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## The Systematics of Hyphomycetes\*

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### I. INTRODUCTION—THE ROLE OF SYSTEMATISTS

Taxonomists inadvertently occupy one of two central positions among biological disciplines, although some of them may not realize it and many of them tacitly reject the responsibility this position involves. Their chief importance to human culture, apart from revealing to their fellow humans the dazzling, almost unbelievable richness and diversity of life on earth, is to collect and collate the information about living organisms acquired by all other disciplines and to construct a system—essentially a four-dimensional web involving space and

\*This chapter is dedicated to the memory of Pat Talbot, whose untimely death robbed the mycological fraternity of a distinguished colleague, and me of the chance to benefit from his wisdom and experience during my stay in Australia.

time—which will link all these millions of multifarious organisms, extant and extinct, and show how they are related to one another (not how they relate to one another—that is ecology, the other central discipline).

Although the beginning taxonomist is often initially fascinated by the beauty, complexity, and essential strangeness of the particular group he has chosen to work with, he often eventually awakens to a realization of his deeper role and is sometimes foolhardy enough to embrace it, with all its attendant pitfalls, because it is a challenge worthy of a true Renaissance man. (No sexual bias intended: other possible constructions are too clumsy.)

## II. THE TROUBLE WITH ANAMORPHS

But before the great web can be woven and the overall pattern made apparent, our understanding and arrangement of each group must be scientifically and intellectually satisfying. And it is always easy, from one's own vantage point, working with a particular group of organisms and only too aware of the difficulties and deficiencies of its systematics, to assume that the taxonomy of other groups is in much better condition than that of one's own. My later comments on ascomycetous and basidiomycetous teleomorphs will reveal the surprise I felt when I first realized the inadequacy of their systematics. But despite my attempts to compensate for a negative bias in my own thinking, I remain convinced that the systematics of conidial anamorphs is particularly disorganized. This conclusion does not imply that taxonomists of conidial fungi are any less competent, diligent, or inspired than their brethren in other groups: I am sure that this is not the case, since I know from personal acquaintance what penetrating, analytic and original minds the best of them have. No, the truth is that we have been faced with some extremely difficult problems, the most important of which is that we usually work with only part of an organism—only one phase of its life cycle. This problem has recently been extensively and intensively explored in *The Whole Fungus* (Kendrick, 1979). In a nutshell: The anamorphic or asexual phase of a dikaryomycotan fungus and its teleomorphic or sexual phase are capable of metamorphosing, each into the other, but we do not as yet understand the factors which bring about the phase change (Müller, 1979) and so cannot control them. So we know the full dual (or sometimes multiple) nature—the holomorph—of only a small percentage of the Dikaryomycota (Ascomycetes plus Basidiomycetes). And some may well have lost their anamorphic or their teleomorphic expression, although this is still difficult to prove. Because of such factors, I feel that any complacency at the appearance of so many useful books on conidial fungi during the last few years would be ill-founded. All these publications do no more than establish a baseline from which we can measure future progress. The conidial fungi remain an enigmatic—and an artificial—group.

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### III. CLASSIFICATION—THE STATUS QUO

To paraphrase a passage from *The Peter Principle*: “A classification may be incompetent in itself—that is, unable to do regularly and accurately the work for which it was designed . . . [and] even when competent in itself, a classification vastly magnifies the results of incompetence in its operators.”

One of the most critical phrases in this passage is “the work for which it was designed.” A classification may be admittedly artificial, based on only part of what we know about the organisms and designed simply and solely to facilitate identification—application of the “correct” binomial to unknown organisms—or it may be much more subtly constructed, based on everything we know about the organisms, with the aim of being natural and of expressing relationships, hence phylogeny. This prompts me to make two position statements. First, I do not believe that an effective hierarchical classification of conidial fungi now exists at either of these levels of sophistication. Second, since we aim ultimately to attain the higher level, a phylogenetic scheme, I cannot in this chapter discuss conidial anamorphs without some reference to teleomorphs, since only the whole fungus can be properly classified (Kendrick, 1979).

How can I say that no respectable classification exists when I frequently succeed in identifying hyphomycetes myself? The answer is that I do so not by referring to any published hierarchical scheme but rather by searching in my own memory bank (or herbarium specimens or generic monographs or “picture books”). I do not make this claim lightly, since part of the blame for the absence of a proper scheme may be laid at my door: Though in self-defense I must say that I have spent several years working on two comprehensive arrangements of hyphomycete genera (Kendrick and Carmichael, 1973; Carmichael *et al.*, 1980). If these do not represent “good” systems, what excuses or reasons can I offer for their deficiencies? The body of this chapter is devoted to answering this question.

A hierarchical scheme requires the recognition of taxa of higher and higher rank (species, genus, family, order, class, and so on). If the scheme is to withstand scrutiny, so must the taxa at all levels. Unfortunately for any existing schemes, but happily for the future of mycology, the artificiality and the misleading connotations of relatedness that mar many of the widely recognized fungal taxa are now being increasingly perceived and will be discussed below. Suffice it to say at this point that a formal high-ranking anamorph-taxon such as Deuteromycotina is of marginal use, even in a scheme aimed solely at identification, and must be anathema to anyone dedicated to the concept of the whole fungus. Kendrick and Nag Raj (1979) have seriously questioned the procrustean segregation of conidial anamorphs into the currently used anamorph-classes Coelomycetes and Hyphomycetes (and thus incidentally the rationale for dealing with them in separate chapters of this book). And below the class level, one

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encounters no widely accepted suprageneric categories—the orders and families of Saccardo began to wither away many years ago, and none of the more recently proposed ordinal or familial names (whether morphologically or ontogenetically based) have met with widespread approval.

So we have in effect a large number of anamorph-genera composed of anamorph-species. And even here the taxonomic concepts have been principally morphological, and often applied very broadly or very narrowly, depending on author and group. Compilations such as those by Barron (1968), Ellis (1971), Kendrick and Carmichael (1973), von Arx (1974), Ellis (1976), and Carmichael *et al.* (1980) are very useful and permit identification of an increasing number of anamorphs, but those of us who have made these compilations know only too well how much our confidence in the taxa varies and what an enormous task of generic reassessment and revision remains to be done. And meanwhile, the flood of new anamorph-taxa continues unabated. At their inception, very few of these anamorph-taxa are linked to a known teleomorph, so yet another vital job is usually left to be done later.

Perhaps this would be a good point at which to bring this general survey to a close and to begin analyzing specific areas in detail.

#### IV. HIGHER TAXA OF FUNGI—HETEROGENEITY

In his key to classes of Basidiomycotina, Ainsworth (1973) separated Hymenomycetes and Gasteromycetes, as has been common practice among mycologists. He noted that the Gasteromycetes are phylogenetically heterogeneous, and we had already been made aware by Heim (1948), Singer and Smith (1960), and Savile (1968) that true phylogenetic relationships in the Holobasidiomycetidae repeatedly cut across the lines separating these classes. Savile compiled no fewer than 14 lineages showing that the family Secotiaceae contains numerous links between Agaricales and gasteromycetous derivatives. Thus both the Secotiaceae and the Gasteromycetes as a whole are revealed as highly polyphyletic. Yet published systems, such as that given in *The Fungi*, Vols. IVA and IVB (Ainsworth *et al.*, 1973a,b), make no serious attempt to replace these categories with more natural ones.

Nobles (1958) showed that many of the families, and even genera, of the higher Basidiomycetes are heterogeneous. Characters of biochemistry and microscopic anatomy effectively dismember older categories based on gross morphology, especially in the polypores. But although many new generic names have been proposed and old ones resurrected as a result of this kind of work revision of the classification is still incomplete, and its altered nature has not yet been fully appreciated or assimilated by the mycological public.

In his key to classes of Ascomycotina, Ainsworth (1973) recognized the Plec

tomycetes. Subsequently Malloch (1979) compiled the recent literature on cleistothecial ascomycetes, with the general conclusion that they are also polyphyletic, being derived in the main from four other presumably more natural groups of Ascomycetes—Pleosporales, Diaporthales, Hypocreales, and Pezizales. Note that these ancestors include bitunicate and unitunicate, perithecial, and apothecial forms. They could hardly be more diverse.

Trappe (1979) writes, "Of the 31 genera of hypogeous Ascomycotina accepted, one is assigned to the monotypic order Elaphomycetales ord. nov. and the rest are placed in the Pezizales. . . . I have discarded the artificial, anachronistic order Tuberales. All hypogeous genera that relate morphologically to families of Pezizales are assigned to those families." The Pezizales are commonly placed in a larger group of fungi which usually have apothecial ascomata and are known as Discomycetes. As one becomes familiar with these same Discomycetes, one is made aware that there are two kinds, those with operculate unitunicate asci and those with inoperculate unitunicate asci. Then one discovers the Patellariaceae and the aberrant *Pseudoscypha* Reid & Piroz. (Reid and Pirozynski, 1966) in which an apothecioid ascoma produces bitunicate asci. Thus one learns that the words "Discomycetes" and "apothecium" are morphologically rather than phylogenetically based. Now Trappe has shown that something classified as an "operculate discomycete" may not even produce an ascoma that is recognizably apothecioid, and that its asci may not be overtly operculate. Trappe has bitten the bullet, and we must applaud this. Unfortunately, for those of us who teach mycology, this means that we now have more explaining to do. The major groups of the Ascomycetes can no longer be recognized by simply examining the gross morphology of their ascomata. Nobody promised that a phylogenetically based classification would be simple or easy to cope with.

#### V. HIGHER TAXA OF FUNGI—EPHEMERAL OR PROTEAN?

Let us now examine the recent history of orders in the bitunicate ascomycetes. Three major efforts to categorize these fungi have appeared in the 1970s. Barr (1972) recognized three orders, Myriangiales, Dothideales, and Pleosporales. Luttrell (1973) accepted five orders—the three given by Barr plus Hysteriales and Hemisphaeriales. Von Arx and Müller (1975) treated all bitunicates in a single order, Dothideales. Since there is no question as to the experience or reputation of any of the workers just mentioned, we must conclude that they have different ideas about what constitutes an order. Von Arx and Müller obviously used the features of the bitunicate ascus itself as diagnostic. Barr used the three common types of centrum development. Luttrell recognized two additional orders. His Hysteriales accommodates forms in which the ascoma is definitely

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“discomycete-like,” and he admits that this order is probably heterogeneous. He suggests, for example, that the Hysteriaceae could be natural members of the Pleosporales. The Dothioraceae, also apothecioid, have affinity with the Dothideales, and Luttrell placed them in this order. The Patellariaceae have no clear affinities, but their apothecioid ascomata allowed them to be placed in the Hysteriales. Luttrell also accepted the order Hemisphaeriales, while recognizing that it too is heterogeneous, since various of its members show internal structure that may eventually lead to their distribution among the other four orders. They are held together for the present by their dimidiate, appressed ascomata, whose evolutionary significance Luttrell felt it was premature to discount.

Von Arx and Müller had earlier (1954) recognized three orders (Pseudo-sphaeriales, Dothiorales, and Myriangiales) using characters of asci and ascomata, but subsequently found too many intermediates for comfort and ultimately decided that the bitunicates exhibited a virtual continuum of features.

I am sure we have not heard the last of this controversy, and I do not even suggest that such a divergence of opinions is bad for mycology. I simply wish to emphasize that we should not invest the names of some higher taxa with an aura of authority and immutability that they do not deserve. Classes, subclasses, and orders seem to be extraordinarily prone to changes in both name and circumscription.

I can advance two possible explanations for this. The first is that, as our knowledge of such groups grows, we can produce increasingly rational (though altered) taxa—look what electron microscopy and wall chemistry have done for the classification of what we used to call the Phycomycetes. The second is that the highest echelons of fungal taxa (Ascomycotina and Basidiomycotina, for example) are now considered fixed stars, capable only of gaining or losing a little mass (Endomycetes, Ustomycetes), and at the other end of the scale, individual genera and species tend to be revised or monographed by individual specialists only at long intervals and thus often give a possibly misleading appearance of stability. In contrast to the highest and lowest taxa, those at the middle levels of the hierarchy seem to attract attention from many taxonomists. Although it is usually impossible for any one worker to monograph more than a small proportion of the genera in a given order or class, such workers usually develop a concept of the higher taxa uniquely colored by their own experience, which may change considerably during their working lifetime. So it is hardly surprising that current opinions (which are, after all, what many taxa are based on) are so diverse.

How have we gotten along without families of conidial fungi for so many years? This may well be because the family concept is of questionable usefulness. Perhaps the best way to exemplify this is by quoting from some universally known groups of flowering plants. The family Ranunculaceae is very heterogeneous—anything that will not fit into the Papaveraceae or Magnoliaceae

tends to finish up in the Ranunculaceae. And how different *Ranunculus* is from *Aquilegia*. In fact, this example points to a logical corollary regarding the unsatisfactory family: It is usually easy to recognize the genera within it. But consider now the Cruciferae, all members of which share a number of very telling features. This is a good family. But the delimitation of genera within it is fraught with difficulties. It seems, then, that as a general principle, the better defined the family, the more difficult it is to recognize the genera within it (G. Jones, personal communication); ergo, in a large and varied group such as the Hyphomycetes, one may be better off without families.

Perhaps I may be allowed one more comment on high-ranking taxa before returning to my main theme. The higher the rank of a particular taxon, the more indistinct its periphery. I will content myself with a single example. Fungi, a taxon in no danger of disappearing, is variously defined as encompassing or excluding such groups as the Myxomycetes (Mycetozoa?), Labyrinthulomycetes, and Plasmodiophoromycetes. This is one consequence of the high probability that even what we all recognize as true fungi (the hyphal kind) comprise several groups which seem to have evolved separately from protistan ancestors. Other analogous solutions to basic biological problems have evolved many times, so why not the hyphal life style? (After all, we even have a prokaryotic parallel in the Actinomycetes.) Implications of monophyly in particular groups (the avowed goal of most systematists) are therefore limited at several levels of the fungal classification.

## VI. PSEUDOTAXA

I have had to begin with all these unsettling comments about the systematics of the Dikaryomycota because the taxonomy of conidial anamorphic fungi is inextricably bound up with that of the sexual alter egos most of them presumably possess. Specialists in anamorphs have usually, with refreshing candor, admitted that their taxa are in fact pseudotaxa. For a long time these were called form-taxa, but this term has been preempted for use with fossils in a sense differing appreciably from that used in discussing dikaryomycotan anamorphs, and we have adopted the term "anamorph-taxa" for our purposes (see Pirozynski and Weresub, 1979). [*Form-taxa* are maintained for fossils of detached organs which lack diagnostic features indicating natural affinity. The application of this term is not governed by Article 59 of the Botanical Code of Nomenclature. *Anamorph-taxa* are maintained for organs of asexual or somatic reproduction in living fungi. The application of the term *is* governed by Article 59 (Weresub and Hennebert, 1979).]

Those who worked with teleomorphs generally did not admit that the taxa in which they arranged their collections were botanical only in name and based on

an arbitrary, legalistic decision of a botanical congress. In fact, as I think I have already demonstrated clearly, many such taxa of what used to be called perfect fungi have turned out to be just as artificial as—and possibly more so than—some anamorph-taxa.

In the term “Fungi Imperfecti” we have escaped some of the misconceptions engendered by such misleading terms of convenience as “Discomycetes,” “Pyrenomyces,” “Plectomyces,” and “Gasteromyces.” We have always been fully aware that the Fungi Imperfecti are a miscellaneous group, though even here mycological textbooks have erred by relating them more or less exclusively to ascomycetous teleomorphs (we now recognize numerous basidiomycetous anamorphs; see Kendrick and Watling, 1979). We also fully realize that any and all subdivisions that have been proposed within the Fungi Imperfecti have few—or no—phylogenetic pretensions.

As I pointed out in Chapter 1, the term “Coelomyces” was coined by Grove (1919) for anamorphic fungi that produced conidia inside initially covered conidiomata. Perhaps because this concept provided a good foil, an “either-or” alternative to the Hyphomycetes with their conidiophores exposed *ab initio*, it has been widely adopted. But we have gradually come to see that the apparent homogeneity of the Coelomyces is an illusion. We now consider that acervular and pycnidial fungi are not closely related and that pycnidial conidiomata can develop in several fundamentally different ways. Acervular conidiomata grade imperceptibly into sporodochial conidiomata, and thus a link is established between the coelomycetous anamorph-order Melanconiales and the hyphomycetous anamorph-order Moniliales. The walls of pycnidial conidiomata may develop in such a way as to leave an internal cavity, or they can develop as a solid structure within which a secondary lysigenous or schizogenous cavity arises. The conidia may escape through a preformed ostiole or through a secondarily developed lysigenous or schizogenous opening. Although we do not know the phylogenetic significance of such differences, it seems likely that the anamorph-order Sphaeropsidales is internally heterogeneous.

## VII. TELEOMORPH + ANAMORPH(S) = HOLOMORPH

I recently edited a publication entitled *The Whole Fungus* (1979) which was based largely on the deliberations of the second Kananaskis Conference held in 1977. The theme of the conference and the book is the recognition and realization of a unified conceptual approach to all phenotypic manifestations of each fungal genome. Of course this was far too ambitious—anamorph–teleomorph connections are known or suspected for only about 10% of higher fungal species. And there remains the strong possibility—in my mind virtually a certainty—that many

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anamorphs will ultimately be shown to be independent entities that have lost the need and the ability to produce the teleomorph they once had (this idea is further discussed in Section VIII). Just what proportion of conidial fungi will turn out to be anamorphic holomorphs is anyone's guess. And how many are teleomorphic holomorphs is equally obscure. But the number of connections will increase dramatically, and the classification will become increasingly based on data derived from both sexual and asexual phases.

But where do we stand now? Our attempt in *The Whole Fungus* to discern patterns of relationship using both morphs had mixed results. In some areas the process has so far generated more heat than light. And even in a group such as the Nectriaceae, whose anamorphs are comparatively well documented, the picture is far from clear. Booth (1978) has pointed out that *Nectria coccinea* has red, smooth-walled perithecial ascomata without a stroma and has a *Cylindrocarpon* anamorph. *Nectria ralfsii* has yellow, rough-walled perithecia on a well-developed stroma and has a dark-spored *Myrothecium* anamorph. These differences at first sight appear to merit generic segregation, until a wide range of *Nectria* species is examined, when the gaps are bridged and the initially clear-cut hiatus disappears.

Anyone who has read this far must by now be aware that, while the extant classification of the fungi is an inadequate reflection of our knowledge, our knowledge is still inadequate to permit the elaboration of a truly satisfactory classification. We have learned enough about the fungi in recent years to realize that they are sending us back to the drawing board; but we have not yet been granted the insight needed to visualize the grand design.

If the linking of anamorphs with teleomorphs does not give us the breakthrough we are looking for, what does it tell us? I think it tells us that, when species of the same genus evolve into different ecological niches (as they must if they are to be separate species), then evolutionary pressures may well mold anamorph or teleomorph (or both, as in the *Nectria* species mentioned above) into new and different shapes. And since anamorph and teleomorph often develop at different times, and serve different purposes, the fact that each may change independently of the other is not difficult to understand. Nevertheless, the evolutionary process springing from this simple principle has led to situations which challenge the most imaginative mycological system builder.

The expectation that there will be one anamorph per teleomorph is soon dispelled when the connections compiled by Kendrick and DiCosmo (1979) are examined. It is equally clear that this concept breaks down when considered from either side. Anamorph-species of the anamorph-genus *Chrysosporium* are, *pro tem*, associated with representatives of no fewer than 17 ascomycetous genera (*Ajellomyces*, *Anixiopsis*, *Aphanoascus*, *Apinisia*, *Arachniotus*, *Arthroderma*, *Ctenomyces*, *Echinopodospora*, *Emmonsia*, *Gymnoascus*, *Neoxenophila*, *Renispora*, *Rollandina*, *Thielavia*, *Xanthothecium*, *Zendera*, and *Zopfiella*) and 1 basidiomycetous genus (*Phanerochaete*). Species of *Acremonium* are associated

with 30 ascomycetous teleomorphs. More of this later. Looking at the situation from the other side, we find equally spectacular examples of such dissonances. Kendrick and DiCosmo (1979) list connections established between species of the ascomycetous (teleomorphic) genus *Mycosphaerella* and no fewer than 27 anamorph-genera. *Nectria* and *Leptosphaeria* both have connections with 19 anamorph-genera, and *Ceratocystis* and *Hypomyces* with 15 each. This list can easily be extended with less spectacular, but nevertheless disturbing, examples. The figures following the teleomorph names are the numbers of anamorph-genera connected with each: *Physalospora*, 14; *Guignardia*, 14; *Pleospora*, 11; *Cordyceps*, 10; *Cucurbitaria*, 10; *Chaetosphaeria*, 8; *Massaria*, 8; *Botryosphaeria*, 7; *Pezicula*, 7; *Ophiobolus*, 7; *Didymella*, 7; *Godronia*, 7. Of course these "multiple-anamorph" genera do not, like *Chrysosporium*, break the cardinal rule of "one teleomorph per holomorph," but they still present a tangled thicket for mycologists to penetrate.

What do such lists mean? (1) They mean that an element of inaccuracy is involved; mycologists have traditionally been too narrow in their knowledge of the fungal groups. Some teleomorph specialists have had inadequate concepts of the anamorphic genera they encountered, and some anamorph specialists insufficient acquaintance with the teleomorphic genera—or each has obtained bad advice from the other—and so some of the identifications will be found on closer scrutiny to be wrong. (2) They mean that, if the connections are rechecked and found (largely) to be well-founded, then the integrity of the single genus (whether teleomorphic or anamorphic) to which the many are connected must be rigorously examined, since it may be in need of splitting. (3) If the single genus involved on one side of the question is sound, then we have to accept that the phase on the other side of the equation has undergone tremendous radiative evolution.

None of the foregoing should be taken to mean that we can abandon our efforts to link teleomorph and anamorph: Our data base is enriched by every authentic connection made. It simply means that we must not expect too much from this source—it will not solve all our problems.

### VIII. ANAMORPHIC AND TELEOMORPHIC HOLOMORPHS

When one first encounters the pseudotaxa of anamorphs in the guise of Fungi Imperfecti with appropriate binomials, one is told that these pseudotaxa are ephemera and that an eventual and inevitable epiphany will reunite them with their respective teleomorphs (long arrogantly called perfect states, and still the source of all holomorph names where a teleomorph is known). But even today, after a century of effort, connections remain in the minority. As I have already indicated, I find it difficult to maintain this doctrine of the perfectibility of fungi. Apart from the entire absence of teleomorph associations for many anamorph-

genera, we need only look at other groups of organisms to find examples of how under certain circumstances sexual reproduction can apparently be selected against and sometimes lost. As far as is known, some aphids are obligately parthenogenetic; some mosses have never been seen to fruit; among the flowering plants *Lemna minor*, although capable of flowering, normally reproduces indefinitely in the asexual mode with great success; one of the most common and successful weeds around Adelaide, Australia, is *Oxalis pes-caprae*, which is present in Australia only as a completely sterile pentaploid, reproducing by means of bulbils; in addition, many obligate apomicts in the genera *Rubus*, *Taraxacum*, *Alchemilla*, *Poa*, *Cassia*, and others, though retaining the external trappings of sex, in fact avoid genetic recombination completely and produce fruit only as a highly evolved dispersal mechanism.

Of course, organisms which dispense with genetic recombination are hostages to fortune. Although they have a genome which is superbly attuned to existing conditions, if these conditions should change dramatically, the species is likely to be wiped out, while other more flexible organisms adapt and survive.

But if we now look back at the conidial fungi we find that they are not actually devoid of all opportunity for genetic recombination. The phenomenon of parasexuality may well provide an adequate amount of recombination, and haploid organisms producing the huge numbers of conidia common among molds must obviously give rise to mutant strains. Anastomosis between hyphae of different strains, and the heterokaryosis arising from such encounters, must help to buffer the conidial fungi against environmental fluctuations. In Chapter 14 Wicklow expands on the reasons for the transcendent success of conidial anamorphs. Most of these could also, I am sure, be advanced as reasons for loss of sexuality. All in all, I see few objections to the idea of anamorphic holomorphs, although I know it will be very difficult to prove their existence unequivocally.

It may be equally challenging to establish the existence of teleomorphic holomorphs, but it seems very probable that they too can be found. For example, we know of no anamorphs in entire families of the Ascomycetes—Brefeldiaceae, Mesnieraceae, Micropeltidaceae, Microthyriaceae, Piedraceae, Zopfiaceae—and it now seems unlikely that they will be found. Negative proof is usually difficult to establish and, from what Müller (1979) has shown us about the factors inducing phase change, these are as variable and unpredictable as we might expect from organisms with such diverse ecological requirements as the fungi. Nevertheless, I am sure that many presumptive single-phase holomorphs will eventually be confirmed as such.

## IX. SIMPLE ANAMORPHS—SIMPLISTIC TAXA?

This section could be subtitled, "They all look the same to me." One of the difficulties facing those who would systematize conidial anamorphs is the rela-

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tive paucity of morphological features available in a fairly large number of anamorph-genera. *Chrysosporium*, the anamorph-genus mentioned earlier in connection with a plurality of teleomorphic genera, is an example of this. It does not produce a highly characteristic, differentiated, branched, or otherwise complex conidiophore, and its kind of generalized "chlamydosporic" propagules may well have arisen on many occasions—in fact, its seeming violation of the "one teleomorph per holomorph" rule is convincing evidence for this. A second case is presented by *Rhizoctonia* (strictly speaking, this is one of the Mycelia Sterilia and not a conidial anamorph, but we usually have to deal with this fringe group by default). This anamorph-genus often produces poorly defined microsclerotia in the soil. Anamorph-species of this pseudotaxon have been connected in culture to six different teleomorphic genera (*Ascophanus*, *Ceratobasidium*, *Sebacina*, *Thanatephorus*, *Trichophaea*, *Tulasnella*—Warcup and Talbot, 1966, 1967). Considering that two of these teleomorphs are Ascomycetes, while the other four are Basidiomycetes, it is clear that the current concept of *Rhizoctonia* is insufficiently precise. But from the stature of the mycologists who established the connections, we can be sure that the matter of separating ascomycetous from basidiomycetous anamorphs, even at the anamorph-generic level, will be far from easy.

My last example of an oversimplified anamorph-generic concept arising directly from simple morphology is *Acremonium*. This genus produces simple, often individual, phialides. Although the phialidic mechanism of conidium ontogeny is a fairly complex and highly evolved one (Kendrick, 1971, 1979; Cole and Samson, 1979), the physical reality of single, tapering phialides is outwardly simple in the extreme and conducive neither to the segregation of closely related taxa nor even to the separation of such monophialidic anamorphs evolved as parts of very different holomorphs. If a single anamorph-genus such as *Acremonium* is polyphyletic, as is apparent from its association with no fewer than 30 ascomycetous teleomorphic genera (28 unitunicates, 2 bitunicates—see Kendrick and DiCosmo, 1979), then we must also entertain the possibility that morphologically different phialidic genera such as *Penicillium* and *Chalara* may be only distantly related, despite their relatively similar conidium ontogenies. Each of these two anamorph-genera has, as a matter of fact, relatively homogeneous teleomorphs, but both (and especially *Penicillium*) probably include anamorphic holomorphs among their species.

#### X. GUIDELINES FOR SPECIES AND GENUS

The literature of hyphomycete taxonomy has grown without reference to any overall principles and in a completely unregulated manner. This is good in that it has given workers of talent and initiative the freedom to explore new ground, bu

bad in that it has allowed some of the worst taxonomy I have ever seen to enter the literature. I doubt whether a single formal university course has ever been given to train specific individuals to perform this task. Lumpers and splitters, cognoscenti and ignorami—all have added their contributions, ranging from the invaluable to the invalid. I have often thought that all descriptions of new taxa should be submitted to an international screening committee which would be able to veto inadequate, iterative, or incorrect manuscripts. No such body exists in mycology, with the result that each year sees a further accretion of bad taxa or bad descriptions which will eventually have to be sorted out by someone whose time would be better spent doing original work. Thus, although there should be no need to produce guidelines to anamorph-taxa, perhaps the following outline will be helpful to the beginner.

1. Collections sharing great similarity in almost all known morphological and developmental features (often virtual congruence), and usually having similar habitat or host preferences, can be regarded as conspecific: members of the same anamorph-species.

2. Collections which are as similar to each other as those grouped under the first heading, and which share most major features with that group, yet exhibit one or more marked and consistent differences from that group, are regarded as congeneric though not conspecific with it. The two groups constitute distinct anamorph-species belonging to the same anamorph-genus.

3. Collections which, while sharing major features with the first two groups, are significantly more different from both of them than they are from each other can be regarded as belonging to a different anamorph-genus. Thus intergeneric hiatuses (Singer, 1975) are greater than those found between species within a genus.

4. Above the generic level there are no particularly helpful familial or ordinal groupings: All those encountered should be treated with suspicion.

## XI. THE ANAMORPH-SPECIES AND ITS PROBLEMS

The anamorph-species should not present too much difficulty, once it has been perceived by the individual. The gaining of this perception is a most valuable step in the training of a taxonomist. An important principle is not to make the organism fit the literature. As a fledgling mycologist I found a helicosporous hyphomycete which I tried to identify in Linder's excellent monograph of the group (1929). The closest match I could come up with did not seem perfect, yet because it was the nearest thing in the literature I accepted it and applied the name to the fungus I had found. A subsequent trip to Kew and consultation with Martin Ellis soon convinced me that the species I had found simply was not in the

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literature, and I proceeded to describe it as a new species. That hurdle is an important one for anamorph specialists to overcome, because we know that many new taxa remain to be described. But the manner in which the hurdle is overcome is important too, in that the beginner should have the benefit of experienced advice and should seek it out wherever it may be found, lest he or she become too cautious or too confident.

In most situations, members of the same anamorph-species may be regarded as being genuinely genetically related to one another. Note that this is the only point in anamorph taxonomy at which we can now claim such a relationship.

But of course even the anamorph-species, with which we should have the least trouble, can be relied upon to cause problems. The first of these arises when we discover that what appears to be a single anamorph-species is connected to more than one teleomorph. Now while it is all right for one teleomorph to have two or more different anamorphs (see example given earlier), it is axiomatic that any given fungal genome is capable of giving rise to one, and only one, teleomorphic phase. So when we read of dual or multiple teleomorphs, we are justifiably skeptical. Clearly, the anamorph-species can betray us by concealing genetic heterogeneity beneath the mask of morphological congruence. This is usually a result of convergent evolution, though it may also indicate that some inadequate taxonomy has been going on. Which brings me to the second problem, that of standardization of circumscription. Although the species is the foundation of all taxonomy, no one has yet come up with the perfect prescription, let alone persuaded everyone else to adopt such a concept. A species is still what a taxonomist says it is. And although I am not among those who are willing to abandon their taxonomic prerogatives to some numerical or computerized—and hence suspiciously procrustean—scheme, I believe hyphomycete taxonomists should communicate with each other much more than they do and try to establish realistic guidelines. This will call for some sacrifice of individual freedom in the decision-making process, but it would probably lend taxonomy an extra measure of credibility in the eyes of the scientific community at large. Considering our central role, I think we should strive for and earn such acceptance instead of maintaining the aloof, almost Olympian, attitude some of our fraternity espouse. Needless to say, while promulgating the idea of a degree of conceptual standardization, I lack the temerity, as well as the enormous breadth of knowledge, needed to prepare such proposals. Perhaps they could be formulated at a future Kananaskis Conference.

A third problem of the anamorph-species concept is bound up with information retrieval, for example, in genera with very large numbers of species. While in Australia I collected fungi on *Eucalyptus* but usually found myself entirely unable to decide on which of the about 500 species of the host genus the fungus was growing. Another Australian genus, *Acacia*, is equally large and difficult for the nonspecialist. As the task of describing the world's mycoflora moves slowly

toward completion, fungal examples of this kind of problem will inevitably multiply.

A fourth area in which our current species concept is apparently inadequate is that of economically important or intensively worked genera, in which significant differences (e.g., in biochemistry, or in host-pathogen relationships) have been documented in otherwise almost identical organisms. In some groups such as the rust fungi (which have of course anamorphic phases) this has engendered a trinomial nomenclature—and even this cannot cope with our detailed knowledge of the fungi causing some cereal rusts. In other groups, such as *Penicillium* and *Aspergillus*, this has led to the recognition of infrageneric but supraspecific series, which could easily be regarded as an equivalent of the “aggregate species” recognized by angiosperm taxonomists. The actual anamorph-species of *Penicillium* and *Aspergillus* may well be essentially subspecific taxa and indicate that the groups concerned are speciating rapidly under strong selection pressures.

Just to show that such problems are not universal in conidial fungi, I will cite the example of the anamorph-genus *Arthrimum*, whose species share some very distinctive features—the basauxic growth pattern of their conidiophores; the presence in many species of very thick, darkly pigmented cross-walls in the conidiophores; and the production of often strangely shaped, dark, amerosporous conidia, which often have a well-marked germ slit. Surely this anamorph-genus will eventually be proven to be a good botanical entity (or at least the anamorphic expression of one).

## XII. THE ANAMORPH-GENUS AND ITS PROBLEMS

From 1958 to 1965, in a series of six papers, M. B. Ellis described no fewer than 64 species in the anamorph-genus *Sporidesmium*. The breadth of his interpretation of this genus can be appreciated by browsing through these papers (Ellis, 1958, 1959, 1961, 1963a,b, 1965) and perhaps even from studying Fig. 1. He describes the conidiophores as discrete, mononematous, unbranched, and brown; conidiogenous cells as integrated, terminal, determinate, or percurrent; and conidia as solitary, dry, borne apically, unbranched, and of various shapes (straight, curved, sigmoid, cylindrical, fusiform, obclavate, obpyriform, obturbinate, and sometimes beaked). Their color ranges from subhyaline through straw-colored, to pale or dark brown, olivaceous brown, or reddish brown. Their walls may be smooth or rough. They are transversely septate or pseudoseptate. This is obviously a broad circumscription. In fact, in some senses the limits of this anamorph-genus can be best expressed in terms of the features that currently separate other, similar dematiaceous hyphomycetes from it. *Clasterosporium* and *Ceratophorum* both produce hyphopodia, and in *Annellophora* the conidia

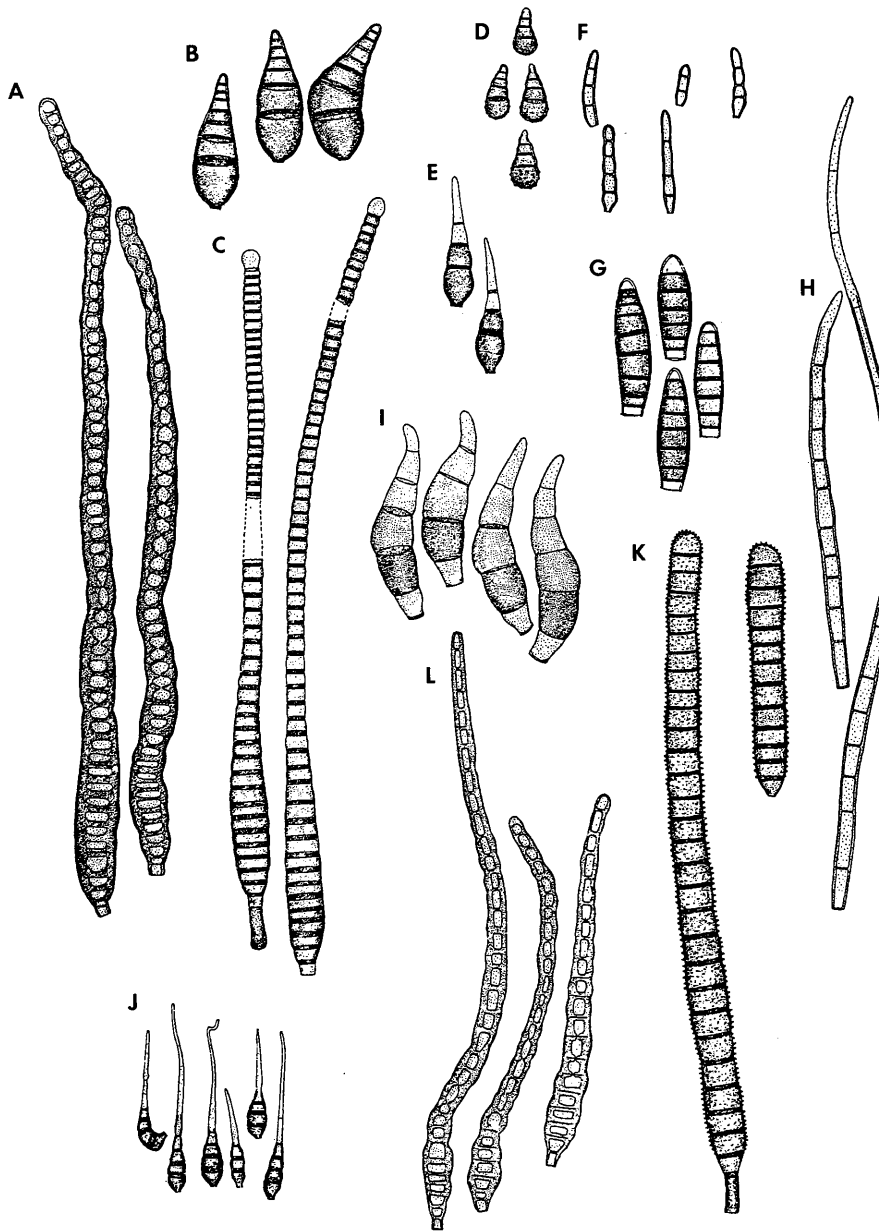


Fig. 1. Conidia of 12 species of *Sporidesmium*, all drawn to the same scale. (A) *Sporidesmium adscendens*; (B) *S. altum*; (C) *S. anglicum*; (D) *S. aturbinatum*; (E) *S. bicolor*; (F) *S. cajani*; (G) *S. cambrense*; (H) *S. eucalypti*; (I) *S. inflatum*; (J) *S. longirostratum*; (K) *S. raphiae*; (L) *S. vagum*. (After M. B. Ellis.)

often proliferate at the apex to form secondary conidiophores and conidia, becoming annellate in the process. *Sporidesmium*, then, lacks hyphopodia, and its conidia do not proliferate. But after these hiatuses have been established, there remains great latitude, which Ellis has clearly made use of. It can be suggested that his generic concept is too broad, that it hinders a ready visualization in the mind's eye of what a *Sporidesmium* looks like. This may be deemed of minor importance, or it may be regarded as a major obstacle to identification of the genus by nonspecialists (think how readily you can visualize some of the common anamorph-genera of the Hyphomycetes—*Aspergillus*, *Penicillium*, *Fusarium*—despite the numerous species each contains). This conflict of interests is one of our perennial problems in information storage and retrieval because, when the generic concept is relatively narrow and easily visualized, species differentiation within the genus is often difficult. When the genus is broadly defined, species differentiation within it may be much easier. We should tread carefully between the extremes I have just outlined, and many taxonomists wander far enough in one direction or the other to exacerbate, rather than minimize, problems of identification—the process of information retrieval may reveal the classification as incompetent. This whole business resembles the family-genus conflict mentioned earlier and seems to be a difficulty inherent in hierarchical schemes. The assignment of characters to the various levels of the hierarchy must be done with great insight and with a fine sense of balance and proportion. Often this is only possible through hindsight, after the units of the classification have initially been established in an *ad hoc* manner (as they usually are) by many different workers at different times.

Because much of hyphomycete taxonomy has so far simply been a matter of convenience, we are burdened with many anamorph-genera which are extremely narrowly defined. The generic characters are either arbitrarily chosen (for example, differences in spore septation) or seem inconsequential to the disinterested (unbiased) observer. I will not cite particular examples, but a number of cases may be discerned with ease from a scrutiny of the plates in Carmichael *et al.* (1980), and some have been discussed in detail by Kendrick (1980).

### XIII. THE INTERGENERIC HIATUS

Booth (1978) pointed out that the evidence for a particular intergeneric hiatus may be drawn from too few collections. Consider species A and G in Fig. 2. The generic constellation to which these two actually belong will ultimately be found to contain 12 species. The catch is that 10 of these have not been collected or described. So A and G may easily be perceived as having a larger taxonomic distance, or hiatus, between them than is actually the case. This may well lead to their being assigned to different genera. In this and other ways, the literature

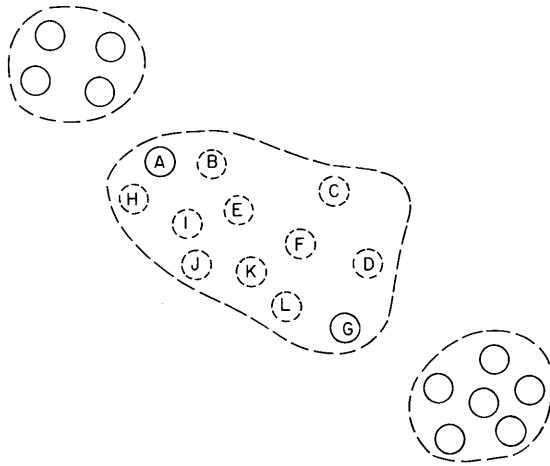


Fig. 2. The intergeneric hiatus.

becomes clogged with genera that will later be recognized as redundant. This process—the description of taxa and their subsequent redundancy—is an inevitable accompaniment of the slow maturation of taxonomy and is not necessarily an indication of any lurking incompetence in those who initially describe these taxa. In some cases, however, the hiatus may be too rigidly and arbitrarily prescribed. Genus X may be defined as having amerosporous conidia, while genus Y, otherwise very similar to X, has didymosporous conidia. Such unthinking reliance on a single generic character is common among the Hyphomycetes and undoubtedly retards taxonomic progress.

#### XIV. THE FOUNDATION

I have printed a rather bleak picture. You may be left with the impression that the work of more than a century has been singularly unproductive. This would not be a fair assessment. I have focused on problem areas and have not discussed the strong points of hyphomycete taxonomy. Perhaps this is a good point at which to try to redress the balance.

We now have hundreds of extremely well-characterized and illustrated anamorph-genera. We have a large number of reliably established connections between anamorph and teleomorph. And despite the fact that no acceptable system has yet emerged, we have many inklings and indications which will serve as intellectual stimuli to the generation of mycologists now gestating in the universities of the world. Let me exemplify these insights.

Hughes (1953) recognized eight ways in which conidial fungi formed their

spores. The proceedings of the first Kananaskis Conference (Kendrick, 1971) reduced the number of basic mechanisms, and we are now aware that, for example, phialidic conidium ontogeny and annellidic conidium ontogeny are more closely related than we believed then. Hughes's initial analytic exercise was parent to all subsequent versions (inevitably it too had antecedents, for which refer to Kendrick, this volume, Chapter 1). Without the initial splitting, the subsequent refinements would never have been realized. I have often stressed the usefulness of an initial splitting process in erecting classifications. This prevents loss of information during the subsequent (and almost inevitable) lumping that ensues when the disguise of superficial differences is penetrated and underlying similarities are perceived. Barron (this series, Vol. II, Chapter 20) suggests that, with one exception, all the adhesive-spored Hyphomycetes which are endoparasites of minute soil animals are probably related to *Verticillium*: this despite the fact that they have been described in *Cephalosporium*, *Harposporium*, *Meria*, *Plesiospora*, *Cephalosporiopsis*, and *Paecilomyces*. Barron thinks they are probably all derived from verticillate ancestors and are more closely related to each other than to other species of the genera in which they were described.

I had earlier (in Schenck *et al.*, 1977) arrived at similar conclusions about a number of nematode-trapping Hyphomycetes with sympodially proliferating conidiophores, and conidia which were amerosporous, didymosporous, or phragmosporous. Although they were distributed among the anamorph-genera *Arthrobotrys*, *Dactylaria*, *Candelabrella*, and *Genicularia*, the last two names may be considered as doubtfully distinct from *Arthrobotrys*, which is much the earliest name, and the nematode-trapping *Dactylaria* species were separated from *Arthrobotrys* only by their phragmosporous conidia. *Arthrobotrys* was traditionally treated as being exclusively didymosporous, but at least two amerosporous species have now been described, and it seems illogical to exclude phragmosporous but otherwise similar *Dactylaria* species, especially when the type species of this genus grows on wood and does not trap nematodes.

For many years, obligately dimorphic anamorph-genera bedeviled our attempts to establish a classification of anamorphs. We recently (Carmichael *et al.*, 1980) took what seems to us the eminently sensible step of applying the appropriate generic name (if one existed) to each of the associated morphs. Thus the dimorphic name *Chalaropsis* is now recognized as a pleomorphic anamorph, with morphs in *Chalara* and in *Humicola*. The pleomorphic anamorph-genus *Diheterospora* is logically dissected into its *Stemphyliopsis* and *Verticillium* morphs.

From ongoing studies of such groups as the nectrioid fungi we are learning more about relationships which override such Saccardoan features as conidiophore aggregation or the lack of it. We have learned, the hard way, that the grouping of anamorphs by morphological similarity alone is often misleading, and we are looking more deeply into this. The anamorph specialist must now

learn to spot characters more subtle yet more basic than any used so far. What are these features, and where does the future lie?

I once wrote that I thought the future lay in an understanding of fungal ecology and the impact that ecological pressures had made on fungal phenotypes during the course of evolution. I still believe this will be of enormous help. But I also feel that we need as many other kinds of data as possible to make up for the relative dearth of fossils (or, rather, knowledge about them) and the relative morphological simplicity of most fungi. To follow the lead of botanists, we need to establish our species on a more nearly genetic base. This means, among other things, chromosome counts. I used to think this was a pipedream as far as the conidial fungi were concerned, since their nuclei are small and the chromosomes have been assumed to be extremely contracted or compacted together, and thus very difficult if not impossible to count and characterize. But this kind of information is now within reach, as Robinow shows (this series, Vol. 2, Chapter 25). I am confident that other now apparently inaccessible kinds of data will become available in the years ahead and will ultimately make it possible to produce a truly rational classification of the conidial anamorph, dovetailed into that of the whole fungus.

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