How should we look at anamorphs?

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Abstract: Biological, taxonomic and nomenclatural aspects of anamorphs in the Ascomycetes are considered. Anamorphs serve dispersive or survival functions in ascomycete life cycles. Some are narrowly or broadly distributed, reproductively isolated clones, derived from sexually competent populations. Strictly asexually reproducing lineages probably occur, although cryptic sexuality has now been demonstrated for some 'anamorphic species'. Some anamorphic species are apparently hybrids between known sexually or asexually reproducing species. Anamorphs are phenotypes that can be interpreted as organs produced as part of a fungal life cycle. Examples of morphological continua among anamorphs of closely related holomorphs argue against the sometimes arbitrary tendency to emphasize certain features as 'anamorph generic characters'. Synanamorphs can be categorized as mononematous, conidiomatal, mycelial, germination, survival, yeast-like, spermatial and vegetative anamorphs, which may represent expressions of different sets of genes and thus not always be homologous. Fungal taxonomy should move towards unit nomenclature, but we believe that anamorphic taxonomic names will still be used in some form in this taxonomic system.

Key words: pleomorphic fungi, synanamorphs, nomenclature, morphological systematics, clonal populations, hybridization.

Introduction

Most ascomycetes produce anamorphs. This simple fact has preoccupied mycologists for nearly 200 years and has stimulated many debates on how these structures should be interpreted biologically, taxonomically and nomenclaturally. The temptation to treat anamorphs in a uniform, pigeon-hole fashion is understandable, but the structures identified by this term arise by diverse biological mechanisms. We hope to show that there are different kinds of anamorphs, different genetic and evolutionary mechanisms that have led to anamorph speciation, and several patterns of relationships between anamorphs and teleomorphs. The sometimes academic arguments over anamorphs and their taxonomy have practical consequences, affecting identification keys, the most appropriate name and hence classification of a taxon, and nomenclatural stability.

The independent taxonomy of anamorphic fungi was established in the founding works of Tode, Persoon, Link, Fries, Corda and others, who gave Latin names to these morphs. Fuckel (1870) proposed the Fungi Imperfecti as a taxonomic class for these asexual organisms, a suggestion subsequently adopted by Saccardo in the *Sylloge Fungorum*. The link between asexual and sexual fungi was described more than 150 years ago when deBary (1854) proved the association between *Aspergillus glaucus* Link and a sexual fungus, *Eurotium herbariorum* (Wiggers) Link. Tulasne & Tulasne (1863) illustrated the physical link between perithecia and conidiophores through common mycelia. Thirty years later, Brefeld & von Tavel (1891) cultivated ascospores of a diversity of fungi and described the conidia developing in cultures. Thus, it was clear from an early time that at least some asexual fungi belong to life cycles that

include sexual reproduction. However, mycologists chose to maintain a system of 'dual nomenclature', in which separate generic and species names were allowed for the sexual and asexual form(s) of one species. This has been a persistent concept, despite the fact that it violates Principle IV of the International Code of Botanical Nomenclature (the *Code*) that each organism should have only one scientific name. The utility of binomial nomenclature reflects the fact that asexual fungi are a large proportion of known fungi, as well as the difficulties inherent in experimentally proving anamorph–teleomorph connections. Rossman (this volume) has estimated that teleomorphs are unknown for approximately 50% of the fungi associated with plants in the United States. This alone suggests that anamorph names will be used in mycology long into the future, although within the last decade, nucleic acid sequences have been used to integrate presumably asexual fungi into teleomorph taxonomy at the order (e.g. Glenn *et al.*, 1996), family (e.g. Rehner & Samuels, 1995), genus (e.g. Berbee & Taylor, 1992; LoBuglio & Taylor, 1993) and species (e.g. Kuhls *et al.*, 1996) levels.

Anamorphs and terminology

The terminology applied to what we now call anamorphs (both as taxonomic entities and for their constituent parts) has never been particularly stable. Today, two terminological systems are widely used, the 'morph' terminology (*holomorph, teleomorph, anamorph*) recommended by the *Code* and the 'karyological' terminology (*meiosporic* or *meiotic* state, *mitosporic* or *mitotic* state) used in the 8th edition of the *Dictionary of the Fungi* (Hawksworth *et al.*, 1995), and advocated by those who consider the 'morph' terminology confusing or inadequate.

Although early definitions of 'anamorph' led to some confusion, the present wording of the *Code* overcomes most ambiguities. In fact, Article 59.1 of the Tokyo *Code* (Greuter *et al.*, 1994) considered the 'morph' and 'karyological' sets of terms identical, using one to define the other. Hennebert and Weresub (1979) defined anamorphs as every part of the life cycle exclusive of the site of actual nuclear fusion; this included any asexual propagules but also the mycelium and tissue of the ascoma. In practice, the term anamorph has been used to refer to dehiscent or indehiscent, asexually produced propagules and the structures that form them. In a generalized life cycle, the sexual spore germinates to produce the mycelium from which asexual propagules form, and the process repeats itself. Because of the irregularity of these events, terminology based on 'stage' or

'phase' in connection with 'sexual' and 'asexual' has now been deliberately abandoned. Hennebert (1987) refined the terms *anamorph* and *synanamorph* to refer to "reproductive, propagative, or vegetative organs recognized by the morphological and morphogenetic characters used as criteria in the taxonomy of the Deuteromycotina".

The recently introduced karyological terminology appears to have arisen out of a misinterpretation of the morph terminology. The term *pleomorphy* is used by mycologists to refer to a multiplicity of forms, by convention usually different modes of sporulation. Reynolds and Taylor (1993) and Sutton (1993) suggested that use of *pleoanamorphy* implied the existence of a known teleomorph. By extension, use of *anamorph* was considered to imply the existence of a known teleomorph. According to this logic, *anamorph* should not be used for fungi lacking teleomorphs. From this perspective, the karyological terminology was designed for those fungi lacking known teleomorphs, for which the *morph* terminology was considered inadequate. The proponents of the karyological terminology also felt that the relationship to well-known karyological events (meiosis and mitosis) would make the terminology more accessible to students and other biologists familiar with Eukaryotes. Thus, morph-based terms with the prefix *conidi-* were replaced with terms based on the prefix *mitosporo-*, hence *mitosporophore* for *conidiophore*, *mitosporogenous cell* for *conidiogenous cell*, and *mitospore* for *conidium*. Although these descriptive terms have rarely been used, the form taxon 'Mitosporic Fungi' is now seen with some frequency.

We consider the karyological terminology superfluous, at least for taxonomic purposes, given the equivalence with morph terminology implied in article 59.1. The term anamorph was never intended to be applied exclusively to fungi with known teleomorphs, neither by Hennebert & Weresub (1979) nor by the *Code*. In our opinion, use of *both* sets of terms involves karyological assumptions (that particular spores are produced by meiosis, for example) that have usually not been proven. The form taxon 'Mitosporic fungi' is equivalent to all other names applied to these fungi (i.e. Fungi Imperfecti, Deuteromycetes, Anamorphic Fungi). Continued use of the now well-established *morph*-based terminology will remind us that teleomorphs and anamorphs are ultimately both morphologically defined phenotypes, and subsets of what taxonomists presume to classify, i.e. the genome.

Anamorphs and life cycles

Teleomorphs and anamorphs both produce propagules that perpetuate the life cycle of individuals, but meiotically and mitotically produced propagules have different roles. Ascospores normally result from outcrossing and perpetuate parental genes rearranged into new genotypes. Conidia usually disseminate carbon copies of the parental genome, and the resulting individuals are generally assumed to be clonal. Both types of spores are dispersed and then compete in the environment. Conidia are often produced in great quantities, saturating particular environments for which they may be perfectly adapted. The formation of such anamorphs is not unique to Ascomycetes; Zygomycetes, 'phycomycetes', rusts, smuts, hetero- and (less so) homobasidiomycetes often produce iterative organs. Taxonomic conventions in these groups have discouraged the proposal of additional taxonomic names for their anamorphs. Because asexual organs of ascomycetes can be conspicuous and are often found apart from sexual organs, they are often given formal Latin names.

There is little data about the timing of conidial formation outside of temperate and boreal regions; even there, most information is based on random collections rather than experimental studies. Many temperate, saprobic ascomycetes produce ascomata in dead plant material and have viable ascospores in the autumn. Ascospores germinate and colonize the dead substratum and the mycelium produces conidia in the spring, cycling through a number of anamorphic generations before ascospore production occurs again the following autumn. In other fungi, particularly plant pathogens, ascospore production coincides with new growth of the host plant, ensuring that new genotypes produced by outcrossing are ready to infect newly emerging host tissue. For example, ascospores of *Monilinia fructicola* (Winter) Honey are discharged in the spring from apothecia that develop from soil-borne sclerotia, infecting young twigs and leaves of stone fruit. Conidia that develop from the infected tissue initiate a secondary infection in flowers that ultimately spreads to fruit and other twigs (Alexopoulos *et al.*, 1996).

Anamorphs generally serve to disperse or ensure the survival of one genotype. Most asexual propagules (i.e. conidia) are dispersed by wind, water, animals or by host movements and serve to restart the life of an individual genotype in a physically different place. Distribution can be local or intercontinental or both. Survival anamorphs, such as sclerotia, thick-walled chlamydospores or aleuriospores, transmit the genotype through time, sometimes persisting for years in soil. Asexually derived propagules also sometimes act as spermatizing agents and are necessary for outcrossing (e.g. cladorrhinum-like microconidia of species of *Neurospora* Shear & B. Dodge, Alexopoulos *et al.*, 1996; sphacelia-like and *Ephelis* Fr. conidia of some balansioid ascomycetes, Bultman & White, 1988; Bultman *et al.*, 1998, see also White *et al.*, this volume). In some fungi, conidia serve a dual role as spermatizing agents and dispersive agents, for example, in some species of *Fusarium* Link (Klittich & Leslie, 1988; Kuhlman, 1982).

In axenic culture, anamorphs generally form more readily than teleomorphs. In cultures of ascomycetous fungi, one often observes less complex anamorphs than occur in nature. Conidiomata are often poorly formed on conventional agar media, reduced to conidiogenous cells on simple, nonaggregated conidiophores [e.g. the 'free-form' cultural anamorph produced in cultures of *Tubercularia lateritia* (Berk.) Seifert illustrated by Seifert 1985]. What is observed in these cultures can be regarded as cultural anamorphs, although improved cultivation techniques may bring the anamorph closer to its wild-type form (cf. the concept of "Hochkultur" in *Fusarium*). There is a widespread assumption that at least some anamorphs are cultural manifestations that do not occur in nature. An alternative explanation is that simple cultural phenotypes are genetically distinct from the phenotypes commonly observed in nature. For example, species of *Epichloë* (Fr.) Tul. produce an acremonium-like anamorph, *Neotyphodium* Glenn, Bacon & Hanlin in culture, which is sometimes interpreted as a cultural expression of the stromatic sphacelia-like anamorph found in nature on grass culms, causing the characteristic 'choke' symptoms. However, it is now known that *Neotyphodium* conidiophores and conidia form on grass leaves in nature (White *et al.*, 1996; this volume). The so-called black yeasts, including species of *Aureobasidium* Viala & Boyer, *Hormonema* Lagerb. & Melin and *Exophiala* Carmichael, are commonly assumed to be cultural anamorphs. The pleoanamorphy of many of these species (see Untereiner, this volume) suggests the possibility that each form of sporulation occurs in a particular niche. Could some apparently cultural anamorphs, produced on agar media with relatively high water activity, be found in water-saturated environments such as submerged organic material?

Anamorphs and phylogeny

ANAMORPH SPECIATION

Mycologists have often asked whether we can assume that a species is strictly asexual simply because

sexual reproduction has not been directly observed. The recent discovery of the *Microascus* Zukal teleomorph of the very common mould *Scopulariopsis brevicaulis* (Sacc.) Bainier by Abbott *et al.* (1998), suggests that mating experiments need to be tried more routinely before we declare a fungus completely anamorphic. Studies of the population genetics of apparently clonal fungal species reveal allelic frequencies that can be explained by infrequent recombination and the subsequent development of new genotypes (see Taylor *et al.*, 1999; Geiser *et al.*, 1998; Gordon & Martyn, 1997). This phenomenon has been referred to as cryptic sexuality. For example, Geiser *et al.* (1998) found genetic diversity in populations of the presumably asexual *Aspergillus flavus* Link that could only be explained by recombination in nature, although that recombination was not necessarily sexual. There appears to be a gradation from outcrossing organisms that have both ascomata and conidia in more or less equal proportion, through those that undergo sexual outcrossing infrequently, to those that may be undergoing recombination through some means other than sex. For example, Leslie & Klein (1996) have estimated that different species within the *Gibberella fujikuroi* (Sawada) Wollenw. clade have ratios of sexual:asexual generations varying from 1:15 to 1:2300. Apparently strictly anamorphic species appear in the same clade (O'Donnell *et al.*, 1998). That these diverse reproductive strategies exist in single clades suggests that genetic mechanisms occur in the ascomycetes that favour the development of new clonal lines that diverge from their parent, sexually competent lineages. *Trichoderma reesei* E. G. Simmons has been considered a possible clonal derivative of *Hypocrea jecorina* Berk. & Broome, a common tropical fungus (Kuhls *et al.*, 1996). It has never been observed to produce perithecia in culture, whereas perithecia form readily in cultures of *H. jecorina* when colonies of the appropriate mating type are paired (Lieckfeldt *et al.*, 2000). So far, there is little evidence for ancient anamorphic lineages, and most studies of monophyletic groups suggest that anamorphic lineages have been derived by independent teleomorph losses (e.g. LoBuglio & Taylor, 1993).

In general, the geographic distribution of the constituent morphs of a holomorph coincide, that is, if the anamorph is widely dispersed, so too is the teleomorph. Increasingly, examples of geographically limited teleomorphs are coming to light that have more widely distributed anamorphs (Table 1). Discordant geographic distribution of morphs is an aspect of the biogeography of species that has rarely been considered. These distribution patterns may simply indicate a shortage of collections of teleomorphs that may be produced in very specific environments in narrow time frames. However, well-adapted genotypes (especially pathogens) can quickly spread over vast geographical distances by anamorphic propagation and this type of episodic selection can quickly lead to speciation, for example when single mating types are introduced into new environments (Brasier, 1995). Several well-known species of *Curvularia* Boedijn apparently consist only of single mating types, phylogenetically separated from their *Cochliobolus* Drechsler progenitors and representing truly anamorphic species (Turgeon, 1998). Populations that were originally anamorphic clones might diversify and become something akin to inverse biological species, defined by an absence of mating with other species. Evolutionary theory suggests these isolated asexual populations will accumulate lethal mutations during asexual reproduction. However, we cannot preclude parasexual genetic mechanisms for allowing widespread genetic exchange within anamorph species and for stabilizing their genomes.

One other type of anamorphic speciation has now been convincingly demonstrated. Some species of the anamorph genus *Neotyphodium* are apparently truly asexual, having arisen through hybridization of sexual *Epichloë* species (Tsai *et al.*, 1994; Schardl *et al.*, 1994). This was suspected first through the appearance of multiple electromorphs of certain proteins in isozyme analyses, then confirmed through the sequencing of the multiple copies of some protein coding genes (mostly β-tubulin) in these anamorphic species. Individual copies have sequences identical with those of known, sexually competent, ancestral *Epichloë* species. The anamorphic species presumably cannot recombine because their ploidy levels prevent successful mating with their parent species. Similarly, a speciation event from the hybridization of the anamorphic fungi *Verticillium albo-atrum* Reinke & Berthold and *V. dahliae* Kleb., yielding *V. longisporum* (Stark) Karapapa *et al.*, has been demonstrated by Karapapa *et al.* (1997). It is intriguing to speculate how common this type of speciation might be. Reevaluation of isozyme studies of anamorphic fungi from the past decades may reveal clues as to whether anamorphic speciation by hybridization is a common event in the ascomycetes.

ANAMORPH CHARACTER PATTERNS

The phylogenetic position of an anamorphic fungus can sometimes be predicted based upon already demonstrated trends in the ascomycetes. Most ascomy-

Table 1. Examples of fungi with broadly occurring anamorphs and teleomorphs with a restricted distribution.

Holomorph	Teleomorph distribution	Anamorph	Anamorph distribution	Reference
Bisporella resinicola (Baranyay & Funk) Carpenter & Seifert	Pacific northwest of N. America	*Eustilbum aureum* (Pers.) Seifert & Carpenter	North temperate	Seifert & Carpenter, 1987
Nectria stilbellae Samuels & Seifert	tropical America	*Stilbella aciculosa* (Ellis & Everhart) Seifert	North temperate	Samuels & Seifert, 1991
Hypocrea schweinitzii (Fr.) Sacc.	Europe, N. America	*Trichoderma citrinoviride* Bissett	Europe, N & S America, SE Asia	Turner *et al.*, 1997
powdery mildews	temperate	various genera	tropical & temperate	Yarwood, 1957
Mycosphaerella suttoniae Crous & M.J. Wingf.	Indonesia, South Africa	*Phaeophleospora epicoccoides* (Cooke & Massee) Crous et al.	Cosmopolitan	Crous, 1998
Epichloë spp.	temperate	*Neotyphodium* spp.	temperate & tropical	White *et al.*, this volume

cetes produce conidia that are colourless and unicellular. Such conidia, generally speaking, are not phylogenetically informative. However, conidia can also be lightly pigmented to heavily melanized; they come in a wide diversity of forms, each apparently adapted to a particular environment or niche. Pigmentation of conidia and/or conidiophores can indicate possible relationships and eliminate others (e.g. darkly pigmented conidia are unlikely to occur in the *Hypocreales* or *Clavicipitales*, hyaline conidiophores are unexpected in the *Chaetosphaeriaceae*). Conidial form sometimes mimics ascospore form (Müller, 1973). This occurs in cases where neither ascospore nor conidium are morphologically exceptional (e.g. species of *Botryosphaeria* Ces. & De Not. with *Fusicoccum* Corda anamorph, see Denman *et al.*, this volume), as well as more fungi with more complex spores [e.g. *Broomella vitalbae* (Berk. & Broome) Sacc. with a *Truncatella* Steyaert anamorph, see Müller, 1973].

The form of morphologically simple conidiophores is often not phylogenetically informative. Conidiophores may bear single conidiogenous cells (e.g. *Acremonium* Link, *Phialophora* Medlar, *Sporothrix* Hektoen), terminal clusters of conidiogenous cells (e.g. *Penicillium* Link, *Gliocladium* Corda, *Trichoderma* Pers.), or conidiogenous cells along the length in some sort of a whorl (e.g. *Verticillium* Nees, *Zanclospora* S. Hughes & W.B. Kendr.). Pigmentation of conidiophores and the type of conidiogenesis can be more or less predictive. Combined attributes of the conidiophore (pigmentation, wall thickening, branching pattern), conidiogenesis and the conidia tend to be conserved within clades. For example, conidia of the *Hypocreales* are brightly or lightly coloured, typically develop from phialides and are held in wet masses, whereas conidia and/or conidiophores of the *Xylariales* are pigmented, dry and develop holoblastically. Conidia of the *Eurotiales* (e.g. *Penicillium, Aspergillus*) are connected to each other in persistant chains (Subramanian, 1971; Gams, 1978).

The presence of conidiomata, once considered worthy of form-family rank, is now widely discounted in anamorph taxonomy because of the occurrence of mononematous and conidiomatal anamorphs in closely related groups of holomorphs. Many anamorph genera include species with a variable degree of aggregation of conidiophores in nature, independent of any suboptimal development in culture. For example, the conidiophores of species of *Clonostachys* Corda show a continuum between truly mononematous, scattered arrangements to sporodochia with basal stromata (Schroers, this volume). The example of *Tubercularia* Tode, including species

with conidiomata varying from pycnidial to sporodochial to synnematous was discussed by both Samuels & Seifert (1987) and Seifert & Okada (1990). But despite this tendency for continua in the arrangement of conidiophores into conidiomata, some conidiomatal fungi have distinctive anatomies that are phylogenetically informative. Sutton (1980) and Nag Raj (1993) used details of conidiomal anatomy as critical elements of their generic concepts for the coelomycetes. In the hyphomycetes, Seifert (1987) illustrated the synnemata of *Batistia annulipes* (Mont.) Ciferri (anamorph: *Acrostroma annellosynnema* Seifert) and *Fluviostroma wrightii* Samuels & E. Müller [anamorph: *Stromatographium stromaticum* (Berk.) Höhne], both of which have characteristic stipe anatomies that distinguish them from the synnemata produced by other superficially similar anamorphs.

Some groups of ascomycetes are not known to produce anamorphs, such as the *Boliniaceae*. Characters of the teleomorph of the *Boliniaceae* could suggest relationships to the *Xylariaceae* or the *Diatrypaceae*, among other families, but the absence of clues given by an anamorph diminishes arguments for placement of the family among the pyrenomycetes.

Anamorphs as phenotypes

SYNANAMORPHY AND HOMOLOGY

Ascomycetes are *organisms*. That is, individuals comprise organs and/or tissues: hyphae, ascomatal structures where nuclear pairing, fusion and meiosis take place and that enclose asci, and structures (conidiophores) that asexually produce propagules (conidia, chlamydospores etc.) that ensure vegetative propagation of the individual. In the filamentous ascomycetes, neither anamorph nor teleomorph is an organism by itself; neither can exist without mycelium. The three morphs, teleomorph–mycelium–anamorph, are often physically interconnected and occur at the same time. In other cases, the relationship is sequential, conidiation ceasing before the appearance of ascomata, or conidia produced after the teleomorph has matured and disseminated its spores.

It seems likely that all anamorphs are not homologous, but fungal taxonomists have traditionally attempted to classify them in a single system. Ascomycete life cycles often include two or more anamorphs, which are called synanamorphs. The original concept for differentiating synanamorphs was introduced by Hughes (1979), who considered morphs to be different when they were generically distinct, thus a taxonomic concept rather than a functional one.

Gams (1982) considered conidium ontogeny a primary criterion for deciding whether two synanamorphs should be designated with different generic names.

The existence of distinct synanamorphs within one species is evidence that all anamorphs are not homologous structures. We can assume that synanamorphs play different roles in the survival strategies of organisms, perhaps with different sets of genes as starting points (but see below). The following categories are proposed as a means of evaluating the role of synanamorphs in life cycles of individual species, and by extension, as a means of categorizing anamorphs produced by monoanamorphic taxa. These concepts differ from the commonly used terminology for synanamorphs based on relative conidium sizes, i.e. macroconidium vs microconidium [and also by extension mesoconidium (Pascoe, 1990) and megaconidium (Crous & Seifert, 1998)], or terms based on order of appearance, i.e. primary anamorph and secondary anamorph (cf. Schroers, this volume). We suggest that considerations of biology and homology should precede the taxonomic question of whether or not various synanamorphs are congeneric. Our intention is to ensure the comparison of homologous structures in taxonomic analyses.

(i) *Mycelial anamorphs:* Comprising mycelium growing above the substratum, lacking stromatic elements; these include hyphomycete structures lacking well-defined, anchored conidiophores, in which conidiogenous cells are borne in superficial mycelial growths; they are also commonly synanamorphs of conidiomatal or mononematous species. Like most kinds of conidial anamorphs, mycelial anamorphs are iterative, i.e. there are repeated cycles of asexual sporulation and dissemination without interceding sexual reproduction. Sometimes they also have spermatial roles (see below). These anamorphs are commonly given generic and or specific names. Examples: *Acremonium*, *Chrysosporium* Corda, *Cladorrhinum* Sacc. & Marchal, *Fusarium* 'microconidia'.

(ii) *Mononematous anamorphs:* Well-differentiated conidiophores anchored to the substratum, lacking stromatic elements; these include the majority of hyphomycete genera traditionally classified in the Moniliales. They are iterative or sometimes spermatial. These anamorphs are commonly given generic and/or specific names. Examples: *Aspergillus* Link, *Periconia* Tode, *Arthrobotrys* Corda.

(iii) *Conidiomatal anamorphs:* Fruit-bodies anchored to or embedded in the substratum, independent from, following or preceding, or derived from the teleomorph stroma; these include coelomycetes, synnematous and sporodochial hyphomycetes. They are iterative or sometimes spermatial. These ana-

morphs are commonly given generic and/or specific names. Examples: *Phoma* Sacc., *Colletotrichum* Corda, *Tubercularia*, *Graphium* Corda, *Fusarium.*

(iv) *Germination anamorphs*: Comprising conidiogenous cells emerging directly from germinating ascospores or conidia. Iterative. These anamorphs are rarely given generic names, although they are often compared with existing genera of mononematous or mycelial anamorphs and are likely to be expressions of the same sets of genes. See Hanlin (1994) for a review of this kind of anamorph (also called repetitive germination or microcyclic germination). Examples: Selenosporella-like, phialophora-like.

(v) *Survival anamorphs*: Single-celled or multi-celled, indehiscent propagules, often with thick walls or dark pigments, usually referred to as chlamydospores, aleuriospores and sclerotia. Noniterative. These are rarely given generic or specific names because they tend to lack diagnostic characters, although there are several older generic names for this kind of anamorph (such as *Sclerotium* Tode, *Sepedonium* Link) that are still widely used. Some characteristic and conspicuous survival anamorphs can be easily identified to species, such as *Desmidiospora myrmecophila* Thaxter.

(vi) *Yeast-like anamorphs*: Masses of wet or slimy blastically budding cells or thallic arthric cells, adapted for survival in high moisture environments. Iterative or assimilative. True yeasts have their own taxonomic system, and yeast synanamorphs of mycelial fungi have rarely been given generic or species names (but cf. *Phaeococcomyces* de Hoog, synanamorphs of some mycelial *Exophiala* spp.). Yeast-like anamorphs with true mycelium have been described in genera such as *Aureobasidium*, *Hormonema* and *Hyphozyma* de Hoog & M. Th. Smith.

(vii) *Spermatial anamorphs*: Also called andromorphs (Parbery, 1996). Dispersive conidia that do not germinate to form mycelium (spermatia in the strict sense), or that can germinate and form mycelium, but serve as gametes. This function has rarely been proven, but is probably a common function for conidia. Anamorphs of discomycetes are often assumed to be spermatial; spermatial anamorphs of the *Sclerotiniaceae* that produce minute, presumably water-borne conidia, have been classified in *Myrioconium* Sydow. In species of *Mycosphaerella* Johanson, purportedly spermatial, asteromella-like anamorphs are often formed alongside hyphomycetous anamorphs (Sivanesan, 1984; Verkley & Priest, this volume).

(viii) *Vegetative mycelium anamorphs*: Formerly called mycelia sterilia or Agonomycetes. No propagules are produced, thus these are probably as-

similative organs, but characteristic mycelium allows the identification of anamorph genera and species. The best known example is *Rhizoctonia* DC. The practice of proposing Latin names for vegetative mycelium, relatively common in the early days of fungal taxonomy (e.g. *Anthina* Fr., see Treu & Rambold 1992), has generally been abandoned outside of *Rhizoctonia*-like fungi and medically important fungi such as *Madurella* Brumpt, *Lacazia* Taborda *et al.*, and some species of *Trichophyton* Malmsten.

Table 2 lists some pleoanamorphic species in the *Hypocreales*, with constituent synanamorphs classified according to the categories defined above. As is clear from this table, the categories are sometimes not discrete, and may grade into each other. The gradation may include distinctly separated synanamorphs, synanamorphs arising from a common hypha, or synanamorphs occurring on a shared conidiophore. Some examples were illustrated by Wang (1979).

Although our concepts suggest that some synanamorphs are not homologous, there is likely to be a continuum of degrees of homology in some fungi. Some genes may be expressed in the development of multiple synanamorphic phenotypes (e.g. the genes involved in producing mononematous conidiophores or phialides). *Basifimbria spinosa* Buffin & Hennebert (1985) was described with a synanamorph (attributed to *Arthrobotrys*) sometimes occurring on the same conidiophore; both morphs have sympodially proliferating conidiogenous cells, but differently shaped, and morphologically distinctive conidia. Some genes involved in the production of the teleomorph may also be involved with the anamorph (e.g. genes involved in stroma development, cf. Schroers, this volume). However, this approach allows us to consider whether morphological phenotypes being compared are homologous, partially homologous, or heterologous (whether they be anamorphs of different species, synanamorphs of one fungus, or teleomorphs and anamorphs).

In fungi with synanamorphs, there is a tendency to produce one dispersive anamorph (thin-walled conidia) and one survival anamorph (resistant chlamydospores or aleurioconidia), especially fungi that spend part of their life cycle in soil, such as species of *Gibberella* (*Fusarium*) and *Neonectria* Wollenw. (*Cylindrocarpon* Wollenw.). Less frequently, two dispersive anamorphs occur within a single life cycle.

Often, the biological implications of morphological distinctions between the forms are obvious (e.g. wall pigmentation and thickness). Sometimes morphological distinctions are obvious, but the res-

Table 2. An interpretation of synanamorphs in the *Hypocreales*. See text for details on categories of synanamorphs.

Within each holomorph, the synanamorphs are assumed not to be homologous, but comparisons between species become complicated by intergradations between mycelial and mononematous and mononematous and conidiomatal types; in these cases, the anamorph is placed in an intermediate position in the table. Holomorph names based on teleomorphs are indicated with an asterisk (*); all other holomorph names are based on one of the anamorphs.

Holomorph	Mycelial anamorphs	Mononematous anamorph(s)[1]	Conidiomatal anamorph(s)[1]	Survival anamorph[1]
Bionectria ochroleuca (Schw.) Schroers & Samuels*	———————————— verticillium–like ————————————		*Clonostachys rosea*	none
Clonostachys compactiuscula (Sacc.) D. Hawksw. & W. Gams	———————————— verticillium-like ————————————		*Clonostachys*	none
'Nectria' radicicola Gerlach & L. Nilsson*	microconidia	none	*Cylindrocarpon destructans*	chlamydospores
Cylindrodendrum album Bonord.	*Cylindrodendrum*	*Cylindrocarpon hydrophilum*	none	none
Gliocladium aurifilum (Gerard) Seifert *et al.*	———————————— verticillium-like ————————————		*Gliocladium*	none
G. penicillioides Corda	none	none	*Gliocladium*	none
Fusarium sporotrichioides Sherb.	'meso-'conidia (fusiform)	'micro'-conidia (globose)	sporodochial or 'macro'-conidia	chlamydospores
Harposporium cerberi W. Gams *et al.*	arthroconidia	A – *Harposporium* B – *Hirsutella*	none	none
Cordyceps kniphophioides H. C. Evans & Samson*	none	none	A – *Synnematium jonesii* B – *Hirsutella stilbelliformis*	none
Hirsutella petchabunensis Hywel-Jones *et al.*	none	none	*Hirsutella*	*Helicoma*
Hirsutella subramanianii Samson & H. C. Evans	none	*Hirsutella*	none	A – sclerotia B – 'resting bodies'
Hirsutella formicarum Petch	none	none	*Hirsutella*	A – *Desmidiospora myrmecophila* B– 'hyphal bodies'
Torrubiella clavata Samson & H.C. Evans*	*Granulomanus*	none	*Gibellula clavata*	none
Stilbocrea gracilipes (Tul. & C. Tul.) Samuels & Seifert*	none	none	A – *Stilbella clavulata* B – *Gracilistilbella*	none
Stilbella albocitrina (Ellis & Everhart) Seifert	———————————— acremonium-like ————————————		*Stilbella*	none
Hypocrea cinereoflava Samuels & Seifert*	trichoderma-like	none	*Stilbella flavipes*	chlamydospores
Sorosporella uvella (Krass.) Giard	none	none	*Synglliocladium*	*Sorosporella*
Volutella cf. *minima* Höhnel	———————————— verticillium-like ————————————		*Volutella*	none

[1] When synanamorphs occurring in a single species are considered of the same type, they are designated A and B.

pective biological functions are not, as in the case of the synanamorphs of *Bionectria ochroleuca* (Schw.) Schroers & Samuels. This species produces penicillate conidiophores with imbricate columns or slimy chains of conidia (often aggregated into sporodochia), the most 'typical' morph that conforms to the usual concept of *Clonostachys rosea* (Link) Schroers *et al.* Conidiophores of the verticillium-like synanamorph have whorls of phialides and conidia held in drops of clear, colourless liquid (Schroers *et al.*, 1999). There is neither evidence that conidia of *B. ochroleuca* function as spermatia nor have separate roles been deduced for the respective synanamorphs. Possibly the different conidial slimes are adapted to disperal by insects and water.

Graphing the distribution of anamorphs onto phylogenetic trees to determine whether anamorph taxa are polyphyletic or paraphyletic should consider the question of whether all anamorphs being considered are homologous. For example, if the *Fusarium* anamorphs of species of *Haematonectria* Samuels & Nirenberg (conidiomatal) and the acremonium-like anamorphs of species of *Neocosmospora* E. F. Sm. (mononematous or mycelial) are nonhomologous, does it make sense to compare their respective phylogenetic distributions and use distribution of a mycelial anamorph to claim that a generic concept based on a conidiomatal anamorph is paraphyletic?

Mixing nonhomologous anamorphs into pleomorphic anamorph genera can lead to serious problems. Anamorph taxonomists have a natural desire to circumscribe real anamorph taxa, or pseudobotanical taxa *sensu* Hennebert (1987, see below), in which a single anamorph name encompasses all synanamorphs. The pleomorphic, pseudobotanical concept of *Fusarium* (see Gams and Nirenberg 1989, with slight modifications by Seifert, 2000) is accepted by most specialists. However, it causes serious problems for general hyphomycete taxonomists unfamiliar with the species of that genus. In contrast, the pleomorphic, pseudobotanical concepts for the anamorph genera *Hirsutella* Pat. and *Stilbella* Lindau seem to be unraveling. Evans & Samson (1982) synonymized *Synnematium* Speare with *Hirsutella* because of the co-occurrence of conidiogenous cells of these two morphs on the same synnemata of a single species; later they synonymized *Desmidiospora*, a distinctive survival synanamorph, with *Hirsutella* (Samson *et al.*, 1988). Recently discovered synanamorphs of *Hirsutella* include *Harposporium* Lohde (Hodge *et al.*, 1997) and *Helicoma* Corda (Hywel-Jones *et al.* 1998). These latter anamorph genera include a significant number of species on their own. Deriving a pleomorphic

anamorphic concept by subsuming a small genus into a larger genus is manageable, but as the number of nonhomologous synanamorphs increases, it is difficult to avoid chaos. A similar example concerns *Stilbocrea gracilipes* (Tul. & C. Tul.) Samuels & Seifert, which has two distinct synnematous anamorphs, classified in different subgenera of *Stilbella* (Seifert, 1985). The A-anamorph, corresponding with *Stilbella* in the strict sense (i.e. subgenus *Stilbella*) appears first in culture, and is followed several weeks later by the darker B-anamorph (subgenus *Gracilipedes*). If no species producing only the B-type of anamorph were known, the situation might be sustainable. However, the existence of species with only the B-type anamorph, and other species with only the A-type anamorph, means that these anamorphs cannot be considered homologous and should not be classified in one anamorph genus. The necessary taxonomic changes are made in the Appendix with the proposal of a new genus, *Gracilistilbella*, for the 'B-anamorphs'.

Comparing anamorph and teleomorph taxonomic concepts

Monophyletic groups of species (as defined either by rigorous phenotype comparison or by DNA analysis) have very similar, sometimes identical, ascomata and very similar anamorphs. Sometimes that relationship is of genus to genus (e.g. *Colletotrichum* is *Glomerella* Schrenk & Spaulding; there is no other known teleomorph for *Colletotrichum* although there are *Colletotrichum* species that lack teleomorphs, cf. Sutton, 1992) and sometimes that relationship is at a higher taxonomic level (e.g. *Fusarium* to four genera of the *Nectriaceae*, Guadet *et al.*, 1989; Rossman *et al.*, 1999; *Gliocladium sensu stricto* to two genera of the *Hypocreaceae*; Rehner & Samuels, 1994). The so-called 'genus for genus' hypothesis, which proposes that phenotypic taxonomies be designed so that teleomorph- and anamorph-generic concepts coincide phylogenetically, is described and discussed by a number of authors in this volume (e.g. Rossman; Schoch *et al.*). Although we agree that teleomorph and anamorph taxonomies often coincide, we caution against any tendency to force generic concepts in this direction. Anamorph-generic names sometimes have an inherent information value that is far more important than an arbitrary desire to declare them *de facto* synonyms of their respective teleomorph-generic names. In particular, we have reservations about this concept when nonhomologous anamorphs are being compared (see above), or when taxonomic concepts based on plesiomorphic phenotypes (teleomorph or

anamorph) are being compared to synapomorphic phenotypes.

Holomorphic species or generic differences are not always manifested in teleomorphs. At the generic level, *Ceratocystis* Ellis & Halsted and *Ophiostoma* Syd. & P. Syd., which have essentially identical teleomorph morphologies, were often considered synonymous in the past, but were then separated by fundamental differences in their anamorphs (see Samuels, 1993) and are now considered members of different orders. At the species level, collections of *Hypocrea* that can be readily identified as *H. rufa* (Pers.) Fr. by perithecial characters can be separated into different species when their anamorphs are known (Samuels, unpublished). Similarly, despite the many described species of *Fusarium*, there are rather few described species of *Gibberella*. *Gibberella* species are classically distinguished on the basis of size and septation of ascospores, but it would be impossible to identify a collection of a *Gibberella* species with certainty unless the *Fusarium* anamorph was known (Samuels *et al.*, 2000). There are many other examples of the use of anamorph characters to delimit holomorph genera or monophyletic groups in this volume (see Rossman; Schoch *et al.*; Réblová).

Often, the anamorphs of closely related species are classified in different genera. Phylogenetically, this may be an indication of nested monophyletic groups, i.e. an ancient teleomorph phenotype (i.e. plesiomorphic teleomorphs) exists in a group of species where anamorph phenotypes have continued to radiate (synapomorphic anamorphs). The preliminary results suggesting the monophyly of the morphologically homogeneous genus *Mycosphaerella*, combined with the discovery that at least some of the associated anamorph genera are also monophyletic, nested inside the larger *Mycosphaerella* clade, may eventually provide a compelling example of this (Crous *et al.*, this volume).

However, discordant generic concepts may also reflect artificially circumscribed anamorph genera for groups of species expressing what have classically been considered generic characters, but which may actually be variations on a theme. In *Chaetosphaeria* Tul. & C. Tul. *sensu stricto*, about 20 dematiaceous hyphomycete genera have been described that share an easily recognized morphological pattern (see Réblová, this volume). The genera have been separated based on differences in conidiophore fasciculation and branching, morphology and development of phialides and conidia. Phylogenetic analyses demonstrate that some anamorph characters do delineate monophyletic groups. Despite our suspicion that many anamorph genera have been delimited using phylogenetically trivial characters, we caution against the assumption that characters used to delineate teleomorph genera are necessarily more phylogenetically informative.

In Ascomycete taxonomy, the abundance of anamorph-generic and -specific names varies among taxonomic groups, a difference that sometimes may relate more to the practices of taxonomists than to the biology of the organisms. For example, while the *Hypocreales* is rich with named teleomorphs and anamorphs, taxonomists studying the often profusely conidiating *Xylariaceae*, in contrast, have generated few anamorph-generic and -specific names. This has its benefits (a less cluttered nomenclature), but also a side-effect that the number of characters inherent in anamorph morphology may be underestimated, and the corresponding descriptions sometimes minimal compared to the complete treatments given to teleomorphs.

Anamorphs and nomenclature

The naming of anamorphs is governed by Article 59 of the *Code*. This article was specifically written for fungi and allows dual (or multiple) nomenclature. A single fungal genome may have two or more Latin binomials, each binomial referring to a specific morphotype. Hennebert (1987) outlined three different nomenclatural systems currently being applied to anamorphs, viz. the pseudobotanical system (in which anamorph names are considered mimics of real taxa, and hence can be pleomorphic, and by extension, representative of an entire life cycle), the anatomical system (in which the taxa are monomorphic and considered artificial or form taxa), and an anatomical system with cross-reference names [e.g. *Fusarium* anamorph of *Gibberella zeae* (Schw.) Petch].

Nonspecialists are often surprised that a single fungal genome can have separate binomials for the teleomorph, the sometimes multiple iterative anamorphs, the chlamydospores, the sclerotia and even the vegetative mycelium, one of which is officially sanctioned as the 'holomorph' name (but often rarely used). In situations where the teleomorph is infrequently seen (and perhaps described long after the anamorph, or known only from mating experiments *in vitro*), there may be a subconscious perception that the biologically active organism is actually an anamorph. Although a culture producing fusarium conidia may be isolated from a diseased plant, for example, it is not the fusarium that causes the disease but rather a fungus that also produces mycelium, fusarium conidia and sometimes perithecia (a *Gibberella*). The disease-causing 'agent' of the fungus is actually the mycelium, from which both conidia and perithecia

ultimately arise. This situation sometimes puts contemporary taxonomy at odds with those who oppose name changes to common or important organisms, when the most frequently used name is that of the anamorph.

Traditionally, the name of the teleomorph has been considered the official name of a species. Usually, anamorph names are thought to have special status simply because they are allowed by an explicit article of the *Code*. However, by restricting the applicability of anamorph names, it is actually teleomorph names that receive special, sanctioned status. In many species with a validly described teleomorph name, the anamorph name is still often widely used. Gams (1995) excused this practice in the case of genetically distinct holomorphs that have morphologically similar anamorphs, when the diagnostic teleomorph has not been seen, but we suggest that using such a binomial without some sort of qualification [e.g. just *Fusarium solani* (Mart.) Sacc. instead of *F. solani* clade or *F. solani* complex] implies fictitious taxonomic precision.

A holomorph name represents the entire genome of a fungus, while anamorph and teleomorph names represent subsets of the genome responsible for the production of cells and tissues comprising these morphological structures. It is axiomatic that teleomorphs and anamorphs are phenotypes. What is presently changing in fungal taxonomy is the pretense that one of these phenotypes, the teleomorph, is the final arbiter of phylogenetic relationships. The sample of the genome being sequenced is now assumed to represent the genome as a whole, and the entire genome is being classified, not just one of its phenotypes. This has been a difficult shift for many taxonomists. There is still a perception that taxa defined by teleomorph phenotypes are inherently superior to taxa defined by anamorph (or other) phenotypes.

In discussions on the desirability of unit nomenclature (i.e. one fungus, one name), the assumption has generally been that teleomorph names will maintain their special status. Cannon & Kirk (this volume) suggest that all names should compete equally for priority, irrespective of whether they represent anamorphs or teleomorphs, irrespective of whether the entire life cycle of the organism is encompassed by the protologue. In our opinion, this is the only logical solution. Otherwise nothing will have changed; it will still be necessary to erect new anamorph names for newly discovered anamorphic taxa, and then eventually to replace them with 'new' holomorph names if teleomorphs are discovered. However, even without formal changes to the *Code*, there are other possibilities for dealing with anamorphic taxa. Frisvad &

Samson (this volume) suggest a convention for referring to anamorphic species whose phylogenetic affinities are inferred from molecular or other data, for example *Fusarium oxysporum* (*aff. Gibberella*).

Conclusions

Anamorphs can function as parts of life cycles of sexually-competent fungi, or be independant clonal populations diverging from such sexual fungi. Episodic selection may favour the evolution of anamorphic species from isolated populations with only a single mating type. In some cases, anamorph species may evolve through hybridization events.

Questions of homology should be considered in the interpretation and classification of anamorphs. In some cases, the relationships between teleomorph genus and anamorph genus are so intimate that the anamorph genus is equivalent to the teleomorph; in other cases, either the teleomorph or the anamorph phenotype is plesiomorphic and there is no equivalence.

Our taxonomic tradition is morphocentric, but the new paradigm of DNA sequence based taxonomy, cladistics and phylogenetic nomenclature is forcing us to reevaluate many of our practices. If teleomorphs and anamorphs are organs of one organism, then it is superfluous to name both phenotypes as though they were separate organisms. A single nomenclaturally valid name is sufficient. It is possible that the special nomenclatural status for the teleomorphic phenotype should be abandoned, at least in selected groups of fungi.

Mycologists now know enough about anamorphs to treat them in a less capricious fashion. We should emphasize their roles as parts of life cycles and recognize their diversity. Their nomenclatural significance can be deemphasized without discounting them as sources of taxonomic characters.

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Appendix

GRACILISTILBELLA Seifert, *gen. nov.*

≡ *Stilbella* subgenus *Gracilipedes* Seifert, Stud. Mycol. 27: 84. 1985.

The Latin diagnosis for this taxon appears at the cited page in Seifert (1985). The species produce lightly pigmented to dematiaceous synnemata with phialidic conidiogenous cells and globose to ellipsoidal ameroconidia accumulating in slime. The most distinctive character is the presence of globose to ellipsoidal, warted ornamenting cells on the marginal hyphae of the stipe. Five species are known to date (Seifert 1985, 1990), two with proven *Stilbocrea* teleomorphs.

Species typica: **Gracilistilbella clavulata** (Mont.) Seifert, *comb. nov.*, anamorphosis *Stilbocrea gracilipes* (Tul. & C. Tul.) Samuels & Seifert, Stud. Mycol. 42: 73. 1999.

≡ *Stilbum clavulatum* Mont., Annls. Sci. nat. Bot. Sér. 2, 18: 248. 1842 (basionym).

For additional synonyms see Seifert (1985).

Other accepted species:

Gracilistilbella aterrima (Welw. & Curr.) Seifert, *comb. nov.*

≡ *Stilbum aterrimum* Welw. & Curr., Trans. Linn. Soc. Lond. 26: 291. 1870 (basionym).

For additional synonyms see Seifert (1985).

Gracilistilbella bambusae (Pat. & Gaill.) Seifert, *comb. nov.*

≡ *Stilbum bambusae* Pat. & Gaill., Bull. Soc. Mycol. Fr. 4: 125. 1888 (basionym).

For additional synonyms see Seifert 1985.

Gracilistilbella anamorph of *Stilbocrea macrostoma* (Berk. & M. A. Curtis) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Natuurwiss. Kl., Abt. 1, 118: 1185. 1909.

= B anamorph of *S. macrostoma sensu* Seifert (1985, sub *Nectria*).

The available anamorphic names in the synonym list of Seifert (1985) all refer to the so-called A-anamorph.

Gracilistilbella pseudobambusae (Seifert) Seifert, *comb. nov.*

≡ *Stilbella pseudobambusae* Seifert, Mem. New Yord Bot. Gard. 59: 143. 1990 (basionym).