„Subdivision Deuteromycotina" – a fungal chimera

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I want to begin by paying homage to the achievements of Dr. VON ARX. His work covered an amazingly wide range of fungi, and the conceptual rapprochement between yeasts and filamentous fungi which he single-handedly crafted was a mycological milestone. It was always a stimulating experience to correspond and collaborate with him. Dr. VON ARX was one of the pivotal figures of twentieth-century mycology, and his death is a great loss for us and our discipline. The paper which follows attempts to perceive and follow the kind of logical and consistent intellectual path which was so characteristic of Dr. VON ARX'S work.

I should explain a few basic concepts as background for my main theme. The first concept can be stated as a general case equation, and it has been widely accepted for some years: **Holomorph = Teleomorph + Anamorph(s)**. This means that the reproductive expressions of an entire fungal genome (the holomorph) may include a sexually reproducing phase or morph (the teleomorph) and one or more asexually reproducing phases or morphs (the anamorph[s]). There is some implication in the equation that most, if not all, fungi may ultimately be expected to exhibit both sexually and asexually reproducing morphs. In the real world, however, the fungi depart significantly from such ideal behaviour.

The second expression: **Holomorph = Teleomorph**, is generally regarded as a reduced derivative of the first, and many mycologists assume that this means either that the teleomorph never had an associated anamorph, or that the anamorph ceased to play a significant role in perpetuating the species, and was selected against. No-one seems too upset about this concept: indeed, many mycologists who work with teleomorphs seem to worry little, if at all, about the possible existence of anamorphs as part of the life cycles of their organisms, and make no mention of their presence or absence.

The third expression: **Holomorph = Anamorph(s)**, is a more recent and perhaps more radical concept, but carries equally serious evolutionary implications, because it implies that sexual reproduction can be abandoned, and the entire burden of maintaining the species placed on the asexual phase(s). Many mycologists still consider this concept heretical, despite the existence of a growing body of supporting evidence.

What are the implications of those expressions for fungal taxonomy? Part of the problem lies in the way ascomycetes and basidiomycetes are defined, not only in elementary survey courses, but also in respected reference works. I quote the *Dictionary of the Fungi* (HAWKSWORTH et al., 1983), which defines the Subdivision Ascomycotina as „The largest group of Fungi, for which the ascus ... is the diagnostic character." Although anamorphs are given some prominence in the treatment of some of the various orders of ascomycetes which follows the definition, nowhere is it stated that anamorphs alone can be regarded as ascomycetes. This omission is significant. If the ascus is indeed accepted as the single, overriding diagnostic feature of ascomycetes, then it is hardly surprising that mycologists who must deal with the many moulds (almost all ascomycetous anamorphs minus teleomorphs) which are typically isolated from soil, plant substrates and air, look for another pigeonhole for the conidial fungi.

The situation is equally problematic for the basidiomycetes. The *Dictionary of the Fungi* pronounces as follows: „The diagnostic character of this Subdivision is the presence of a basidium ..." This statement leaves a large number of sturdily independent basidiomycetous anamorphs (KENDRICK & WATLING, 1979) in taxonomic limbo.

Let me examine for a moment the way in which the other major fungal groups, the zygomycetes and oomycetes, are treated. If we find a *Mucor* that is producing only asexual sporangia, we do not suggest that it belongs to some other group. Mycologists apparently assume (correctly, in my opinion) that somewhere in its genome lies, or once lay, the potential to produce zygosporangia. This appropriate inference may spring at least partly from the fact that no-one has ever suggested a separate slate of names for zygomycetous anamorphs. *Mucor* without its zygosporangia is still *Mucor,* and it is still very much a member of the Division Zygomycota. This may be because *Mucor* was originally named on the basis of the sporangial anamorph long before the zygosporangia were discovered. Interestingly enough, the zygomycetes are not accorded an official definition in the *Dictionary of the Fungi.* But that might conceivably be because there is so little controversy about it.

Perhaps I may be excused for characterizing the Division

Oomycota by *Phytophthora infestans,* the causal organism of late blight of potato. When it arrived in Europe in the 1840's, only one strain of this heterothallic species made the trip, so no oospores could be found. Despite this gaping hole in the life cycle of the organism, it reproduced more than adequately in its anamorphic incarnation, created incredible havoc, and was eventually understood to be an oomycete. Again, no-one has proposed a separate system of names for oomycetous anamorphs, despite the fact that these can develop in the complete absence of the supposedly diagnostic teleomorph. I note that the *Dictionary of the Fungi* states that „Oospores (occasionally absent) and biflagellate zoospores (absent in some terrestrial spp. where the vegetative spore is a conidium) are characteristic." In that definition, with its built-in caveats, there seems to be a tacit assumption that we can actually recognize an oomycete without either of those diagnostic features.

I would assert that it is equally possible to recognize a member of the Division Dikaryomycota in the absence of asci or basidia. It is often possible to tell whether an anamorph with regularly septate hyphae belongs to the ascomycetes or the basidiomycetes. Dikaryotic basidiomycetous anamorphs frequently bear clamp connections (sometimes even between the cells of phragmo- or stauroconidia), and monokaryotic or dikaryotic basidiomycetous anamorphs can often be placed by mycelial characters, by biochemical tests for the presence of xylose, or by electron microscopy that reveals the multilayered nature of the hyphal wall and the presence of dolipore septa. DNA fingerprinting is now an additional possibility. Despite the existence of these diagnostic tools, the „Deuteromycotina" has been widely recognized, and used as a dump for thousands of conidial fungi.

This seems to be at least partly because mycologists long ago began to give separate binomials to dikaryomycotan anamorphs, simply because they did not know what the teleomorphs were. Eventually this process appears to have generated the impression that this growing collection of names needed a special high-ranking taxon of its own, and a separate kind of classification within that taxon. The latter is justified: the former is not.

In all fairness I must mention that many dikaryomycotan anamorphs (actually a large majority) have not been connected to teleomorphs, and that even in cases where the connections are known, the separate binomials are legally permitted to coexist because so many anamorphs develop remote from their known teleomorphs in time, in space, and even in substrate. The two phases also look completely different from one another, so they lend themselves to classification on the basis of different characters, and they can be „connected" only by painstaking observational or cultural

techniques (KENDRICK et al., 1979). DNA techniques will help solve this problem.

Entirely separate schemes of taxonomy grew up for the anamorphic and teleomorphic assemblages, and their truly interconnected nature was widely overlooked, or deliberately ignored. Even where connections between anamorphs and teleomorphs had been made in culture, it was unsafe to extrapolate from a single observation to every similar anamorph collected, since some groups of easily separable teleomorph genera apparently shared virtually indistinguishable anamorphs, while other groups of almost identical teleomorph genera were individually associated with very different anamorphs.

And there was another more practical problem: if we filed anamorphs in herbaria under the name of the teleomorph, it would be a common occurrence to discover whole folders full of specimens bearing only anamorphs, with never a teleomorph to be found. This biased situation could arise because the anamorph is often common throughout the growing season on conspicuous substrates, while the teleomorph may either be intrinsically rare, or be produced only briefly, for example in Spring, on cryptic substrates.

In the earlier days of mycology there might have been some excuse for erecting a separate major taxon for anamorphs. But now that we know literally thousands of connections (mainly in the Ascomycetes [KENDRICK & DICOSMO, 1979], but also in the Basidiomycetes [KENDRICK & WATLING, 1979]), there can no longer be any reason to perpetuate this confusing situation.

We must accept that, just as there are microcyclic rust fungi (Uredinales, Teliomycetes), there are almost certainly microcyclic ascomycetes and basidiomycetęs. On the one hand, some which are exclusively teleomorphic will have lost their anamorph(s), while others may never have had such morphs. On the other hand, we assume that all anamorphs which no longer have teleomorphs did produce them at some earlier time, but must have lost them as a result of selection pressure. We cannot as yet prove that the second and third expressions at the beginning of this paper are true representations of the real world, since a single positive observation can override a thousand false negatives. But there is much circumstantial evidence which strongly suggests that there are teleomorphic holomorphs, and also anamorphic holomorphs.

The *Dictionary of the Fungi* defines „Subdivision Deuteromycotina" as follows: „The diagnostic characteristics of this miscellaneous assemblage is [sic] the absence of a teleomorph ... It is convenient, though not strictly correct, to treat them as a Subdivision. Other Subdivisions of the Eumycota are separated not by the anamorph ... but by characteristics of the teleomorph." Unfor-

tunately, this caveat is rather cryptic, and is, in any case, overlooked by many mycologists who are not directly concerned with the issue. In my view, it is conceptually dangerous and misleading to speak of the „Deuteromycotina" as if they constituted an actual Subdivision, with all the evolutionary implications that entails.

As the *Dictionary of the Fungi* goes on to say: „Most deuteromycetes are anamorphs of ascomycetes, a few have basidiomycetous affinities." Exactly. We are talking about **Ascomycetes** and **Basidiomycetes**. The fact that they do not, in this particular incarnation (phenotype), produce asci or basidia, is irrelevant. Do we worry that, because a Lepidopteran larva does not have six legs, it might not be an insect? Are we fooled, by the absence of sexually reproductive flowers from many Angiosperms during eleven months of the year, into believing that they are not flowering plants? Then why do we still insist that the anamorphic expressions of ascomycetous and basidiomycetous genomes be placed in a separate, and entirely spurious, taxon?

Part of the trouble may also spring from the International Code of Botanical Nomenclature (Voss et al. [Eds.] 1983). Article 59 deals with the names of fungi with a pleomorphic life cycle, and although it does not actually pronounce on the ultimate taxonomic disposition of anamorphs without teleomorphs, it does seem to frown on their possible recognition as holomorphs. It does so by insisting (Para. 59.1) that „the correct name covering the holomorph (i.e., the species in all its morphs) is – except for lichen-forming fungi – the earliest legitimate name typified by an element representing the teleomorph, i.e. the morph characterized by the production of asci/ascospores, basidia/basidiospores, teliospores, or other basidium-bearing organs." The second-class status of the anamorph is confirmed by Para. 59.4, which states that „The priority of names of holomorphs at any rank is not affected by the earlier publication of names of anamorphs judged to be correlated morphs of the holomorph." Such strictures should have the effect of making people cautious about erecting high-rank taxa for anamorphs, since the lower ranking taxa of which they are composed may disappear at any second. But their exclusion from the holomorphic elite has apparently had the opposite effect. On the one hand, mycologists expect the taxa to be submerged in later-named teleomorphs; on the other hand, anamorph-taxa are considered worthy of their own Subdivision. Logically, we cannot have it both ways.

The successful anamorph genera *Penicillium* and *Aspergillus* are worth examining as practical examples of the difficulties involved in the taxonomic placement of anamorphs. A considerable number of species of *Aspergillus* are known to be the anamorphs of named species in the ascomycete genera *Chaetosartorya, Dichlaena,*

Edyuillia, Emericella, Eurotium, Fennellia, Gymnoeurotium, Harpezomyces, Hemicarpenteles, Neosartorya, Petromyces, Sclerocleista and*Warcupiella* (KENDRICK & DICOSMO, 1979). But many more species of *Aspergillus* have **not** been connected to any known teleomorph. Likewise, a large number of species of *Penicillium* are known to be the anamorphs of named species in the ascomycete genera *Eupenicillium, Talaromyces* and *Trichocoma;* but an even larger number of species of *Penicillium* have **not** been connected to any known teleomorph. It is interesting to note that, although at least sixteen different ascomycete genera have been shown to contain teleomorphs of *Aspergillus* and *Penicillium,* all sixteen have been placed in a single family, the Trichocomaceae of the order Eurotiales. I see no reason whatsoever to doubt that the other aspergilli and penicillia are also members of the same family and order. The fact that they do not produce asci must not place them in some kind of taxonomic limbo. This does raise the question of when they may be expected to take their place among the properly connected holomorphs. To which my answer is: any of the following – this year, next year, sometime, never. New connections will continue to be established for many years to come. But we have no reason to anticipate that this herculean task will ever be completed. Many of those missing teleomorphs may no longer exist. It is probable, if not certain, that many anamorphic fungi have become so well adapted to life in the conidial lane, with its heterokaryotic flexibility, and its parasexual recombinatoric possibilities, that the teleomorph has become redundant, and has been effectively dropped from the life cycle altogether.

Our suspicions that this may indeed be the outcome of our search are aroused by the fact that the number of new anamorph taxa being described far exceeds the number of connections being made. This is not proof, because the process of making connections is slow and painstaking compared to that of description. But there is other evidence. One of the best ways of establishing anamorph-teleomorph relations is to germinate single ascospores and see if anamorphs develop. As this is done in more and more groups of ascomycetes, an interesting trend has emerged. The anamorphs that do develop are frequently not the common, well-known yet unconnected taxa, but are new anamorph species (SAMUELS, pers. comm.) This reinforces my conviction that many common anamorphs will never be linked to teleomorphs and will ultimately be demonstrated to be anamorphic holomorphs.

The „Deuteromycotina" might well have been established for taxa such as these, because although it is obvious that an unconnected *Penicillium* is nevertheless representative of a Eurotialean genome, there are many other anamorph taxa for which the disposi-

tion of the teleomorph is far less obvious. And of course there is the difficulty of telling ascomycetous and basidiomycetous anamorphs apart in the absence of any knowledge of their teleomorphs. For the purposes of the present discussion, this difficulty is reduced, though not eliminated, by treating the Ascomycotina and the Basidiomycotina as Subdivisions within the Division Dikaryomycota: all true conidial fungi can reliably be termed Dikaryomycotan anamorphs.

The „Deuteromycotina" were not always so formally named: they were formerly known as the „Fungi Imperfecti". This quaint term, which served several generations of mycologists, implied that only the part of the life cycle exhibiting sexual reproduction could be regarded as „perfect". Young mycologists were raised in the fervent hope and belief that eventually, the „imperfect" fungi would pass away, and would all be known in their perfect, sexually reproducing condition. As I have already indicated, many of us have long since abandoned that faith in favour of a more pragmatic philosophy. But it is still possible to see how this earlier example of wishful thinking influences the way in which many non-specialists think. Long after a classification has changed, or a taxonomic concept has been abandoned in favour of a better one, the ghost of the old idea continues to haunt and confuse us. While it is obviously necessary and acceptable to establish anamorph genera and anamorph species, the extrapolation of this idea to the rank of Subdivision was, in my view, a mistake. A Subdivision must represent a single, distinct evolutionary pathway. The spurious „Subdivision Deuteromycotina" includes conidial forms of two divergent evolutionary lines, and some authors speak of conidial zygomycetes and conidial morphs of oomycetes as well, though these do not have separate binomials.

From this mycologist's point of view, one of the interesting minutiae gleaned from the book *Pleomorphic Fungi: The Diversity and its Taxonomic Implications* (Sugiyama [Ed.], 1987), is that of the no fewer than 17 authors who contributed to the book, only one mentions the taxonomic Subdivision „Deuteromycotina" by name. This might be regarded as an aberration, considering that the mycological literature as a whole is fairly littered with references to this „taxon". But if we examine an almost equally recent volume: *Evolutionary Biology of the Fungi* (Rayner et al. [Eds.], 1986), we will notice an almost equal reticence with regard to this word – it is found on only two pages out of 448. Such neglect may be accidental, a mere oversight on the part of almost all of the 51 contributors to the two volumes. But although none of them addresses the issue directly, I believe that the omission is deliberate, and represents a healthy trend. In the first place, these are very general volumes, dealing respectively with most, and with all, of the fungal spectrum. Secondly, one of the books is concerned almost entirely with

anamorph-teleomorph connections and their taxonomic and evolutionary implications; and those implications surely extend to members of anamorph-genera such as *Penicillium* and *Aspergillus* for which connections haven't yet been made – even to those for which they may never be made. Thirdly, the matter of life cycles is of basic concern to evolutionists, and a large taxon that encompasses the asexual phase of many thousands of fungi could hardly be overlooked by anyone concerned with „the big picture". It looks as if the „D"-word is on its way out, at least as far as the cognoscenti are concerned. This article is an attempt to assist it on its way to a well deserved obscurity.

If we must have a name for unconnected dikaryomycotan anamorphs, it should be of such a nature as to clearly indicate that it is an informal group, and not a part of the regular taxonomic hierarchy – **Conidial Fungi** or **Fungi Anamorphici** would seem to fill the bill.

And while we are at it, we might reconsider the current misuse of our formal Class terminology for the assemblages of anamorphs now placed in the „Classes" Hyphomycetes and Coelomycetes. These, too, are artificial categories, which are not even particularly distinct. If we examine such anamorph genera as *Conicomyces* (Sinclair & al., 1983; Illman & White, 1985), *Koorchaloma* (Nag Raj, 1984), *Leptoxyphium* (Roquebert & Bury, 1988), *Myrothecium* (Nag Raj, pers. comm.; Tulloch, 1972), *Pycnofusarium* (Kendrick & Nag Raj, 1979; Nag Raj, 1981; Sutton, 1986), and *Thyrsidina* (Nag Raj & Dicosmo, 1978), we will see that they produce conidiomata that can be interpreted as intermediate between those diagnostic of the Hyphomycetes and those characteristic of the Coelomycetes. It is also worth pointing out that both groups contain ascomycetous and basidiomycetous anamorphs, and so cannot be regarded as monophyletic, unless we go back many millions of years to the presumed common ancestor of the Ascomycetes and Basidiomycetes.

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