, J.W. (2001): Fungal molecular evolution: gene trees and geological time. In: *The Mycota*, vol. 7B, *Systematics and evolution* (eds. D.J. McLaughlin, E.G. McLaughlin and P.A. Lemke). Springer-Verlag, New York: 229-245.
- Berch, S.M., Allen, T.R. and Berbee, M.L. (2002). Molecular detection, community structure and phylogeny of ericoid mycorrhizal fungi. *Plant and Soil* 244: 55-66.
- Bessey, E.A. (1950). *Morphology and Taxonomy of Fungi*. Constable and Company Limited, London: 1-21.
- Bever, J.D. and Morton, J. (1999). Heritable variation and mechanisms of inheritance of spore shape within a population of *Scutellospora pellucida*, an arbuscular mycorrhizal fungus. *American Journal of Botany* 86: 1209-1216.
- Binder, M. and Hibbett, D.S. (2006). Molecular systematics and biological diversification of *Boletales*. *Mycologia* 98: 971-981.
- Bischoff, J.F. and White, J.F. Jr. (2004). *Torrubiella piperis* sp. nov. (*Clavicipitaceae*, *Hypocreales*), a new teleomorph of the *Lecanicillium* complex. *Studies in Mycology* 50: 89-94.

- Blackwell, M., Hibbett, D.S., Taylor, J.W. and Spatafora, J.W. (2006). Research Coordination Networks: a phylogeny for kingdom *Fungi* (Deep Hypha). *Mycologia* 98: 829-837.
- Braun, U., Crous, P.W., Dugan, F., Groenewald, J.Z. and Hoog, de G.S. (2003). Phylogeny and taxonomy of *Cladosporium*-like hyphomycetes, including *Davidiella* gen. nov., the teleomorph of *Cladosporium* s. str. *Mycological Progress* 2: 3-18.
- Bruns, T.D., White, T.J. and Taylor, J.W. (1991). Fungal Molecular Systematics. *Annual Review of Ecology and Systematics* 22: 525-564.
- Bruns, T.D., Vilgalys, R., Barns, S.M., Gonzalez, D., Hibbett, D.S., Lane, D.J., Simpson, L., Stickel, S., Szaro, T.M., Weisburg, W.G. and Sogin, M.L. (1992). Evolutionary relationships within the fungi: analysis of nuclear small subunit rRNA sequences. *Molecular Phylogenetics and Evolution* 1: 231-241.
- Bryant, H.N. and Cantino, P.D. (2002). A review of criticisms of phylogenetic nomenclature: Is taxonomic freedom the fundamental issue? *Biological Reviews* 77: 39-55.
- Burgess, T.I., Barber, P.A., Sufaati, S., Xu, D., Hardy, G.E. StJ. and Dell, B. (2007). *Mycosphaerella* spp. on *Eucalyptus* in Asia; new species, new hosts and new records. *Fungal Diversity* 24: 135-157.
- Burnett, J. (2003). *Fungal Populations and Species*. Oxford University Press, Oxford.
- Burt, A., Carter, D.A., Koenig, G.L., White, T.J. and Taylor, J.W. (1996). Molecular markers reveal cryptic sex in the human pathogen *Coccidioides immitis*. *Proceedings of the National Academy of Sciences of the United States of America* 93: 770-773.
- Cai, L., Zhang, K.Q. and Hyde, K.D. (2003). Freshwater ascomycetes. *Fungal Diversity Research Series* 10: 275-324.
- Cai, L., Zhang, K.Q. and Hyde, K.D. (2005). *Ascoyunnania chameleonina* gen. et sp. nov. a freshwater fungus collected from China and its microcyclic conidiation. *Fungal Diversity* 18: 1-8.
- Campbell, J., Shearer, C.A. and Marvanová, L. (2006). Evolutionary relationships among aquatic anamorphs and teleomorphs: *Lemonniera*, *Margaritispota*, *Goniopila*. *Mycological Research* 110: 1025-1033.
- Cannon, P.F. and Kirk, P.M. (2000). The philosophy and practicalities of amalgamating anamorph and teleomorph concepts. *Studies in Mycology* 45: 19-25.
- Cantino, P.D. and de Queiroz, K. (2007). International Code of Phylogenetic Nomenclature. Version 3a. Part 1: Clade Names. Available at URL: <http://www.ohiou.edu/phylocode/>
- Carlile, M.J. and Watkinson, S.C. (1994). *The Fungi*. Academic Press, London.
- Carmichael, J.W., Kendrick, B., Connors, I.L. and Sigler, L. (1980). *Genera of Hyphomycetes*. University of Alberta Press, Edmonton: 1-386.
- Cavalier-Smith, T. (1998). A revised six-kingdom system of life. *Biological Reviews* 73: 203-266.
- Cavalier-Smith, T. (2001). What are fungi? In: *The Mycota*, vol. 7A, *Systematics and evolution* (eds. D.J. McLaughlin, E.G. McLaughlin and P.A. Lemke). Springer-Verlag, New York, USA: 3-37.
- Celio, G.J., Padamsee, M., Dentinger, B.T.M., Bauer, R. and McLaughlin, D.J. (2006). Assembling the Fungal Tree of Life: Constructing the Structural and Biochemical Database. *Mycologia* 98: 850-859.
- Chaverri, P. and Samuels, G.J. (2003). *Hypocrea/Trichoderma* (Ascomycota, Hypocreales, Hypocreaceae): Species with green ascospores. *Studies in Mycology* 48: 1-113.
- Chaverri, P., Castlebury, L.A., Samuels, G.J. and Geiser, D.M. (2003). Multilocus phylogenetic structure within the *Trichoderma harzianum/Hypocrea lixii* complex. *Molecular Phylogenetics and Evolution* 27: 302-313.

- Chaverri, P., Bischoff, J.F., Evans, H.C. and Hodge, K.T. (2005). *Regiocrella*, a new entomopathogenic genus with a pycnidial anamorph and its phylogenetic placement in the *Clavicipitaceae*. *Mycologia* 97: 1225-1237.
- Chou, H.-H. and Wu, W.-S. (2002). Phylogenetic analysis of internal transcribed spacer regions of the genus *Alternaria*, and the significance of filament-beaked conidia. *Mycological Research* 106: 164-169.
- Cole, G.T. and Kendrick, B. (1981). *Biology of conidial fungi*. Academic Press, New York.
- Cortinas, M.N., Crous, P.W., Wingfield, B.D. and Wingfield, M.J. (2006). Multi-gene phylogenies and phenotypic characters distinguish two species within the *Colletogloeopsis zuluensis* complex associated with *Eucalyptus* stem cankers. *Studies in Mycology* 55: 133-146.
- Crous, P.W. (1998). *Mycosphaerella* spp. and their anamorphs associated with leaf spot diseases of *Eucalyptus*. *Mycologia Memoir* 21:1-170.
- Crous, P.W. (2002). Taxonomy and pathology of *Cylindrocladium* (*Calonectria*) and allied genera. APS Press, St Paul, USA.
- Crous, P.W., Hong, L., Wingfield, M.J., Wingfield, B.D. and Kang, J. (1999). *Uwebraunia* and *Dissoconium*, two morphologically similar anamorph genera with distinct teleomorph affinity. *Sydowia* 52: 155-166.
- Crous, P.W., Aptroot, A., Kang, J.C., Braun, U. and Wingfield, M.J. (2000). The genus *Mycosphaerella* and its anamorphs. *Studies in Mycology* 45: 107-121.
- Crous, P.W., Kang, J.C. and Braun, U. (2001). A phylogenetic redefinition of anamorph genera in *Mycosphaerella* based on ITS rDNA sequence and morphology. *Mycologia* 93: 1081-1101.
- Crous, P.W., Groenewald, J.Z., Risède, J.-M., Simoneau, P., Hywel-Jones, N.L. (2004). *Calonectria* species and their *Cylindrocladium* anamorphs: Species with sphaeropedunculate vesicles. *Studies in Mycology* 50: 415-430.
- Crous, P.W., Groenewald, J.Z., Groenewald, M., Caldwell, P., Braun, U. and Harrington, T.C. (2006a). Species of *Cercospora* associated with grey leaf spot of maize. *Studies in Mycology* 55: 189-197.
- Crous, P.W., Groenewald, J.Z., Risède, J.-M., Simoneau, P. and Hyde, K.D. (2006b). *Calonectria* species and their *Cylindrocladium* anamorphs: Species with clavate vesicles. *Studies in Mycology* 55: 213-226.
- Crous, P.W., Slippers, B., Wingfield, M.J., Rheeder, J., Marasas, W.F.O., Phillips, A.J.L., Alves, A., Burgess, T., Barber, P. and Groenewald, J.Z. (2006c). Phylogenetic lineages in the *Botryosphaeriaceae*. *Studies in Mycology* 55: 235-253.
- Crous, P.W., Wingfield, M.J., Mansilla, J.P., Alfenas, A.C. and Groenewald, J.Z. (2006d). Phylogenetic reassessment of *Mycosphaerella* spp. and their anamorphs occurring on *Eucalyptus*. II. *Studies in Mycology* 55: 99-131.
- Cunfer, B.M. and Ueng, P.P. (1999). Taxonomy and identification of *Septoria* and *Stagonospora* species on small grain cereals. *Annual Review of Phytopathology* 37: 267-284.
- Cunnington, J.H., Takamatsu, S., Lawrie, A.C. and Pascoe, I.G. (2003). Molecular identification of anamorphic powdery mildews (*Erysiphales*). *Australasian Plant Pathology* 32: 421-428.
- De Beer, Z.W., Harrington, T.C., Vismer, H.F., Wingfield, B.D. and Wingfield, M.J. (2003). Phylogeny of the *Ophiostoma stenoceras-Sporothrix schenckii* complex. *Mycologia* 95: 434-441.

- De Beer, Z.W., Begerow, D., Bauer, R., Pegg, G.S., Crous, P.W. and Wingfield, M.J. (2006). Phylogeny of the *Quambalariaceae* fam. nov., including important *Eucalyptus* pathogens in South Africa and Australia. *Studies in Mycology* 55: 289-298.
- Den Breeÿen, A., Groenewald, J.Z., Verkley, G.J.M. and Crous, P.W. (2006). Morphological and molecular characterisation of *Mycosphaerellaceae* associated with the invasive weed, *Chromolaena odorata*. *Fungal Diversity* 23: 89-110.
- Denman, S., Crous, P.W., Taylor, J.E., Kang, J.C., Pascoe, I. and Wingfield, M.J. (2000). An overview of the taxonomic history of *Botryosphaeria* and a re-evaluation of its anamorphs based on morphology and ITS rDNA phylogeny. *Studies in Mycology* 45: 129-140.
- Dodd, S.L., Crowhurst, R.N., Rodrigo, A.G., Samuels, G.J., Hill, R.A. and Stewart, A. (2000). Examination of *Trichoderma* phylogenies derived from ribosomal DNA sequence data. *Mycological Research* 104: 23-34.
- Dodd, S., Lieckfeldt, E. and Samuels, G.J. (2003). *Hypocrea atroviridis* sp. nov., the teleomorph of *Trichoderma atroviride*. *Mycologia* 95: 27-40.
- Donoghue, M.J. and Gauthier, J.A. (2004). Implementing the PhyloCode [2]. *Trends in Ecology and Evolution* 19: 281-282.
- Druzhinina, I.S., Kopchinskiy, A.G., Komo, M., Bissett, J., Szakacs, G. and Kubicek, C.P. (2005). An oligonucleotide barcode for species identification in *Trichoderma* and *Hypocrea*. *Fungal Genetics and Biology* 42: 813-828.
- Druzhinina, I.S., Kopchinskiy, A.G. and Kubicek, C.P. (2006). The first 100 *Trichoderma* species characterized by molecular data. *Mycoscience* 47: 55-64.
- Du, M., Schardl, C.L., Nuckles, E.M., and Vaillancourt, L.J. (2005). Using mating-type gene sequences for improved phylogenetic resolution of *Colletotrichum* species complexes. *Mycologia* 97: 641-658.
- Dubois, A. (2007). Naming taxa from cladograms: A cautionary tale. *Molecular Phylogenetics and Evolution*, 42: 317-330.
- Duong, L.M., Crous, P., Lumyong, S. and Hyde, K.D. (2007). Phylogenetic relationships of *Guignardia* species. *Fungal Diversity* (in press)
- Dyer, P.S., Paoletti, M. and Archer, D.B. (2003). Genomics reveals sexual secrets of *Aspergillus*. *Microbiology* 149: 2301-2303.
- Edman, J.C., Kovacs, J.A., Masur, H., Santi, D.V., Elwood, H.J. and Sogin, M.L. (1998). Ribosomal RNA sequence shows *Pneumocystis carinii* to be a member of the fungi. *Nature* 334: 519-522.
- Ellis, M.B. (1958). *Clasterosporium* and some allied dematiaceae-phragmosporae I. *Mycological Papers* 70: 1-89.
- Ellis, M.B. (1963). Dematiaceous Hyphomycetes. V. *Mycological Papers* 93: 1-33.
- Ellis, M.B. (1971a). *Dematiaceous Hyphomycetes*. Commonwealth Mycological Institute, Kew, Surrey, England.
- Ellis, M.B. (1971b). Dematiaceous Hyphomycetes. X. *Mycological Papers* 125: 1-31.
- Ellis, M.B. (1972). Dematiaceous Hyphomycetes. XI. *Mycological Papers* 131: 1-25.
- Ellis, M.B. (1976). *More Dematiaceous Hyphomycetes*. Commonwealth Mycological Institute, Kew, Surrey, England.
- Feau, N., Hamelin, R.C. and Bernier, L. (2006). Attributes and congruence of three molecular data sets: Inferring phylogenies among *Septoria*-related species from woody perennial plants. *Molecular Phylogenetic and Evolution* 40: 808-829.
- Fell, J.W., Boekhout, T., Fonseca, A., Scorzetti, G. and Statzell-Tallman, A. (2000). Biodiversity and systematics of basidiomycetous yeasts as determined by large-subunit

- rDNA D1/D2 domain sequence analysis. *International Journal of Systematic and Evolutionary Microbiology* 50: 1351-1371.
- Fernández, F.A. and Huhndorf, S.M. (2005). New species of *Chaetosphaeria*, *Melanopsammella* and *Tainosphaeria* gen. nov. from the Americas. *Fungal Diversity* 18: 15-57.
- Fernández, F.A., Lutzoni, F.M. and Huhndorf, S.M. (1999). Teleomorph-anamorph connections: The new pyrenomycetous genus *Carpoligna* and its *Pleurothecium* anamorph. *Mycologia* 91: 251-262.
- Fernández, F.A., Miller, A.N., Huhndorf, S.M., Lutzoni, F.M. and Zoller, S. (2006). Systematics of the genus *Chaetosphaeria* and its allied genera: morphological and phylogenetic diversity in north temperate and neotropical taxa. *Mycologia* 98: 121-130.
- Gams, W. (1995). How natural should anamorph genera be? *Canadian Journal of Botany* 73: S747-S753.
- Gams, W. (2000). *Phialophora* and some similar morphologically little-differentiated anamorphs of divergent ascomycetes. *Studies in Mycology* 45: 187-199.
- Gams, W., Korf, R.P., Pitt, J.I., Hawksworth, D.L., Berbee, M.L., Kirk, P.M. and Seifert, K.A. (2003). Has dual nomenclature for fungi run its course? the article 59. *Mycotaxon* 88: 493-508.
- Geiser, D.M., Jiménez-Gasco, M.D.M., Kang, S., Makalowska, I., Veeraraghavan, N., Ward, T.J., Zhang, N. and O'Donnell, K. (2004). FUSARIUM-ID v. 1.0: A DNA sequence database for identifying *Fusarium*. *European Journal of Plant Pathology* 110: 473-479.
- Geiser, D.M., Gueidan, C., Miadlikowska, J., Lutzoni, F., Kauff, F., Hofstetter, V., Fraker, E., Schoch, C.L., Tibell, L., Untereiner, W.A. and Aptroot, A. (2006). *Eurotiomycetes: Eurotiomycetidae* and *Chaetothyriomycetidae*. *Mycologia* 98: 1053-1064.
- Glenn, A.E., Bacon, C.W., Price, R. and Hanlin, R.T. (1996). Molecular phylogeny of *Acremonium* and its taxonomic implications. *Mycologia* 88: 369-383.
- Goh, T.K. and Hyde, K.D. (1996). *Spadicoides cordanoides* sp. nov., a new dematiaceous hyphomycete from submerged wood in Australia, with a taxonomic review of the genus. *Mycologia* 88: 1022-1031.
- Goh, T.K. and Hyde, K.D. (1998). A synopsis of and a key to *Diplococcium* species, based on the literature, with a description of a new species. *Fungal Diversity* 1: 65-83.
- Goodwin, S.B., Dunkle, L.D. and Zismann, V.L. (2001). Phylogenetic analysis of *Cercospora* and *Mycosphaerella* based on the internal transcribed spacer region of ribosomal DNA. *Phytopathology* 91: 648-658.
- Goos, R.D. (1987). Fungi with a twist: the helicosporous hyphomycetes. *Mycologia* 79: 1-22.
- Green, S. and Castlebury, L.A. (2007). Connection of *Gnomonia intermedia* to *Discula betulina* and its relationship to other taxa in *Gnomoniaceae*. *Mycological Research* 111: 62-69.
- Guarro, J., Gene, J. and Stchigel, A.M. (1999). Developments in fungal taxonomy. *Clinical Microbiology Reviews* 12: 454-500.
- Guba, E.F. (1929). Monograph of the genus *Pestalotia* de Notaris. Part 1. *Phytopathology* 19: 191-232.
- Guerber, J.C. and Correll, J.C. (2001). Characterization of *Glomerella acutata*, the teleomorph of *Colletotrichum acutatum*. *Mycologia* 93: 216-229.
- Hajibabaei, M., Janzen, D.H., Burns, J.M., Hallwachs, W. and Hebert, P.D.N. (2006). DNA barcodes distinguish species of tropical *Lepidoptera*. *Proceedings of the National Academy of Sciences the United States of America* 103: 968-971.

- Halleen, F., Schroers, H.-J., Groenewald, J.Z. and Crous, P.W. (2004). Novel species of *Cylindrocarpon* (*Neonectria*) and *Campylocarpon* gen. nov. associated with black foot disease of grapevines (*Vitis* spp.). *Studies in Mycology* 50: 431-455.
- Halleen, F., Schroers, H.-J., Groenewald, J.Z., Rego, C., Oliveira, H. and Crous, P.W. (2006). *Neonectria liriodendri* sp. nov., the main causal agent of black foot disease of grapevines. *Studies in Mycology* 55: 227-234.
- Hambleton, S. and Sigler, L. (2005). *Meliniomyces*, a new anamorph genus for root-associated fungi with phylogenetic affinities to *Rhizoscyphus ericae* (= *Hymenoscyphus ericae*), *Leotiomyces*. *Studies in Mycology* 53: 1-27.
- Hambleton, S., Nickerson, N.L. and Seifert, K.A. (2005). *Leohumicola*, a new genus of heat-resistant hyphomycetes. *Studies in Mycology* 53: 29-52.
- Hammond, P. (1992). Species inventory. In: *Global biodiversity: status of the earth's living resources* (ed. B. Groombridge). Chapman and Hall, London: 17-39.
- Hansen, K. and Pfister, D.H. (2006). Systematics of the *Pezizomycetes* - the operculate discomycetes. *Mycologia* 98: 1029-1040.
- Harrington, T.C., McNew, D., Steimel, J., Hofstra, D. and Farrell, R. (2001). Phylogeny and taxonomy of the *Ophiostoma piceae* complex and the dutch elm disease fungi. *Mycologia* 93: 111-136.
- Hawksworth, D.L. (ed.) (1994). *Ascomycete systematics: problems and perspectives in the nineties*. Plenum Press, New York.
- Hawksworth, D.L. and Kalin-Arroyo, M.T. (1995). Magnitude and distribution of biodiversity. In: *Global biodiversity assessment* (ed. V.H. Heywood). Cambridge University Press, London: 107-191.
- Hebert, P.D.N. and Gregory, T.R. (2005). The promise of DNA barcoding for taxonomy. *Systematic Biology* 54: 852-859.
- Hebert, P.D.N., Cywinska, A., Ball, S.L. and deWaard, J.R. (2002). Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London Series B* 270: 313-321.
- Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H. and Hallwachs, W. (2004a). Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of the America* 101: 14812-14817.
- Hebert, P.D.N., Stoeckle, M.Y., Zemplak, T.S. and Francis, C.M. (2004b). Identification of birds through DNA barcodes. *PLoS Biology* 2: e312.
- Hennebert, G.L. (1987). Pleoanamorphy and its nomenclatural problem. In: *Pleomorphic Fungi: The Diversity and its Taxonomic Implications* (ed. J. Sugiyama). Kodansha Ltd., Tokyo: 263-290.
- Hennebert, G.L. (1991). Art. 59 and the problem with pleoanamorphic fungi. *Mycotaxon* 40: 479-496.
- Hennebert, G.L. (2003). Fundamentals for suppression of dual nomenclature in pleomorphic fungi and integration of anamorphic fungi (deuteromycetes) into the *Ascomycota* and *Basidiomycota*. *Mycotaxon* 88: 509-514.
- Hennebert, G.L. and Weresub, L.K. (1977). Terms for states and forms of fungi, their names and types. *Mycotaxon* 6: 207-211.
- Hernández-Gutiérrez, A. and Sutton, B.C. (1997). *Imimyces* and *Linkosia*, two genera segregated from *Sporidesmium sensu lato*, and redescription of *Polydesmus*. *Mycological Research* 101: 201-209.
- Hibbett, D.S. (2006). A phylogenetic overview of the *Agaricomycotina*. *Mycologia* 98: 917-925.

- Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Lücking, R., Lumbsch, T., Lutzoni, F., Matheny, P.B., Mclaughlin, D.J., Powell, M.J., Redhead, S., Schoch, C.L., Spatafora, J.W., Stalpers, J.A., Vilgalys, R., Aime, M.C., Aptroot, A., Bauer, R., Begerow, D., Benny, G.L., Castlebury, L.A., Crous, P.W., Dai, Y.-C., Gams, W., Geiser, D.M., Griffith, G.W., Gueidan, C., Hawksworth, D.L., Hestmark, G., Hosaka, K., Humber, R.A., Hyde, K.D., Ironside, J.E., Køljalg, U., Kurtzman, C.P., Larsson, K.-H., Lichtwardt, R., Longcore, J., Midlikowska, J., Miller, A., Moncalvo, J.-M., Mozley-Standridge, S., Oberwinkler, F., Parmasto, E., Reeb, V., Rogers, J.D., Roux, C., Ryvarde, L., Sampaio, J.P., Schüßler, A., Sugiyama, J., Thorn, R.G., Tibell, L., Untereiner, W.A., Walker, C., Wang, Z., Weir, A., Weiß, M., White, M.M., Winka, K., Yao, Y.-J., Zhang, N. (2007). A higher-level phylogenetic classification of the Fungi. *Mycological Research* 111: 509-547.
- Hidayat, I., Jeewon, R., To-anun, C. and Hyde, K.D. (2006). The genus *Oxydothis*: New palmicolous taxa and phylogenetic relationships within *Xylariales*. *Fungal Diversity* 23: 159-179.
- Hillis, D.M. (2007). Constraints in naming parts of the tree of life. *Molecular Phylogenetics and Evolution* 42: 331-338.
- Hinrikson, H.P., Hurst, S.F., Lott, T.J., Warnock, D.W. and Morrison, C.J. (2005). Assessment of ribosomal large-subunit D1-D2, internal transcribed spacer 1, and internal transcribed spacer 2 regions as targets for molecular identification of medically important *Aspergillus* species. *Journal of Clinical Microbiology* 43: 2092-2103.
- Hoog, G.S. de (1979) Deductive classification - worked examples using anamorph and teleomorph data in the Ascomycetes. In: *The Whole Fungus*. Vol. 1B. (ed. B. Kendrick). National Museums of Canada, Ottawa: 215-239.
- Hoog, G.S. de and Hermanides-Nijhof, E.J. (1977). Survey of the black yeasts and allied fungi. *Studies in Mycology* 15: 178-221.
- Hoog, G.S. de and Smith, M.Th. (2005). Ribosomal gene phylogeny and species delimitation in *Geotrichum* and its teleomorphs. *Studies in Mycology* 50: 489-515.
- Hosaka, K., Bates, S.T., Beaver, R.E., Castellano, M.A., Colgan, W., III, Dominguez, L.S., Nouhra, E.R., Geml, J., Giachini, A.J., Kenney, S.R., Simpson, N.B., Spatafora, J.W. and Trappe, J.M. (2006). Molecular phylogenetics of the gomphoid-phalloid fungi with the establishment of the new subclass *Phallomycetidae* and two new orders. *Mycologia* 98: 949-959.
- Hughes, S.J. (1953). Conidiophores, conidia and classification. *Canadian Journal of Botany* 31: 577-659.
- Hughes, S.J. (1979). Relocation of species of *Endophragma* auct. with notes on relevant generic names. *New Zealand Journal of Botany* 12: 139-188.
- Hunter, G.C., Crous, P.W., Wingfield, B.D., Pongpanich, K. and Wingfield, M.J. (2006a). *Pseudocercospora flavomarginata* sp. nov., from *Eucalyptus* leaves in Thailand. *Fungal Diversity* 22: 71-90.
- Hunter, G.C., Wingfield, B.D., Crous, P.W. and Wingfield, M.J. (2006b). A multi-gene phylogeny for species of *Mycosphaerella* occurring on *Eucalyptus* leaves. *Studies in Mycology* 55: 147-161.
- Hyde, K.D. (1993): Fungi from palms. VI. Reflections on *Oxydothis* and related genera. *Sydowia* 45: 204-225.
- Hyde, K.D. (1994): Fungi from palms. XIII. The genus *Oxydothis*, a revision. *Sydowia* 46: 265-314.

- Index Fungorum, (2007): An online database currently coordinated and supported by CABI Bioscience, CBS and Landcare Research, available at www.speciesfungorum.org
- Jacobs, K.A. and Rehner, S.A. (1998). Comparison of cultural and morphological characters and ITS sequences in anamorphs of *Botryosphaeria* and related taxa. *Mycologia* 90: 601–610.
- Jaklitsch, W.M., Komon, M., Kubicek, C.P. and Druzhinina, I.S. (2006). *Hypocrea crystalligena* sp. nov., a common European species with a white-spored *Trichoderma* anamorph. *Mycologia* 98: 499-513.
- James, T.Y., Kauff, F., Schoch, C.L., Matheny, P.B., Hofstetter, V., Cox, C.J., Celio, G., Gueidan, C., Fraker, E., Miadlikowska, J., Lumbsch, H.T., Rauhut, A., Reeb, V., Arnold, A.E., Amtoft, A., Stajich, J.E., Hosaka, K., Sung, G.H., Johnson, D., O'Rourke, B., Crockett, M., Binder, M., Curtis, J.M., Slot, J.C., Wang, Z., Wilson, A.W., Schussler, A., Longcore, J.E., O'Donnell, K., Mozley-Standridge, S., Porter, D., Letcher, P.M., Powell, M.J., Taylor, J.W., White, M.M., Griffith, G.W., Davies, D.R., Humber, R.A., Morton, J.B., Sugiyama, J., Rossman, A.Y., Rogers, J.D., Pfister, D.H., Hewitt, D., Hansen, K., Hambleton, S., Shoemaker, R.A., Kohlmeyer, J., Volkmann-Kohlmeyer, B., Spotts, R.A., Serdani, M., Crous, P.W., Hughes, K.W., Matsuura, K., Langer, E., Langer, G., Untereiner, W.A., Lucking, R., Budel, B., Geiser, D.M., Aptroot, A., Diederich, P., Schmitt, I., Schultz, M., Yahr, R., Hibbett, D.S., Lutzoni, F., McLaughlin, D.J., Spatafora, J.W. and Vilgalys, R. (2006a). Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature* 443: 818-822.
- James, T.Y., Letcher, P.M., Longcore, J.E., Mozley-Standridge, S.E., Porter, D., Powell, M.J., Griffith, G.W. and Vilgalys, R. (2006b). A molecular phylogeny of the flagellated fungi (*Chytridiomycota*) and description of a new phylum (*Blastocladiomycota*). *Mycologia* 98: 860-871.
- Jeewon, R., Liew, E.C.Y. and Hyde, K.D. (2002). Phylogenetic relationships of *Pestalotiopsis* and allied genera inferred from ribosomal DNA sequences and morphological characters. *Molecular Phylogenetics and Evolution* 25: 378-392.
- Jeewon, R., Liew, E.C.Y. and Hyde, K.D. (2003a). Molecular systematics of the *Amphisphaeriaceae* based on cladistic analyses of partial LSU rDNA sequences. *Mycological Research* 107: 1392-1402.
- Jeewon, R., Liew, E.C.Y., Simpson, J.A., Hodgkiss, I.J and Hyde, K.D. (2003b). Phylogenetic significance of morphological characters in the taxonomy of *Pestalotiopsis* species. *Molecular Phylogenetics and Evolution* 27: 372-383.
- Jeewon, R., Liew, E.C.Y. and Hyde, K.D. (2004). Phylogenetic evaluation of species nomenclature of *Pestalotiopsis* in relation to host association. *Fungal Diversity* 17: 39-55.
- Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F. and Donoghue, M.J. (2002). *Plant Systematics: A Phylogenetic Approach, Second Edition*. Sinauer Associates, Inc., Sunderland: 1-39.
- Judson, O.P. and Normark, B.B. (1996). Ancient asexual scandals. *Trends in Ecology and Evolution*. 11: 41-46.
- Kaiser, W.J., Wang, B.-C. and Rogers, J.D. (1997). *Ascochyta fabae* and *A. lentis*: Host specificity, teleomorphs (*Didymella*), hybrid analysis, and taxonomic status. *Plant Disease* 81: 809-816.
- Keeling, P.J. (2003). Congruent evidence from alpha-tubulin and beta-tubulin gene phylogenies for a zygomycete origin of microsporidia. *Fungal Genetics and Biology* 38: 298-309.

- Kendrick, B. (ed.) (1979). *The Whole Fungus: The Sexual-Asexual Synthesis*. Volume 1-2. National Museums of Canada, Ottawa.
- Kendrick, B. (2000). *The Fifth Kingdom*, the third edition, Focus Publishing, R. Paulins Company, Newburyport, Massachusetts, USA: 4.
- Kendrick, B. and DiCosmo, F. (1979). Anamorph-Teleomorph connections in ascomycetes. In: *The Whole Fungus* vol. 1. (ed. W.B. Kendrick). National Museums of Canada, Ottawa: 283-410.
- Kim, J.-J., Lim Y.W, Seifert K.A., Kim S.H., Breuil C. and Kim, G.-H. (2005). Taxonomy of *Ophiostoma radiaticola* sp. nov. (*Ophiostomatales*, *Ascomycetes*), the teleomorph of *Pesotum pini*, isolated from logs of *Pinus radiata*. *Mycotaxon* 91: 481-496.
- Kirk, P.M. (1982). New or interesting microfungi VI. *Sporidesmiella* gen. nov. (hyphomycetes). *Transactions of the British Mycological Society* 79: 479-489.
- Kirk, P.M., Cannon, P.F., David, J.C. and Stalpers J.A. (2001). *Ainsworth & Bisby's Dictionary of the Fungi, ninth edition*, CAB International, Wallingford, Oxon, UK.
- Kirschner, R. and Chen, C.-J. (2004). *Helicomysa everhartioides*, a new helicosporous sporodochial hyphomycete from Taiwan with relationships to the *Hyaloriaceae* (*Auriculariales*, *Basidiomycota*). *Studies in Mycology* 50: 337-342.
- Kodsueb, R., Jeewon, R., Dhanasekaran, V., McKenzie, E.H.C., Lumyong, P., Lumyong, S. and Hyde, K.D., (2006a). Systematic revision of *Tubeufiaceae* based on morphological and molecular data. *Fungal Diversity* 21: 105-130.
- Kodsueb, R., Vijaykrishna, D., Aptroot, A., Lumyong, S., McKenzie, E.H.C. and Hyde, K.D. (2006b). The family *Pleosporaceae*: Intergeneric relationships and phylogenetic perspectives based on sequence analyses of partial 28S rDNA. *Mycologia* 98: 571-583.
- Kolarik, M., Kubatova, A., Pazoutova, S., and Srutka, P. (2004). Morphological and molecular characterisation of *Geosmithia putterillii*, *G. pallida* comb. nov. and *G. flava* sp. nov., associated with subcorticolous insects. *Mycological Research* 108: 1053-1069.
- Köljalg, U., Larsson, K.-H., Abarenkov, K., Nilsson, R.H., Alexander, I.J., Eberhardt, U. and Erland, S. and Ursing, B.M. (2005). UNITE: A database providing web-based methods for the molecular identification of ectomycorrhizal fungi. *New Phytologist* 166: 1063-1068.
- Kress, W.J., Wurdack, K.J., Zimmer, E.A., Weigt, L.A. and Janzen, D.H. (2005). Use of DNA barcodes to identify flowering plants. *Proceedings of the National Academy of Sciences the United States of America* 102: 8369-8374.
- Kullnig-Gradinger, C.M., Szakacs, G. and Kubicek, C.P. (2002). Phylogeny and evolution of the genus *Trichoderma*: A multigene approach. *Mycological Research* 106: 757-767.
- Kurtzman, C.P. and Robnett, C.J. (1998). Identification and phylogeny of ascomycetous yeasts from analysis of nuclear large subunit (26S) ribosomal DNA partial sequences. *Antonie van Leeuwenhoek* 73: 331-371.
- Lang, B.E., O'Kelly C., Nerad, T., Gray, M.W. and Burger, G. (2002). The closest unicellular relative to animals. *Current Biology* 12: 1773-1778.
- Larsson, K.H., Parmasto, E., Fischer, M., Langer, E., Nakasone, K.K. and Redhead, S.A. (2006). *Hymenochaetales*: a molecular phylogeny for the hymenochaetoid clade. *Mycologia* 98: 926-936.
- Lee, S., Groenewald, J.Z. and Crous, P.W. (2004). Phylogenetic reassessment of the coelomycete genus *Harknessia* and its teleomorph *Wuestneia* (*Diaporthales*), and the introduction of *Apoharknessia* gen. nov. *Studies in Mycology* 50: 235-252
- Lee, S., Crous, P.W. and Wingfield, M.J. (2006). Pestalotioid fungi from *Restionaceae* in the Cape Floral Kingdom. *Studies in Mycology* 55: 175-187.

- Lieckfeldt, E. and Seifert, K.A. (2000). An evaluation of the use of ITS sequences in the taxonomy of the *Hypocreales*. *Studies in Mycology* 45: 35-44.
- Liu, B., Liu, X.Z. and Zhuang, W.Y. (2005). *Orbilium querci* sp. nov. and its knob-forming nematophagous anamorph. *FEMS Microbiology Letters* 245: 99-105.
- Liu, M. and Hodge, K.T. (2005). *Hypocrella zhongdongii* sp. nov., the teleomorph of *Aschersonia incrassata*. *Mycological Research* 109: 818-824.
- Liu, Y.J., Whelen, S. and Hall, B.D. (1999). Phylogenetic relationships among ascomycetes: Evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16: 1799-1808.
- Liu, Y.J. and Hall, B.D. (2004). Body plan evolution of ascomycetes, as inferred from an RNA polymerase II phylogeny. *Proceedings of the National Academy of Sciences the United States of America* 101: 4507-4512.
- Liu, Y.J., Hodson, M.C. and Hall, B.D. (2006). Loss of the flagellum happened only once in the fungal lineage: Phylogenetic structure of Kingdom *Fungi* inferred from RNA polymerase II subunit genes. *BMC Evolutionary Biology* 6: Article No. 74.
- Liu, Z.Y., Yao, Y.J., Liang, Z.Q., Liu, A.Y., Pegler, D.N. and Chase, M.W. (2001). Molecular evidence for the anamorph–teleomorph connection in *Cordyceps sinensis*. *Mycological Research* 105: 827-832.
- Lucas, J.A., Dyer, P.S. and Murray, T. (2000). Pathogenecity, host specificity, and population biology of *Tapesia* spp., causal agents of eyespot disease of cereals. *Advances in Botanical Research* 33: 225-258.
- Luque, J., Martos, S. and Phillips, A.J.L. (2005). *Botryosphaeria viticola* sp. nov. on grapevines: a new species with a *Dothiorella* anamorph. *Mycologia* 97: 1111-1121.
- Lutzoni, F., Kauff, F., Cox, C.J., McLaughlin, D., Celio, G., Dentinger, B., Padamsee, M., Hibbett, D., James, T. Y., Baloch, E., Grube, M., Reeb, V., Hofstetter, V., Schoch, C., Arnold, A. E., Miadlikowska, J., Spatafora, J., Johnson, D., Hambleton, S., Crockett, M., Shoemaker, R., Sung, G.H., Lucking, R., Lumbsch, T., O'Donnell, K., Binder, M., Diederich, P., Ertz, D., Gueidan, C., Hansen, K., Harris, R. C., H., Kentaro, L., Young-W., Matheny, B., Nishida, H., Pfister, D., Rogers, J., Rossman, A., Schmitt, I., Sipman, H., Stone, J., Sugiyama, J., Yahr, R. and Vilgalys, R. (2004). Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *American Journal of Botany* 91: 1446-1480.
- Maddison, D. R. and Schulz, K.-S. (eds.) (1996-2006). The Tree of Life Web Project. Internet address: <http://tolweb.org>
- Magee, P.T. and Magee, B.B. (2004). Through a glass opaquely: The biological significance of mating in *Candida albicans*. *Current Opinion in Microbiology* 7: 661–665.
- Matheny, P.B. (2005). Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; *Agaricales*). *Molecular Phylogenetics and Evolution* 35: 1-20.
- Matheny, P.B., Curtis, J.M., Hofstetter, V., Aime, M.C., Moncalvo, J.M., Ge, Z.W., Yang Z.L., Slot, J.C., Ammirati, J.F., Baroni, T.J., Bougher, N.L., Hughes, K.W., Lodge, D.J., Kerrigan, R.W., Seidl, M.T., Aanen, D.K., DeNitis, M., Daniele, G.M., Desjardin, D.E., Kropp, B.R., Norvell, L.L., Parker, A., Vellinga, E.C., Vilgalys, R. and Hibbett, D.S. (2006). Major clades of Agaricales: a multilocus phylogenetic overview. *Mycologia* 98: 982-995.
- Mayr, E. (1942): *Systematics and the origin of species*. Columbia University Press, New York: 1-334.

- Metz, A.M., Haddad, A., Worapong, J., Long, D.M., Ford, E.J., Hess, W.M., Strobel, G.A. (2000). Induction of the sexual stage of *Pestalotiopsis microspora*, a taxol-producing fungus. *Microbiology* 146: 2079-2089.
- Miadlikowska, J., Kauff, F., Hofstetter, V., Fraker, E., Grube, M., Hafellner, J., Reeb, V., Hodkinson, B.P., Kukwa, M., Lücking, R., Hestmark, G., Otalora, M.G., Rauhut, A., Büdel, B., Scheidegger, C., Timdal, E., Stenroos, S., Brodo, I., Perlmutter, G.B., Ertz, D., Diederich, P., Lendemer, J.C., May, P., Schoch, C.L., Arnold, A.E., Gueidan, C., Tripp, E., Yahr, R., Robertson, C. and Lutzoni, F. (2006). New insights into classification and evolution of the *Lecanoromycetes* (*Pezizomycotina*, *Ascomycota*) from phylogenetic analyses of three ribosomal RNA and two protein-coding genes. *Mycologia* 98: 1088-1103.
- Miller, M.G. and Johnson, A.D. (2002). White-opaque switching in *Candida albicans* is controlled by mating-type locus homeodomain proteins and allows efficient mating. *Cell* 110: 293-302.
- Miller, S.L., Larsson, E., Larsson, K.H., Verbeken, A. and Nuytinck, J. (2006). Perspectives in the new *Russulales*. *Mycologia* 98: 960-970.
- Min, X.J. and Hickey, D.A. (2007). Assessing the effect of varying sequence length on DNA barcoding of fungi. *Molecular Ecology Notes* 7: 365-373.
- Minter, D.W., Kirk, P.M. and Sutton, B.C. (1982). Holoblastic phialides. *Transactions of the British Mycological Society* 79: 75-93.
- Minter, D.W., Kirk, P.M. and Sutton, B.C. (1983). Thallic phialides. *Transactions of the British Mycological Society* 80: 39-66.
- Mo, M.H., Huang, X.W., Zhou, W., Huang, Y., Hao, Y.E. and Zhang, K.Q. (2005). *Arthrotrrys yunnanensis* sp. nov., the fourth anamorph of *Orbilia auricolor*. *Fungal Diversity* 18: 107-115.
- Moncalvo, J.-M. (2005). Molecular systematics: major fungal phylogenetic groups and fungal species concepts. In: *Evolutionary genetics of Fungi* (ed. J.P. Xu). Horizon Scientific Press, Norfolk: 1-33.
- Moncalvo, J.M., Nilsson, R.H., Koster, B., Dunham, S.M., Bernauer, T., Matheny, P.B., Porter, T.M., Margaritescu, S., Weiß, M., Garnica, S., Danell, E., Langer, G., Langer, E., Larsson, E., Larsson, K.H. and Vilgalys, R. (2006). The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. *Mycologia* 98: 937-948.
- Monsch, K.A. (2006). The PhyloCode, or alternative nomenclature: Why it is not beneficial to paleontology, either. *Acta Palaeontologica Polonica* 51: 521-524.
- Moore, G. (1998). A comparison of traditional and phylogenetic nomenclature. *Taxon* 47: 561-579.
- Morgan-Jones, G. and White, J.F. (1987). Notes on Coelomycetes. III. Concerning *Microsphaeropsis concentrica*: morphology and ultrastructure. *Mycotaxon* 30:177-187.
- Mostert, L., Crous, P.W., Groenewald, J.Z., Gams, W. and Summerbell, R.C. (2003). *Togninia* (*Calosphaeriales*) is confirmed as teleomorph of *Phaeoacremonium* by means of morphology, sexual compatibility and DNA phylogeny. *Mycologia* 95: 646-659.
- Mostert, L., Groenewald, J.Z., Summerbell, R.C., Gams, W., Crous, P.W. (2006). Taxonomy and pathology of *Togninia* (*Diaporthales*) and its *Phaeoacremonium* anamorphs. *Studies in Mycology* 54: 1-115.
- Müller, E. (1957). Haupt- und Nebenfruchtformen bei *Guignardia* Viala et Ravaz. *Sydowia Beiheft* 1: 210-224.
- Nag Raj, T.R. (1993). *Coelomycetous Anamorphs with Appendage Bearing Conidia*. Mycologue Publications, Waterloo.

- Nag Raj, T.R. and Kendrick, W.B. (1975). A monograph of *Chalara* and allied genera. Wilfrid Laurier University Press, Waterloo.
- Nilsson, R.H., Ryberg, M., Kristiansson, E., Abarenkov, K., Larsson, K., and Kõljalg, U. (2006) Taxonomic Reliability of DNA Sequences in Public Sequence Databases: A Fungal Perspective. PLoS ONE 1: e59.
- Nilsson, S. (1964). Freshwater hyphomycetes: taxonomy, morphology and ecology. *Symbolae Botanicae Upsaliensis* 18: 1-130.
- Normark, B.B., Judson, O.P. and Moran, N.A. (2003). Genomic signatures of ancient asexual lineages. *Biological Journal of the Linnean Society* 79: 69-84.
- O'Donnell, K., Lutzoni, F.M., Ward, T.J. and Benny G.L. (2001). Evolutionary relationships of among mucoralean fungi (*Zygomycota*): evidence for family polyphyly on a large scale. *Mycologia* 93: 286-296.
- O'Donnell, K., Ward, T.J., Geiser, D.M., Kistler, H.C. and Aoki, T. (2004). Genealogical concordance between the mating type locus and seven other nuclear genes supports formal recognition of nine phylogenetically distinct species within the *Fusarium graminearum* clade. *Fungal Genetics and Biology* 41: 600-623.
- Okada, G., Seifert, K.A., Takematsu, A., Yamaoka, Y., Miyazaki, S., and Tubaki, K. (1998). A molecular phylogenetic reappraisal of the *Graphium* complex based on 18S rDNA sequences. *Canadian Journal of Botany* 76: 1495-1506.
- Okada, G., Jacobs, K., Kirisits, T., Louis-Seize, G.W., Seifert, K.A., Sugita, T., Takematsu, A. and Wingfield, M.J. (2000). Epitypification of *Graphium penicillioides* corda, with comments on the phylogeny and taxonomy of graphium-like synnematosus fungi. *Studies in Mycology* 45: 169-186.
- Overton, B. E., Stewart, E. L., Geiser, D. M. and Jaklitsch, W. M. (2006). Systematics of *Hypocrea citrina* and related taxa. *Studies in Mycology* 56: 1-38.
- Paoletti, M., Rydholm, C., Schwier, E.U., Anderson, M.J., Szakacs, G., Lutzoni, F., Debeauvais, J.P., Latge, J.P., Denning, D.W. and Dyer, P.S. (2005). Evidence for sexuality in the opportunistic fungal pathogen *Aspergillus fumigatus*. *Current Biology* 15: 1242-1248.
- Paulin, A. and Harrington, T.C. (2000). Phylogenetic placement of anamorphic species of *Chalara* amongst *Ceratocystis* species and other ascomycetes. *Studies in Mycology* 45: 209-222.
- Paulin-Mahady, A.E., Harrington, T.C. and McNew, D. (2002). Phylogenetic and taxonomic evaluation of *Chalara*, *Chalaropsis*, and *Thielaviopsis* anamorphs associated with *Ceratocystis*. *Mycologia* 94: 62-72.
- Peever, T.L., Su, G., Carpenter-Boggs, L. and Timmer, L.W. (2004). Molecular systematics of citrus-associated *Alternaria* species. *Mycologia* 96: 119-134.
- Peever, T.L., Carpenter-Boggs, L., Timmer, L.W., Carris, L.M., and Bhatia, A. (2005). Citrus black rot is caused by phylogenetically distinct lineages of *Alternaria alternata*. *Phytopathology* 95: 512-518.
- Peever, T.L., Barve, M.P., Stone, L.J. and Kaiser, W.J. (2007). Evolutionary relationships among *Ascochyta* species infecting wild and cultivated hosts in the legume tribes *Cicereae* and *Vicieae*. *Mycologia* 99: 59-77.
- Pennycook, S.R. and Samuels, G.J. (1985). *Botryosphaeria* and *Fusicoccum* species associated with ripe fruit rot of *Actinidia deliciosa* (Kiwifruit) in New Zealand. *Mycotaxon* 24: 445-458.
- Phillips, A.J.L., Oudemans, P.V., Correia, A. and Alves, A. (2006). Characterisation and epitypification of *Botryosphaeria corticis*, the cause of blueberry cane canker. *Fungal Diversity* 21: 141-155.

- Phillips, A.J.L., Crous, P.W and Alves, A. (2007). *Diplodia seriata*, the anamorph of “*Botryosphaeria*” *obtusa*. *Fungal Diversity* 25: 141-155.
- Photita, W., Taylor, P.W.J., Ford, R., Lumyong, P., McKenzie, E.H.C. Hyde, K.D. and Lumyong, S., (2005). Morphological and molecular characterization of *Colletotrichum* species from herbaceous plants in Thailand. *Fungal Diversity* 18: 117-133.
- Pitt, J.I. and Samson, R.A. (1993). Species names in current use in the *Trichocomaceae*. In: *Names in current use in the families Trichocomaceae, Cladoniaceae, Pinaceae and Lemnaceae (NCU-2)* (ed. W. Greuter). *Reg Veg* 128: 13-57.
- Pringle, A., Baker, D.M., Platt, J.L., Wares, J.P., Latge, J.P. and Taylor, J.W. (2005). Cryptic speciation in the cosmopolitan and clonal human pathogenic fungus *Aspergillus fumigatus*. *Evolution* 59: 1886-1899.
- Pryor, B.M. and Bigelow, D.M. (2003). Molecular characterization of *Embellisia* and *Nimbya* species and their relationship to *Alternaria*, *Ulocladium* and *Stemphylium*. *Mycologia* 95: 1141-1154.
- Queiroz, K. de, and Gauthier, J. (1990). Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. *Systematic Zoology* 39: 307-322.
- Queiroz, K. de, and Gauthier, J. (1992). Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 23: 449-480.
- Queiroz, K. de, and Gauthier, J. (1994). Toward a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution* 9: 27-31.
- Queiroz, K. de (2006). The PhyloCode and the distinction between taxonomy and nomenclature. *Systematic Biology* 55: 160-162.
- Ratnasingham, S. and Hebert, P.D.N. (2007). BOLD: The Barcode of Life Data System. *Molecular Ecology Notes* 7: 355-364.
- Réblová, M. (1999a). Studies in *Chaetosphaeria sensu lato* I. The genera *Chaetosphaerella* and *Tengiomyces* gen. nov. of the *Helminthosphaeriaceae*. *Mycotaxon* 70: 387-420.
- Réblová, M. (1999b). Teleomorph-anamorph connections in Ascomycetes 3. Three new lignicolous species of *Helminthosphaeria*. *Sydowia* 51: 223-244.
- Réblová, M. (2000). The genus *Chaetosphaeria* and its anamorphs. *Studies in Mycology* 45: 149-168.
- Réblová, M. and Seifert, K.A. (2004). *Cryptadelphina* (*Trichosphaeriales*), a new genus for holomorphs with *Brachysporium* anamorphs and clarification of the taxonomic status of *Wallrothiella*. *Mycologia* 96: 343-367.
- Réblová, M. and Seifert, K.A. (2005). *Conioscyphascus*, a new ascomycetous genus for holomorphs with *Conioscypha* anamorphs. *Studies in Mycology* 50: 95-108.
- Réblová, M. and Seifert, K.A. (2007). A new fungal genus, *Teracosphaeria*, with a phialophora-like anamorph (*Sordariomycetes*, *Ascomycota*). *Mycological Research* 111: 287-298.
- Réblová, M. and Winka, K. (2000). Phylogeny of *Chaetosphaeria* and its anamorphs based on morphological and molecular data. *Mycologia* 92: 939-954.
- Réblová, M. and Winka, K. (2001). Generic concepts and correlations in ascomycetes based on molecular and morphological data: *Lecythothecium duriligni* gen. et sp. nov. with a *Sporidesmium* anamorph, and *Ascolacicola austriaca* sp. nov. *Mycologia* 93: 478-493.
- Réblová, M., Seifert, K.A. and White, G.P. (2006). *Chaetosphaeria tortuosa*, the newly discovered teleomorph of *Menispora tortuosa*, with a key to known *Menispora* species. *Mycological Research* 110: 104-109.
- Redecker, D. and Raab, P. (2006). Phylogeny of the *Glomeromycota* (arbuscular mycorrhizal fungi): recent developments and new gene markers. *Mycologia* 98: 885-895.

- Rehner, S.A. and Buckley, E. (2005). A *Beauveria* phylogeny inferred from nuclear ITS and EF1-alpha sequences: Evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97: 84-98.
- Rensburg, J.C.J. van, Lamprecht, S.C., Groenewald, J.Z., Castlebury, L.A., Crous, P.W. (2006). Characterisation of *Phomopsis* spp. associated with die-back of rooibos (*Aspalathus linearis*) in South Africa. *Studies in Mycology* 55: 65-74.
- Reynolds, D.R. (1993). The fungal holomorph: An overview. In: *The fungal holomorph: Mitotic, meiotic and pleomorphic speciation in fungal systematics* (eds. D.R. Reynolds and J.W. Taylor). CAB International, Oxon: 15-25.
- Reynolds, D.R. and Taylor, J.W. (eds.) (1993). *The fungal holomorph: Mitotic, meiotic and pleomorphic speciation in fungal systematics*. CAB International, Oxon.
- Rice, A.V. and Currah, R.S. (2005a). *Oidiodendron*: A survey of the named species and related anamorphs of *Myxotrichum*. *Studies in Mycology* 53: 83-120.
- Rice, A.V. and Currah, R.S. (2005b). Profiles from Biolog FF plates and morphological characteristics support the recognition of *Oidiodendron fimicola* sp. nov. *Studies in Mycology* 53: 75-82.
- Rieppel, O. (2006). The PhyloCode: A critical discussion of its theoretical foundation. *Cladistics* 22: 186-197.
- Roets, F., De Beer, Z.W., Dreyer, L.L., Zipfel, R., Crous, P.W. and Wingfield, M.J. (2006). Multi-gene phylogeny for *Ophiostoma* spp. reveals two new species from *Protea* infructescences. *Studies in Mycology* 55: 199-212.
- Rossmann, A.Y. (2000). Towards monophyletic genera in the holomorphic *Hypocreales*. *Studies in Mycology* 45: 27-34.
- Rossmann, A.Y., McKemy, J.M., Pardo-Schultheiss, R.A., Schroers, H.-J. (2001). Molecular studies of the *Bionectriaceae* using large subunit rDNA sequences. *Mycologia* 93: 100-110.
- Rossmann, A.Y., Samuels, G.J., Rogerson, C.T. and Lowen, R. (1999). Genera of *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* (*Hypocreales*, *Ascomycetes*). *Studies in Mycology* 42: 1-248.
- Saccone, C., Giorgi, C.D., Gissi, C., Pesole, G. and Reyes, A. (1999). Evolutionary genomics in Metazoa: the mitochondrial DNA as a model system. *Gene* 238: 195-209.
- Samson, R.A. and Frisvad, J.C. (eds.) (2004). *Penicillium* subgenus *Penicillium*: new taxonomic schemes, mycotoxins and other extrolites. *Studies in Mycology* 49: 1-257.
- Samson, R.A., Seifert, K.A., Kuijpers, A.F.A., Houbraken, J.A.M.P. and Frisvad, J.C. (2004). Phylogenetic analysis of *Penicillium* subgenus *Penicillium* using partial Beta-tubulin sequences. *Studies in Mycology* 49: 175-200.
- Samuels, G.J. (2006). *Trichoderma*: Systematics, the sexual state, and ecology. *Phytopathology* 96: 195-206.
- Samuels, G.J. and Singh, B. (1986). *Botryosphaeria xanthocephala*, cause of stem canker in pigeon pea. *Transactions of the British Mycological Society* 86: 295-299.
- Samuels, G.J., Candoussau, F. and Magni, J.F. (1997). Fungicolous pyrenomycetes 1. *Helminthosphaeria* and the new family *Helminthosphaeriaceae*. *Mycologia* 89: 141-155.
- Sanders, I.R., Alt, M., Groppe, K., Boller, T. and Wiemken, A. (1995). Identification of ribosomal DNA polymorphisms among and within spores of the *Glomales*: application to studies on the genetic diversity of arbuscular mycorrhizal fungal communities. *New Phytologist* 130: 419-427.

- Sanders, I.R., Clapp, J.P. and Wiemken, A. (1996). The genetic diversity of arbuscular mycorrhizal fungi in natural ecosystems – a key to understanding the ecology and functioning of the mycorrhizal symbiosis. *New Phytologist* 133: 123-134.
- Sanders, I.R., Koch, A. and Kuhn, G. (2003). Arbuscular mycorrhizal fungi: genetics of multigenomic, clonal networks and its ecological consequences. *Biological Journal of the Linnean Society* 79: 59-60.
- Saunders, G.W. (2005) Applying DNA barcoding to red macroalgae: a preliminary appraisal holds promise for future applications. *Philosophical Transactions of the Royal Society of London Series B* 360: 1879–1888.
- Schmidt, O. and Moreth, U. (2002). Data bank of rDNA-ITS sequences from building-rot fungi for their identification. *Wood Science and Technology* 36: 429-433.
- Schoch, C.L., Crous, P.W., Wingfield, M.J. and Wingfield, B.D. (2000). Phylogeny of *Calonectria* and selected hypocrealean genera with cylindrical macroconidia. *Studies in Mycology* 2000: 45-62.
- Schoch, C.L., Crous, P.W., Wingfield, B.D. and Wingfield, M.J. (2001). Phylogeny of *Calonectria* based on comparisons of Beta-tubulin DNA sequences. *Mycological Research* 105: 1045-1052.
- Schoch, C.L., Shoemaker, R.A., Seifert, K.A., Hambleton, S., Spatafora, J.W. and Crous, P.W. (2006). A multigene phylogeny of the *Dothideomycetes* using four nuclear loci. *Mycologia* 98: 1041-1052.
- Schroers, H.-J. (2000). Generic delineation of *Bionectria* (*Bionectriaceae*, *Hypocreales*) based on holomorph characters and rDNA sequences. *Studies in Mycology* 45: 63-82.
- Schroers, H.-J. (2001). A monograph of *Bionectria* (*Ascomycota*, *Hypocreales*, *Bionectriaceae*) and its *Clonostachys* anamorphs. *Studies in Mycology* 2001: 1-211.
- Schüßler, A., Schwarzott, D. and Walker, C. (2001). A new fungal phylum, the *Glomeromycota*: phylogeny and evolution. *Mycological Research* 105: 1413-1421.
- Scorzetti, G., Fell, J. W., Fonseca, A. and Statzell-Tallman, A. (2002). Systematics of basidiomycetous yeasts: a comparison of large subunit D1/D2 and internal transcribed spacer rDNA regions. *FEMS Yeast Research* 1497: 1-23.
- Seifert, K.A. and Samuels, G.J. (2000). How should we look at anamorphs? *Studies in Mycology* 45: 5-18.
- Seifert, K.A. and Gams, W. (2001). The taxonomy of anamorphic fungi. In: *The Mycota*. Vol. VII (A). *Systematics and Evolution* (eds. D.J. McLaughlin, E.G. McLaughlin and P.A. Lemke), Springer-Verlag, Berlin: 307-347.
- Seifert, K.A., Gams, W., Crous, P.W. and Samuels, G.J. (2000a). Molecules, morphology and classification: towards monophyletic genera in the Ascomycetes. *Studies in Mycology* 45: 1-4.
- Seifert, K.A., Gams, W., Crous, P.W. and Samuels, G.J. (eds.) (2000b). Molecules, morphology and classification: towards monophyletic genera in the Ascomycetes. *Studies in Mycology* 45: 1-231.
- Seifert, K.A., Samson, R.A., deWaard, J.R., Houbraken, J., Lévesque, C.A., Moncalvo, J., Louis-Seize, G. and Hebert, P.D.N. (2007). Prospects for fungus identification using COI DNA barcodes, with *Penicillium* as a test case. *Proceedings of the National Academy of Sciences of the United States of America* 104: 3901–3906.
- Shearer, C.A., Raja, H.A. and Schmit, J.P. (2007). Freshwater Ascomycetes and their anamorphs - website available online at <http://www.life.uiuc.edu/fungi/>
- Shenoy, B.D., Jeewon, R. and Hyde, K.D. (2005). *Oxydothis bambusicola*, a new ascomycete with a huge subapical ascus ring found on bamboo in Hong Kong. *Nova Hedwigia* 80: 511–518.

- Shenoy, B.D., Jeewon, R., Wu, W.P., Bhat, D.J. and Hyde, K.D. (2006). Ribosomal and RPB2 DNA sequence analyses suggest that *Sporidesmium* and morphologically similar genera are polyphyletic. *Mycological Research* 110: 916-928.
- Shoemaker, R.A. and Hambleton, S. (2001). "Helminthosporium" asterinum, *Polydesmus elegans*, *Imimyces*, and allies. *Canadian Journal of Botany* 79: 592-599.
- Sinclair, R.C., Eicker, A. and Bhat, D.J. (1985). Branching in *Spadicoides*. *Transactions of the British Mycological Society* 85: 736-738.
- Sivanesan, A. (1984). *The Bitunicate Ascomycetes and their Anamorphs*. Strauss and Cramer, Vaduz, Germany.
- Sivichai, S. and Jones, E.B.G. (2003). Teleomorphic-anamorphic connections of freshwater fungi. *Fungal Diversity Research Series* 10: 259-272.
- Slippers, B., Crous, P.W., Denman, S., Coutinho, T.A., Wingfield, B.D. and Wingfield, M.J. (2004). Combined multiple gene genealogies and phenotypic characters differentiate several species previously identified as *Botryosphaeria dothidea*. *Mycologia* 96: 83-101.
- Slot, S. and Hibbett, D.S. (2007). Teaching the Fungal Tree of Life. URL: <http://www.clarku.edu/faculty/dhibbett/TFTOL>
- Smith, M.A., Fisher, B.L. and Hebert, P.D.N. (2005). DNA barcoding for effective biodiversity assessment of a hyperdiverse arthropod group: the ants of Madagascar. *Philosophical Transactions of the Royal Society of London Series B* 360: 1825-1834.
- Spatafora, J.W., Sung, G.H., Johnson, D., Hesse, C., O'Rourke, B., Serdani, M., Spotts, R., Lutzoni, F., Hofstetter, V., Miadlikowska, J., Reeb, V., Gueidan, C., Fraker, E., Lumbsch, T., Lücking, R., Schmitt, I., Hosaka, K., Aptroot, A., Roux, C., Miller, A.N., Geiser, D.M., Hafellner, J., Hestmark, G., Arnold, A.E., Büdel, B., Rauhut, A., Hewitt, D., Untereiner, W.A., Cole, M.S., Scheidegger, C., Schultz, M., Sipman, H. and Schoch, C.L. (2006). A five-gene phylogeny of *Pezizomycotina*. *Mycologia* 98: 1018-1028.
- Sreenivasaprasad, S., Mills, P.R., Meehan, B.M. and Brown, A.E. (1996). Phylogeny and systematics of 18 *Colletotrichum* species based on ribosomal DNA spacer sequences. *Genome* 39: 499-512.
- Subramanian, C.V. (1962). The classification of the hyphomycetes. *Bulletin of the Botanical Survey of India* 4: 249-259.
- Subramanian, C.V. (1971). *Hyphomycetes*. Indian Council of Agricultural Research. New Delhi, India: 1-930.
- Subramanian, C.V. (1983). *Hyphomycetes: taxonomy and biology*. Academic Press, London.
- Subramanian, C.V. (1992). A reassessment of *Sporidesmium* (hyphomycetes) and some related taxa. *Proceedings of Indian National Science Academy B* 58: 179-190.
- Subramanian, C.V. and Sekar, G. (1989) (1987). Three bitunicate ascomycetes and their anamorphs. *Kavaka* 15: 87-98.
- Sugiyama, J. (ed.) (1987). *Pleomorphic Fungi: The diversity and its taxonomic implications*. Kodansha Ltd., Tokyo: 1-325.
- Sugiyama, J., Hosaka, K. and Suh, S.O. (2006). Early diverging Ascomycota: phylogenetic divergence and related evolutionary enigmas. *Mycologia* 98: 996-1005.
- Suh, S.O., Blackwell, M., Kurtzman, C.P. and Lachance, M.A. (2006). Phylogenetics of *Saccharomycetales*, the ascomycete yeasts. *Mycologia* 98: 1006-1017.
- Summerell, B.A., Groenewald, J.Z., Carnegie, A.J., Summerbell, R.C. and Crous, P.W. (2006). *Eucalyptus* microfungi known from culture. 2. *Alysidiella*, *Fusculina* and *Phlogicylindrium* genera nova, with notes on some other poorly known taxa. *Fungal Diversity* 23: 323-350.

- Sutton, B.C. (1973). Coelomycetes. In: *The fungi: An advanced treatise*. Vol. IVA. A taxonomic review with keys: *ascomycetes and fungi imperfecti* (eds. G.C. Ainsworth, F.K. Sparrow and A.S. Sussman). Academic Press, New York: 513-582.
- Sutton, B.C. (1980). *Coelomycetes - Fungi Imperfecti with pycnidia, acervuli and stromata*. Commonwealth Mycological Institute, Kew, Surrey, England.
- Sutton, B.C. (1992). The Genus *Glomerella* and its anamorph *Colletotrichum*. In: *Colletotrichum: biology, pathology and control* (eds. J.A. Bailey and M.J. Jeger). CAB International, Wallingford: 1-26.
- Sutton, B.C. and Hennebert, G.L. (1994). Interconnections amongst anamorphs and their possible contribution to ascomycete systematics. In: *Ascomycete Systematics: problems and perspectives in the nineties* (ed. D.L. Hawksworth). Plenum Press, New York: 77-100.
- Talbot, P.H.B. (1971). *Principles of Fungal Taxonomy*. The Macmillan Press, London: 1- 274.
- Tavanti A., Gow, N.A.R., Maiden, C.J., Odds, F.C. and Shaw, D.J. (2004). Genetic evidence for recombination in *Candida albicans* based on haplotype analysis. *Fungal Genetics and Biology* 41: 553-562.
- Taylor, J.W., Jacobson, D. and Fisher, M. (1999). The evolution of asexual fungi: reproduction, speciation and classification. *Annual Review of Phytopathology* 37: 197-246.
- Taylor, J.W. and Berbee, M.L. (2006). Dating divergences in the Fungal Tree of Life: review and new analyses. *Mycologia* 98: 838-849.
- The Anamorph-Teleomorph database, (2007): An online database maintained by Centraalbureau voor Schimmelcultures (CBS), available at www.cbs.knaw.nl/databases
- Tsui, C.K.M. and Berbee, M.L. (2006). Phylogenetic relationships and convergence of helicosporous fungi inferred from ribosomal DNA sequences. *Molecular Phylogenetics and Evolution* 39: 587-597.
- Tsui, C.K.M., Berbee, M.L., Jeewon, R. and Hyde, K.D. (2006a). Molecular phylogeny of *Dictyosporium* and allied genera inferred from ribosomal DNA. *Fungal Diversity* 21: 157-166.
- Tsui, C.K.M., Sivichai, S. and Berbee, M. (2006b). Molecular systematics of *Helicoma*, *Helicomycetes* and *Helicosporium* and their teleomorphs inferred from rDNA sequences. *Mycologia* 98: 94-104.
- Tubaki, K. (1958). Studies on the Japanese Hyphomycetes V. Leaf & Stem Group with a discussion of the classification of Hyphomycetes and their perfect states. *Journal of the Hattori Botanical Laboratory* 20: 142-244.
- Tubaki, K. (1981). *Hyphomycetes – their perfect-imperfect connexions*. J. Cramer, Vaduz: 1-181.
- Tzung K.-W., Williams, R.M., Scherer, S. Federspiel, N., Jones, T., Hansen, N., Bivolarevic, V., Huizar, L., Komp, C., Surzycki, R., Tamse, R., DavisDagger, R.W. and Agabian, N. (2001). Genomic evidence for a complete sexual cycle in *Candida albicans*. *Proceedings of the National Academy of Sciences of the United States of America* 98: 3249-3253.
- Van Wyk, M., Roux, J., Barnes, I., Wingfield, B.D. and Wingfield, M.J. (2006). Molecular phylogeny of the *Ceratocystis moniliformis* complex and description of *C. tribiliformis* sp. nov. *Fungal Diversity* 21: 181-201.
- Vaughan-Martini, A., Kurtzman, C.P., Meyer, S.A. and O'Neill, E.B. (2005). Two new species in the *Pichia guilliermondii* clade: *Pichia caribbica* sp. nov., the ascosporic state of *Candida fermentati*, and *Candida carpophila* comb. nov. *FEMS Yeast Research*. 5: 463-469.

- Verkley, G.J.M. (1999). A monograph of the genus *Pezicula* and its anamorphs. *Studies in Mycology* 44: 1-162.
- Verkley, G.J.M. and Priest, M.J. (2000). *Septoria* and similar coelomycetous anamorphs of *Mycosphaerella*. *Studies in Mycology* 43: 123-128.
- Vijaykrishna, D., Mostert, L., Jeewon, R., Gams, W., Hyde, K.D. and Crous, P.W. (2004). *Pleurostomophora*, an anamorph of *Pleurostoma* (*Calosphaeriales*), a new anamorph genus morphologically similar to *Phialophora*. *Studies in Mycology* 50: 387-395.
- Vijaykrishna, D., Jeewon, R. and Hyde, K.D. (2006). Molecular taxonomy, origins and evolution of freshwater ascomycetes. *Fungal Diversity* 23: 351-390.
- Wainright, P.O., Hinkle G., Sogin, M.L. and Stickel, S.K. (1993). Monophyletic origins of the Metazoa: "an evolutionary link with fungi". *Science* 260: 340-342.
- Walther, G., Garnica, S. and Weiß, M. (2005). The systematic relevance of conidiogenesis modes in the gilled *Agaricales*. *Mycological Research* 109: 525-544.
- Wang, C.J.K. (1976). *Spadicoides* in New York. *Memoirs of the New York Botanical Garden* 28: 218-224.
- Wang, C.J.K. and Sutton, B.C. (1982). New and rare lignicolous hyphomycetes. *Mycologia* 74: 489-500.
- Wang, Z., Johnston, P.R., Takamatsu, S., Spatafora, J.W. and Hibbett, D.S. (2006). Toward a phylogenetic classification of the *Leotiomycetes* based on rDNA data. *Mycologia* 98: 1065-1075.
- Ward, R.D., Zemplak, T.S., Innes, B.H., Last, P.R. and Hebert, P.D.N. (2005). Barcoding Australia's fish species. *Philosophical Transactions of the Royal Society of London B* 360: 1847-1857.
- Ware, S.B., Verstappena, E.C.P., Breedenc, J., Cavaletto, J.R., Goodwin, S.B., Waalwijk, C., Crous, P.W. and Kema, G.H.J. (2007). Discovery of a functional *Mycosphaerella* teleomorph in the presumed asexual barley pathogen *Septoria passerinii*. *Fungal Genetics and Biology* 44: 389-397.
- Webster, J. (1992). Anamorph-teleomorph relationships. In: *The Ecology of Aquatic Hyphomycetes* (ed. F. Bärlocher). Springer-Verlag, Berlin: 99-117.
- Weresub, L.K. and Hennebert, G.L. (1979). Anamorph and teleomorph: terms for organs of reproduction rather than karyological phases. *Mycotaxon* 8: 181-186.
- Wheeler DL, Chappey C, Lash AE, Leipe DD, Madden TL, Schuler GD, Tatusova TA, Rapp BA (2000). Database resources of the National Center for Biotechnology Information. *Nucleic Acids Research* 28:10-14.
- Wheeler, Q.D. (2004). Taxonomic triage and the poverty of phylogeny. *Philosophical Transactions of the Royal Society of London Series B* 359: 571-583.
- White, M.W., James, T.Y., O'Donnell, K., Cafaro, M.J., Tanabe, Y. and Sugiyama, J. (2006). Phylogeny of the *Zygomycota* based on nuclear ribosomal sequence data. *Mycologia* 98: 872-884.
- White, T.J., Bruns, T.D., Lee, S. and Taylor, J.W. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: A Guide to Methods and Applications* (eds. M.A. Innis, D.H. Gelfand, J. Sninsky and T.J. White). Academic Press, San Diego: 315-322.
- Whittaker, R.H. (1969). New concepts of kingdoms of organisms. *Science* 163: 150-160.
- Wingfield, B.D., Viljoen, C.D. and Wingfield, M.J. (1999). Phylogenetic relationships of ophiostomatoid fungi associated with *Protea infructescences* in South Africa. *Mycological Research* 103: 1616-1620.
- Wu, W.P. and Zhuang, W. (2005). *Sporidesmium*, *Endophragmiella* and related genera from China. *Fungal Diversity Research Series* 15: 1-351.

- Zhang, N., Castlebury, L.A., Miller, A.N., Huhndorf, S.M., Schoch, C.L., Seifert, K.A., Rossman, A.Y., Rogers, J.D., Kohlmeyer, J., Volkmann-Kohlmeyer, B. and Sung, G.H. (2006). An overview of the systematics of the *Sordariomycetes* based on a four-gene phylogeny. *Mycologia* 98: 1076-1087.
- Zhao, G.Z., Liu, X.Z. and Wu, W.P. (2007). Helicosporous hyphomycetes from China. *Fungal Diversity* 26: 313-524.
- Zhou, S. and Stanosz, G.R. (2001). Relationships among *Botryosphaeria* species and associated anamorphic fungi inferred from the analyses of ITS and 5.8S rDNA sequences. *Mycologia* 93: 516-527.
- Zhou, X., De Beer, Z.W., Cibrian, D., Wingfield, B.D. and Wingfield, M.J. (2004). Characterisation of *Ophiostoma* species associated with pine bark beetles from Mexico, including *O. pulvinisporum* sp. nov. *Mycological Research* 108: 690-698.
- Zhou, X., De Beer, W.Z. and Wingfield, M.J. (2006). DNA sequence comparisons of *Ophiostoma* spp., including *Ophiostoma aurorae* sp. nov., associated with pine bark beetles in South Africa. *Studies in Mycology* 55: 269-277.
- Zhu, P., Ge, Q., Xu, T. (1991). The perfect stage of *Pestalosphaeria* from China. *Mycotaxon* 50: 129-140.
- Zipfel, R.D., De Beer, Z.W., Jacobs, K., Wingfield, B.D. and Wingfield, M.J. (2006). Multi-gene phylogenies define *Ceratocystiopsis* and *Grosmannia* distinct from *Ophiostoma*. *Studies in Mycology* 55: 75-97.

(Received 30 May 2007; accepted 25 June 2007)