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- A REAPPRAISAL

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## THE GENERIC CONCEPT IN HYPHOMYCETES - A REAPPRAISAL

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### ABSTRACT

It is postulated that there are now too many genera of Hyphomycetes. The characters used to define them are often inadequate, poorly defined or purely monothetic, and the construction of workable keys has become impossible. The condensation of many groups of genera is suggested, and several possible strategies proposed. Several genera centered on *Beltrania* are analyzed in detail; four other groups of genera are also discussed. Finally, the dangers of ignoring convergent evolution are stressed.

### INTRODUCTION

As one of the prime movers in the production of two illustrated compendia of hyphomycete anamorph-genera (Kendrick & Carmichael 1973, Carmichael et al. 1980) I have noted with some despondency the enormously variable amount of confidence we can place in the different descriptions and illustrations scattered through the literature. What a motley assemblage the genera of hyphomycetes are. How could they be anything else, conceived as they have been over a

span of two centuries, and in the minds of hundreds of different authors? But the task of compilation was such that we had to focus all our energies on the main objective, rein in our critical faculties (to some extent), and postpone the issue of revision and rationalization.\*

Yet these compilations surely allow us, for the first time, to survey our generic patrimony as a whole. I hope that from this ability will spring a dialogue among mycologists about the anamorph-generic concept, and the usefulness of existing genera. This paper is intended as a contribution to such a dialogue.

We deplore the lack of a fossil or genetic base for our classification, and generally agree that anamorph-taxa are mainly matters of convenience. It is my thesis that the number of anamorph-genera of hyphomycetes has already risen to a point where it is no longer convenient. Not only that, but new genera are being proposed in increasing numbers. In 1973 Kendrick & Carmichael recognised about 600 'good' genera. This number has now risen to nearly 900 (Carmichael et al. 1980). It seems inevitable that we will be confronted by well over one thousand such genera long before the end of the century.

Why does this matter? It matters because, having decided that an unknown fungus belongs to the anamorph-class hyphomycetes, the seeker-after-identification (the consumer) must immediately choose among this excessively large, and growing, number, and may encounter two serious, and worsening, difficulties. The first involves the characters used in delimiting genera. As the number of genera grows, the taxonomic gaps which should help to define them are being filled in, or are at least narrowing, sometimes to the point of imperceptibility. New genera are being erected on smaller and smaller bases, and existing genera are being carved up by the recognition of segregate genera. Sometimes these activities are justified by

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\* I use this word in the sense of making rational rather than in its frequent interpretation as explaining away irrationality.

differences which, though small, are fundamental (e.g. dolipore septa vs. simple septa - an example of this is cited later in this paper). And, of course, as any experienced taxonomist knows, distinctive segments of the anamorph spectrum remain to be described. But fairly frequently the description of new genera is merely an exercise in splitting hairs. Such exercises serve only to confuse and frustrate the consumer. Here is a powerful reason for a selective but significant reduction in the rate of description of new genera and in the number of genera currently accepted.

The second difficulty involves the mechanics of the system of information storage and retrieval which the consumer must use when trying to identify an unknown. None of the traditional systems can cope properly with 900 genera. Anyone who has picked their way through an extended dichotomous key to hyphomycetes knows that the chance of error increases with each choice made. After encountering a hundred or so couplets, the seeker will usually come up with a name, but may well feel that they have compromised and guessed their way into error. Synoptic keys (Korf 1972, Michaelides et al. 1979) sidestep the endless choosing and allow entry at any point, but are unsuited for use with large numbers of taxa.

If the hyphomycetes could be reasonably classified in a hierarchical manner by means of acceptable orders and families, the monolithic dichotomous key, such as that in Ellis (1971), could be replaced by a number of shorter, more manageable keys: one to the orders; then perhaps one to the families within each order, then one to the genera within each family.

Unfortunately, and probably for the reasons given in detail by Kendrick (1980), hyphomycete taxonomists have largely rejected families and orders for their organisms. Those suprageneric categories erected by Saccardo have fallen into disuse, and those proposed by several more recent authors simply have not caught on, because they ultimately lack credibility. What I wrote about hyphomycetologists in 1971 still holds true: "I often liken a hyphomycete specialist to someone

holding a large bunch of balloons (the better the specialist, the larger the bunch of balloons!) Each balloon is a hyphomycete [genus] and each has a separate, independent string leading to it". The balloons are in danger of becoming unmanageable.

Since we cannot bring ourselves to adopt suprageneric categories, it seems to me that a reasonable alternative would be to attempt some condensation of genera, and shift some of the load from the 'generic key' to the 'species keys' that can easily be constructed for even fairly large genera.

One of the aims of this paper will be to show, by means of selected examples, that such a shift could be implemented.

#### PROPOSED PHASES IN CONDENSATION OF GENERA

I envisage several phases of the condensation process.

1. The first, with which this paper is chiefly concerned, involves the fusion of groups of very similar and, in all probability, truly related genera. The genera in many of these related groups are in fact readily separable in a monothetic way - often by single but well marked characters. Nevertheless, their relatedness enables us to adopt a polythetic generic concept, so that a single larger genus can embrace several extant but narrow genera.

2. A second phase could involve groups of genera in which the very morphological simplicity of the organisms makes one wonder about the convenience and validity of the existing generic delimitations. One such group produces rounded, dark, asexual chlamydo-spores - *Humicola* Traaen, *Gilmaniella* Barron, *Thermomyces* Tsiklinskaya, *Acremoniula* Ciferri, *Desertella* Mouchacca, *Botryoderma* Papendorf & Upadhyay -- and if we extend consideration to dark asexual chlamydo-spores of other shapes, the genera *Rhinocladium* Saccardo & Marchal, *Mammaria* Cesati and *Echinobotryum* Corda can be added.

3. A third phase could involve genera which are morphologically very similar but have different modes of conidiation. Although the fashion in recent years has been to separate such anamorphic fungi, there may be good reasons for reconsidering this position.

For many years von Arx among others has maintained that if the differences between two 'genera' were too inconspicuous to be readily recognised then those genera should not, for all practical purposes, be maintained as separate. His position was well stated by Hennebert (in Kendrick 1971: 115). "Dr. von Arx does not make any distinction between phialides and annelliphores. His keys to genera of Hyphomycetes are based on the assumption that for all practical purposes there are no distinguishing characters. He will assert that, since the conidiogenous cell of *Cryptosporiopsis* looks like a phialide in ordinary light microscopy, and has long been called a phialide, he will maintain that usage. Remember also that we may in future decide that poroconidia are really only blastoconidia, and that many phialides are really annellides when we look at their internal arrangements. So von Arx may have some reason to ignore the fine differences between phialides and annellides. We must be careful in making keys. They are only tools, not classifications. They must be practical. Not everyone can look at fungi with an electron microscope to identify them."

For years, caught up as many of us were in the search for features of conidium development, we rejected von Arx's thesis, and called upon each other to push the light microscope to the limits of resolution, and even bring the electron microscope to bear, in order to distinguish between such annellidic, phialidic and sympodial 'genera' as *Leptographium* Lagerberg & Melin, *Phialocephala* Kendrick and *Verticicladiella* Hughes. But now we have come to realise that ontogeny is often much less conservative, and much more plastic, than we had hoped (Madelin 1979, Kendrick 1978) and it is being relegated to the status of just another character, rather than the character. It also appears that the differences between phialides and annellides are more in their externals than in their inner workings.

In his recent revision of *Cladobotryum* Nees ex Steudel, de Hoog (1978) states that "Although markedly different types of conidiation are present in this group of fungi, these characters alone are not sufficient for the delimitation of the genera. They are used here only in combination with other criteria". And indeed, evidence from anamorph-teleomorph connections often runs counter to that from conidium ontogeny. (See Kendrick & DiCosmo 1979, Madelin 1979). So it seems reasonable, when both morphology and relationship point in the same direction, to reconsider some of the ontogenetically based generic segregations made in recent years. Since *Leptographium*, *Verticicladiella* and *Phialocephala* have very similar, complex conidiphores, and in some cases are associated with teleomorphs in *Ceratocystis* Ellis & Halst., it might be reasonable, as well as convenient, to group them within a single anamorph-genus.

4. A fourth phase might concern itself with recognizing morphological and developmental similarities between some mononematous, synnematos, and possibly even sporodochial and acervular genera, e.g. *Leptographium-Graphium* Corda, *Verticicladiella-Pesotum* Crane & Schoknecht, *Gamsia* Morelet - *Gymmodochium* Masee & Salmon. This phase could explore our growing conviction (Kendrick & Nag Raj 1979) that the gap apparently separating hyphomycetes and coelomycetes is largely illusory. Certainly there seem to be series in which the sporodochial conidioma passes by imperceptible gradations into the acervular conidioma. Genera now placed on opposite sides of this dichotomy might eventually be united. Dr Nag Raj (pers. comm.) is currently exploring this possibility.

In our long search for a more natural basis on which to classify fungi, we must use our growing knowledge of anamorph-teleomorph connections to detect similarities that may underlie and supersede the old categories 'mononematous-synnematous-sporodochial-acervular.' Eventually we may perceive in the ascomycetes and basidiomycetes as a whole a beautifully regular pattern like that found among the anamorphs of the rust fungi, and we must keep such possibilities in mind. This fourth phase might well serve more than one purpose: a glance at the synnematal 'genera' compiled

by Carmichael et al. (1980) shows that a lot of them seem virtually indistinguishable, e.g. *Crinula* Fries - *Dendrostilbella* Höhnelt - *Phialographium* Upadhyay & Kendrick. This is a sure sign that many such genera need to be critically re-examined. Taxonomists please note.

5. A fifth phase could bring about the final and long overdue extirpation of those anamorph-genera obligately based on the co-occurrence of two different anamorphs on the same mycelium, e.g. *Thielaviopsis* Went, *Chalaropsis* Peyronel, *Dimorphospora* Tubaki, *Duosporium* Thind & Rawla, *Diheterospora* Kamyschko, *Dwayabeeja* Subramanian, *Triadelphia* Shearer & Crane, *Mycochlamys* Marchand & Cabral. In most cases generic names already exist for the individual anamorphs of which these composite genera are made up. For example, *Chalaropsis* is an unnecessary name for a *Chalara* (Corda) Rabenhorst and a *Humicola*. *Mycochlamys* comprises a *Humicola* and a *Scytalidium* Pesante.

Other phases may emerge during the debate, but it is time to return to the main theme of this paper - what I have called phase one.

#### PROPOSED AMALGAMATION OF CONTIGUOUS GENERA

Perusing the 129 plates in Carmichael et al. (1980) and the fine illustrations in Ellis (1971, 1976) one is occasionally struck by groups of 'genera' whose members exhibit what might be called a 'family likeness'. These are the first candidates for a more detailed scrutiny. The following 26 groupings will exemplify the idea.

- (*Chalara* - *Chaetochalara* Sutton & Pirozynski)
- (*Catenularia* Grove ex Saccardo - *Chloridium* Link - *Dischloridium* Sutton - *Bisporomyces* van Beyma)
- (*Clonostachys* Corda - *Mariannaea* Arnaud)
- (*Selenosporella* Arnaud ex McGarvie - *Umbellidion* Sutton & Hodges)
- (*Beltrania* Penzig - *Beltraniopsis* Batista & Bezerra
- Ellisiopsis* Batista - *Beltraniella* Subramanian - *Pseudobeltrania* P. Hennings)
- (*Rhinocladiella* Nannfeldt - *Ramichloridium* Stahel ex de Hoog)

- (*Phymatotrichopsis* Hennebert - *Amphobotrys*  
 Hennebert - *Dichobotrys* Hennebert -  
*Glischroderma* Fuckel - *Pulchromyces* Hennebert -  
*Chromelosporium* Corda - *Streptobotrys*  
 Hennebert - *Verrucobotrys* Hennebert - *Botrytis*  
 Persoon ex Fries)  
 (*Haplobasidium* Eriksson - *Echinocatena* Campbell &  
 Sutton - *Lacellinopsis* Subramanian)  
 (*Fulvia* Ciferri - *Alysidiopsis* Sutton - *Cladospo-*  
*rium* Link ex Fries - *Sorocybe* Fries)  
 (*Ovulariopsis* Patouillard & Hariot - *Oidium*  
 Saccardo)  
 (*Staheliella* van Emden - *Botryomonilia* Goos &  
 Pirozynski - *Oidiodendron* Robak)  
 (*Antromycopsis* Patouillard & Trabut - *Sclerostilbum*  
 Povah)  
 (*Arthrinium* Kunze ex Fries - *Cordella* Spegazzini-  
*Pteroconium* Saccardo ex Grove)  
 (*Mycosylva* Tulloch - *Pachmodium* Upadhyay &  
 Kendrick)  
 (*Circinotrichum* Nees ex Persoon - *Gyrothrix* (Corda)  
 Corda - *Ceratocladium* Patouillard)  
 (*Hyphodiscosia* Lodha & Chandra Reddy - *Leptodis-*  
*cella* Papendorf)  
 (*Cylindrotrichum* Bonorden - *Chaetopsis* Greville)  
 (*Cyphellophora* de Vries - *Phialogeniculata*  
 Matsushima - *Phialophora* Medlar)  
 (*Myrothecium* Tode ex Fries - *Septomyrothecium*  
 Matsushima)  
 (*Torula* Persoon ex Fries - *Dwayabeeja* Subramanian -  
*Bahusaganda* Subramanian)  
 (*Septonema* Corda - *Lylea* Morgan-Jones)  
 (*Varicosporium* Kegel - *Dendrospora* Ingold -  
*Dendrosporomyces* Nawawi, Webster & Davey)  
 (*Scorpiosporium* Iqbal - *Tricladium* Ingold)  
 (*Heliscus* Saccardo - *Clavatospora* Nilsson)

Such groups have both morphological and development-  
 al similarities, and many are also cemented by our know-  
 ledge of the respective teleomorphs. It would obviously  
 take far too long to discuss all of them, so I have  
 selected five examples for further consideration. The  
 first of these may be regarded as a test case and has  
 been set forth in considerable detail.

1) *Beltrania*-*Beltraniopsis*-*Ellisiopsis*-*Beltraniella*-*Pseudobeltrania*

The anamorph-genus *Beltrania* Penzig 1882 was erected for the single species *B.rhombica* Penzig. *B.querna* Harkness was added two years later. In 1886 Penzig and Saccardo thought the conidia were didymosporous, and although Penzig's type specimen has been lost, a clearly recognizable concept had been established, and by 1963, when Pirozynski's beautifully illustrated account of the tribe appeared, it had grown to six anamorph-genera with 11 species in all. This despite Pirozynski's recognition of a very broad 'neoconcept' for *B.rhombica*, and his synonymization of *B.indica* Subramanian and *B.multispora* Swart with it.

In the intervening seventeen years the number of species in the tribe has doubled, reflecting the sharply increased concern of mycologists with conidial fungi. Perhaps surprisingly, the number of 'genera' involved has remained constant. My question is whether that number should in fact be reduced. The quotation which follows is from Kendrick & Carmichael (1973) "... the recently recognized form-genera *Beltraniella*, *Ellisiopsis* and *Beltraniopsis* are differentiated from the classical *Beltrania* by characters which could easily be regarded as valid only at the species level ... [the species of these genera] are so similar that they should probably be treated as congeneric in any practical, working classification". These genera are indeed separable by single characters, but they probably represent a luxury we can no longer afford, if our system is to be manageable, so this seems an appropriate place to take up and extend the earlier discussion. The species of the genera *Beltrania*, *Beltraniopsis*, *Beltraniella* and *Ellisiopsis*, as well as those of two other genera, *Pseudobeltrania* and *Hemibeltrania* Pirozynski, which are relevant to the discussion, are all illustrated in Ellis (1971:237-235, 1976:200-207).

Let us first analyze the constellation of characters that make *Beltrania* distinctive. Almost unique among hyphomycetes are the striking biconic conidia which are lightly pigmented but have a narrow hyaline band at the conjunction of upper and lower cones. This

strangely shaped conidium also has a tubular apical appendage and often a basal 'separating cell', swollen in the middle, but narrowly truncate at each end. The separating cells arise from denticles clustered at the apex of unbranched, multiseptate conidiophores which spring from around the radially lobed, rosette-like bases of long, dark, pointed setae.

There is a strong tendency for anamorph-genera to be monothetic; that is, for them to be based on the possession by all member species of a unique feature or features. Among the *Beltrania*-like hyphomycetes this means that an all-or-nothing reliance on one or two characters has led to the recognition of several numerically small genera. The salient features of these genera are analyzed in Table 1. I have tried to rate these features in terms of their frequency of occurrence over the whole spectrum of hyphomycetes. My categories range from: ' \* = unique', through '\*\* = very rare', to '\*\*\* = unusual', to '\*\*\*\* = common'. From the point of view of their value as characters delimiting monothetic genera, we can surely discount the four-star features completely. For example, anamorph-genera with '(1) Conidia amerosporous' fill no fewer than 55 of the 129 plates in Carmichael et al. (1980). '(3) Conidia lightly pigmented' and '(4) Conidia limoniform or obovoid' are less common, but can still be found in scores of genera. '(5) Conidiophores arising from substrate' must describe the majority of all hyphomycetes and is only included as a foil for those arising along the setae.

Let us pass on, then, to the remaining characters. Three (#6-8) are rated as "unusual". '(6) Dark setae' can be found in about 30 anamorph-genera (e.g. *Chaetochalara*, *Codinaea* Maire, *Cordella*, *Lacellina* Saccardo, *Lacellinopsis*, *Mahabalella* Sutton & Patil, *Minimidochium* Sutton, *Septosporium* Corda). This total does not include genera with setiform conidiophores. An interesting situation arises with the publication of *Beltrania mundkurii* and *B. santapauri*, whose setae are often branched, since it is on branched vs. unbranched setae that the genera *Gyrothrix* and *Circinotrichum* are differentiated - see below '(7) Conidiophores

Table 1

Salient Features of the *Beltrania* group and other selected genera

	Frequency rating of characters	<i>Beltrania</i>	<i>Beltraniopsis</i>	<i>Beltraniella</i>	<i>Ellisiopsis</i>	<i>Psuedobeltrania</i>	<i>Hemibeltrania</i>	<i>Rhombostillbella</i>	<i>Chaetendophragma</i>	<i>Subulispora</i>
1. Conidia amerosporous	****	✓	✓	✓	✓	✓	✓	✓	x	x
2. Conidia phragmosporous	****	x	x	x	x	x	x	x	✓	✓
3. Conidia lightly pigmented	****	✓	✓	✓	✓	✓	✓	x	✓	✓
4. Conidia limoniform or obovoid	****	x	x	x	x	x	✓	x	x	x
5. Conidiophores arising from substrate	****	✓	✓	✓	✓	✓	✓	✓	✓	✓
6. Dark setae present	***	✓	✓	✓	✓	x	x	x	x	x
7. Conidiophores arising along setae	***	x	✓	✓	✓	x	x	x	x	x
8. Conidia beaked or apiculate	***	x	✓	x	x	✓	(✓)	✓	✓	✓
9. Conidia with hyaline equatorial band	**	✓	✓	✓	✓	✓	x	x	x	x
10. Bases of setae or conidiophores radially lobed	**	✓	✓	✓	✓	✓	✓	x	✓	✓
11. Conidia biconic	**	✓	✓	(✓)	x	✓	x	✓	x	x
12. Conidia turbinate	*	x	x	✓	✓	x	x	x	x	x
13. Conidia with apical, tubular, non-septate appendage	*	✓	x	x	x	x	x	x	x	x
14. Swollen separating cell often present	*	✓	✓	(✓)	(✓)	x	x	x	x	x

Weighting used in Table 4

\*\*\*\* = 1, \*\*\* = 3, \*\* = 7, \* = 10

No character is included in the key unless it is present in at least two of the fungi and therefore contributes to similarity.

(or conidiogenous cells) arising along setae.' This condition is about as frequent as that described above (#6); examples are *Chaetopsina* Rambelli, *Chaetopsis* Greville, *Conoplea* Persoon, *Cryptophiale* Pirozynski, *Gonytrichum* Nees & Nees, *Hansfordia* Hughes, *Kumanasamuha* Rao & Rao, and *Zanclospora* Hughes & Kendrick. '(8) Conidia beaked or apiculate' Depending on just how it is interpreted, this feature occurs in at least 40 anamorph-genera of hyphomycetes (excluding staurosporous and scolecosporous forms). Examples are: *Echinobotryum*, *Hansfordiella* Hughes, *Hansfordiellopsis* Deighton, *Sessiliospora* Hawksworth, *Sporidesmium* Link, *Toxosporium* Vuillemin, *Walkeromyces* Thaug).

It is apparent that the last six features (#9-14) carry the real taxonomic weight. '(9) Conidia with hyaline equatorial band'. Darker central bands are found in a number of genera, and longitudinal germ slits are not uncommon, but a hyaline band around the body of the conidium is rare. I am aware of such a feature only in *Arthrimum*, *Pteronidium* and *Cordella* (three very similar genera) outside the *Beltrania* group, in which five of the six 'genera' share this character. One species of *Beltraniella*, *B.porosa* Pirozynski & Patil, has several equatorial hyaline pores in place of the continuous band. This configuration is unique, and were the fungus not so obviously a member of the *Beltrania* group, could easily have led to its segregation at the generic level.

'(10) Bases of setae or conidiophores radially lobed' The bases of setae and conidiophores in many genera are swollen (e.g. *Cacumisporium* Preuss, *Sporoschismopsis* Holubová-Jechová & Hennebert, *Circinotrichum*, *Periconia* Tode ex Persoon), but I am aware of the existence of radial lobes in only two genera -- *Chaetendophragma* Matsushima and *Subulispora* Tubaki -- outside the *Beltrania* group. Within the group, species of all six 'genera' possess this feature. Because of its rarity, common possession of this character must raise questions about the possible relationships among the genera concerned. It is difficult to be dogmatic in a group so poorly known genetically and palaeontologically, yet neither *Chaetendophragma* nor *Subulispora* resembles the

*Beltrania* group in most ways: a comparison is given in Table 2. This suggests that the lobing may have arisen separately on at least three occasions as a solution to the common problem of obtaining stability for tall structures.

Table 2

A comparison of anamorph-genera with radially lobed conidiophore bases.

	Beltrania group	Subulispora	Chaetendo- phragmia
conidiophore bases radially lobed	✓	✓	✓
conidia pigmented	✓	x	✓
conidia with apical appendages	(✓)	x	✓
conidia with lateral appendages	x	x	✓
conidiophore proliferating	x	x	✓
conidiophore proliferating sympodially	x	✓	x
separating cells present	✓	x	x
conidia phragmosporous	x	✓	✓
conidia arising on denticles	✓	x	x

'(11) Conidia biconic. Of the six genera in the *Beltrania* group, four share this feature. Only two other hyphomycete genera produce conidia of this shape: the hyaline, synnematous, fungicolous *Rhombostilbella* Zimmermann, and the hyaline, sporodochial *Fusisporella* anamorph of *Nectria pallidula* Cooke. It seems most probable that the similarity in conidium shape is

coincidental, and that neither of these fungi is related to *Beltrania*. As Pirozynski (1963) pointed out, biconic spores are found among the Sphaeriales, Microthyriales and Helotiales, so this shape is not necessarily good evidence for close relationship.

'(12) Conidia turbinate.' This means 'shaped like a child's whipping top.' Such conidia have a rounded or rather flattened apex, and a pointed base. Yet the word turbinate specifies an over-all shape rather than simply those of base and apex. So although it is not hard to find genera whose conidia have a rounded or flattened apex and a tapered base, these usually have little resemblance to *Beltraniella* or *Ellisiopsis*. I think it is fair to suggest that, were the shape of the conidia in these two genera to be fully specified (as in a drawing, rather than as an oversimplified verbal description) it would be essentially unique: the *Exosporiella fungorum* (Fries) Karsten conidium is about the only example I can think of that bears it much resemblance.

'(13) Conidia with one apical, tubular, nonseptate appendage.' Apical appendages are common among coelomycetes, but found in relatively few genera of hyphomycetes, especially if one excludes forms with a simple apical extension like that of some species of *Alternaria* Nees or *Hansfordiella*, and discriminates between the fine non-cellular setulae of such genera as *Codinaea*, *Mahabalella*, *Menispora* Persoon, *Menosporopsis* Hughes, *Minimidochium* and *Mycoleptodiscus* Ostazeski, and the tubular kind that lack cytoplasmic content at maturity. *Camposporium* may have 0-several appendages, sometimes septate; *Chaetendophragma* has one or two lateral appendages in addition to the apical; *Pleiochaeta* (Saccardo) Hughes usually has two or three apical appendages. If one can exclude the 'beaks' of e.g., *Phaeotrichoconis crotalariae* (Salam & Rao) Subramanian and *Blastodictys hibisci* (Hansford) Ellis (which are very appendage-like, and suggest that the word 'appendage' needs some attention), only *Monotrichum* Gaeumann is seen to possess anything comparable to the appendage found in some species of *Beltrania*.

'(14) Swollen separating cell often present.' Separating cells are found in more than twenty anamorph-genera of hyphomycetes. Sometimes they are nothing more than a denticle which has a septum laid down across the base. The denticle may be very short, as in *Dematophora* Hartig, *Conoplea* or *Hansfordia*, and the separating cell therefore disc-like. In other genera the denticle is larger (*Nakataea* Hara, *Pyricularia* Saccardo, *Parapyricularia* Ellis) and in yet others it may be very long in proportion to its width (*Brachysporium* Saccardo, *Paratrichoconis* Deighton & Pirozynski, *Rhombostilbella*). The separating cells of these genera differ from those of the *Beltrania* group in three significant ways. First, they are all cylindrical or tubular - none is swollen in the manner typical of those in *Beltrania*, *Beltraniopsis*, *Beltraniella*\* or *Ellisiopsis*. Second, the cylindrical kind of separating cell usually ruptures when the single conidium it bears secedes, part of the cell going with the conidium, part remaining attached to the conidiogenous cell. In the *Beltrania* group, the swollen separating cell does not usually rupture, but either remains on the conidiophore in its entirety or secedes with the conidium. Third, it is fairly common for a separating cell of the *Beltrania* group to bear more than one conidium: I am not aware of such behaviour among cylindrical separating cells. So, although several other genera have separating cells, those of the *Beltrania* group are unique.

Even a cursory examination of the ratings in Table 1 will convince the reader that the *Beltrania* group occupies a fairly well-defined region of the fungal spectrum. If we look only at the six most unusual features, we find that only one, radially lobed setae or conidiophore base, is present in all six pseudotaxa, though another, the hyaline equatorial band, is found on the conidia of five of the six, and two more (biconic conidia and swollen separating cells) are found in four of the six 'genera'.

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\* Separating cells of *Beltraniella nilagirica* Pirozynski & Patil may be cylindrical, but they are much wider than the denticles from which they arise, and each commonly bear several conidia, as in other *Beltraniella* species.

Table 3 shows the results of cross-matching the various features present in each 'genus' in an unweighted manner. However, in the normal taxonomic approach some features are always given more 'weight' than others. I thought it would be salutary to visualize this usually cerebral process, and assigned weightings of 10, 7, 3 and 1 to the four degrees of rarity recognized earlier. Although this scheme is doubly arbitrary, it produces similarities (Table 4) that do not seem unrealistic when one makes the usual mental comparisons.

I admit that this comparison is made on a limited sample of data, but I am fairly sure that it was upon just these characters that the original 'generic' delimitations were based.

Table 4 makes it clear that *Hemibeltrania* is peripheral or even external to the *Beltrania* group. Although it shares four or five features with each of the other genera in the group, three of these are of the common or garden variety, and only feature 11, the radially lobed conidiophore base, a seven-point character, gives it any semblance of credibility as a member of the group. To drive this point home further, I have compared *Chaetendophragmia triangularia* Matsushima and *Subulispora procurvata* Tubaki with the 'genera' of the *Beltrania* group, extending Table 1 as necessary to include all the main features, and found that each of them was, in fact, just as 'close' to the other members of the *Beltrania* group as is *Hemibeltrania*. Note that this degree of similarity is essentially based on two features, the '3-point' apiculate conidia and the '7-point' radially lobed conidiophore base.

In the conidial fungi we are, as I have recently pointed out at some length (Kendrick 1980), at a considerable disadvantage when speaking about conservatism in characters because we have so little fossil record on which to base conclusions. Yet if we can attach some importance to 'shared rarity' (and how else can we taxonomize organisms) we could suggest that *Chaetendophragmia triangularia* and *Subulispora procurvata*, no less than species of *Hemibeltrania*, may be related in some way to the otherwise closely knit *Beltrania* group. But although there is, as I have tried to demonstrate, a

strong case for condensing the five *Beltrania* genera into one (as their weighted resemblances in Table 4 suggest), there can be little justification for including *Hemibeltrania*, *Chaetendophragma* or *Subulispora* in this expanded generic concept.

Table 3

Positive resemblances between genera (unweighted - out of 10)

	Beltraniopsis	Beltraniella	Ellisiopsis	Pseudobeltrania	Hemibeltrania	Rhombostilbella
Beltrania	8	8	7	6	4	3
Beltraniopsis		9	8	7	5	4
Beltraniella			9	6	4	3
Ellisiopsis				5	4	3
Pseudobeltrania					5	4
Hemibeltrania						3



The five core 'genera' in what I have called the *Beltrania* group contain in all only about 20 species. I suggest that even were the number of species to double (which it well may, as the hyphomycetes of the tropics are more fully enumerated) it would be easier to track down any of them initially under a single generic heading (largely on the basis of qualitative features) then run it down to species by using the remaining qualitative features for subgeneric groupings (which might correspond to the genera now recognized), and finally by means of quantitative differences.

If we adopt the traditional monothetic stance, we can define the *Beltrania* group as producing biconic, or sometimes turbinate, pigmented conidia which have a hyaline equatorial band. But that gives a very inadequate account of the group as a whole, and since other very unusual or even unique characters are also found in the majority of species within the group, it seems more reasonable to include those in the generic constellation, adopting a more polythetic approach.

Among the unusual, rare, or unique features already enumerated, no less than five are present in at least four of the five genera. These five features (# 6,9, 10,11,14 in Table 1) are present in *Beltrania*, *Beltraniopsis* and *Beltraniella*; four of them in *Ellisiopsis*, and three in *Pseudobeltrania*. Only one of the five is found in *Hemibeltrania*. I propose, then, that membership in the expanded, slightly polythetic genus *Beltrania* sensu lato be granted to fungi possessing any three of the five features listed below: (1) dark setae, (2) setae or conidiophores with radially lobed bases, (3) swollen separating cells, (4) biconic conidia (5) conidia with hyaline equatorial band.

Using this polythetic concept, I believe that all species thus far described in *Beltrania*, *Beltraniopsis*, *Beltraniella*, *Ellisiopsis* and *Pseudobeltrania* fall within the limits of the single expanded anamorph-genus. *Hemibeltrania* is clearly excluded.

It is encouraging to note that Pirozynski & Patil (1970) foreshadowed the present paper by reducing *Ellisiopsis* to synonymy with *Beltraniella*.

I have deliberately delayed until this point any consideration of the species most recently described in *Hemibeltrania*, *H. navicularis* Sutton. Sutton (1976) reports that his collections of the new taxon "have not only shown characteristics of *Hemibeltrania* but also extraneous features [sic] not hitherto reported in the family [sic]." Sutton notes that the new species is "similar in morphology and ontogeny of conidia ..... to *Hemibeltrania* species but in addition to solitary conidia it produces short chains of up to 3 conidia. Were it not for this feature there would be no hesitation in placing the species in *Hemibeltrania*, but, if a strict interpretation of the generic limits is imposed, there would be no alternative to the introduction of a new generic name to accommodate it."

I consider that the inclusion of this species in *Hemibeltrania* involves an excessive extension of the generic concept. Not only are the conidia of the two extant species of *Hemibeltrania* obovoid or limoniform and not at all 'navicular' or spindle-shaped, but they never form in chains, and completely lack the swollen separating cells which Sutton invokes as a derivative of the chains found in his fungus. If we can extend the generic limits of *Hemibeltrania* to include an additional shape of conidia, and conidia in chains, how much easier it would be to extend the limits of *Beltrania* to incorporate the other four genera already mentioned, which already have so much in common with the original genus. Sutton's new fungus, even if it can be postulated as having some relationship with the *Beltrania* group - and perhaps it can - must surely be regarded as distinct both from *Beltrania* sensu lato and from *Hemibeltrania*. It possesses none of the constellation of five features that characterize *Beltrania* sensu lato, and is not much more similar to *Hemibeltrania*, as that genus has generally been understood. It could, in fact, be considered more closely allied to *Spondylocycladiopsis* M.B. Ellis, or to *Haplariopsis* Oudemans (see Ellis 1971: 293-294).

Since this is the beginning of the debate, I am deliberately refraining from making the suggested transfers, not wishing to prejudge the outcome, or to clutter the literature with combinations that may, if the argument goes against them, be rendered superfluous.

(2) *Chalara* - *Chaetochalara*

As Nag Raj & Kendrick (1975) showed, *Chalara* is unique in its production of cylindrical, phialidic, asexual or didymosporous conidia from a conidial collar. Unique, that is, except for the contiguous genus *Chaetochalara*, which has exactly the same characteristics, with one addition, that of dark setae. Although Nag Raj & Kendrick were conservative and retained both genera, it seems to me that there is now very little reason to do so. *Chaetochalara* has only six species (Nag Raj & Kendrick 1975) and could be absorbed into *Chalara* with virtually no loss of information, since the six species would constitute a small subgeneric group that could be quickly keyed out on their possession of setae ... (Remember that some members of *Beltrania* sensu lato have setae, while some do not). I propose, therefore, that the concept of the genus *Chalara* be expanded to admit species with setae, *Chaetochalara* becoming a facultative synonym of *Chalara*.

(3) *Circinotrichum* - *Gyrothrix* - *Ceratocladium*

The only feature separating *Circinotrichum*, with six species, from *Gyrothrix*, with twelve, is the unbranched setae of the former vs. the branched setae of the latter (See Pirozynski 1962). Species of these two genera are remarkably similar in every other respect. Referring back to the *Beltrania* discussion, we may note that two species of *Beltrania*, *B. mundkuri* Pirozynski & Patil and *B. santapau* Pirozynski & Patil have recently been described as having branched setae, while the other members of *Beltrania* sensu stricto all have unbranched setae. Although I know it is not always safe to transfer taxonomic conclusions from one situation to another, this is surely a case in which what makes sense in *Beltrania* does so also in *Circinotrichum* - *Gyrothrix*. I therefore suggest unification of the two genera, with *Gyrothrix* becoming a facultative synonym of *Circinotrichum*.

*Ceratocladium* Corda 1839, with one species, *C. microspermum* Corda, has branched setae like *Gyrothrix*, but while the conidiogenous cells in *Gyrothrix* arise from the substrate, the almost identical cells of

*Ceratocladium* arise along the lower part of the setae. This might seem like a reasonable generic distinction, but for the fact that the conidiogenous cells of a recently described *Circinotrichum*, *C. pseudocladum* Pirozynski & Patil, also develop along the lower portion of the setae. Thus *Ceratocladium microspermum* is to *Gyrothrix* what *Circinotrichum pseudocladum* is to the rest of *Circinotrichum*. If *C. pseudocladum* can be accepted as a good species of *Circinotrichum* (and I do not see why it should not be), then *Ceratocladium microspermum* can now be logically and comfortably disposed in *Gyrothrix* - and hence in *Circinotrichum* sensu lato. Once again it is encouraging to note that Pirozynski & Patil (1970) having described *Circinotrichum pseudocladum*, drew attention to the same logical redistribution of *Ceratocladium microspermum*, though they did not go as far as to propose the second step.

(4) *Antromycopsis* - *Sclerostilbum*

*Sclerostilbum septentrionale* Povah has recently been revealed as the synnematal anamorph of *Collybia racemosa* (Persoon ex Fries) Quelet (Watling & Kendrick 1977). Its conidia are formed by the arthric disarticulation of closely clamped hyphae in the head of the synnematal conidioma. Quite independently, it has also been shown that *Antromycopsis broussonetiae* Patouillard & Trabut is the synnematal anamorph of *Pleurotus cystidiosus* O.K. Miller (Jong & Peng 1975, Pollack & Miller 1976). Its conidia form in exactly the same manner as those of *Sclerostilbum*, though the *Pleurotus* also produces an anamorph on the monokaryotic mycelium: this is, of course, not clamped and the arthric conidia are not as distinctive as those of the dikaryon. The literatures of these two basidiomycetous anamorphs have followed separate, if parallel, paths, and the actual comparison between them has been made only very recently (Watling & Kendrick 1977, Kendrick & Watling 1979). It seems that there is little reason to maintain them as separate anamorph-genera, and I propose that *Sclerostilbum* should become a facultative synonym of *Antromycopsis*.

(5) *Heliscus* - *Clavatospora*

*Heliscus lugdunensis* Saccardo & Therry, the type species of *Heliscus* Saccardo, has tetra- or sporous, phialidic conidia in which the three upwardly directed arms are comparatively short (Carmichael et al. 1980, Fig. 117D). Because those of *H. longibrachiatus* Ingold were much longer, Nilsson established the segregate genus *Clavatospora* Nilsson ex Marvanova & Nilsson for it. The only significant difference between *H. lugdunensis* and *C. longibrachiata* (Ingold) Nilsson (Carmichael et al. 1980, Fig. 119A) lies in the respective lengths of the three upper arms of their conidia. Since both species are amphibious, and the conidia of both are basically amero-staurosporous and phialidic, I consider their segregation to have been unnecessary. I therefore suggest that *Clavatospora* should become a facultative synonym of *Heliscus*.

## EXCEPTIONS DUE TO CONVERGENCE

I must now sound a note of warning. The staurosporous conidia of *Varicosporium*, *Dendrospora* and *Dendrosporomyces* share a basic pattern of construction even to the constrictions at the base of each branch or arm of the conidium. Yet Nawawi et al. (1977) showed unequivocally that *Dendrosporomyces prolifer* Nawawi, Webster & Davey has dolipore septa, and must therefore be a basidiomycetous anamorph. *Dendrospora erecta* Ingold, on the other hand, has simple septal pores, and is therefore assumed to be an ascomycetous anamorph. The status of *Varicosporium* has not yet been resolved.

*Spiniger* Stalpers was erected for basidiomycetous anamorphs that in most ways resemble *Oedocephalum* Preuss. We may expect to encounter other unclamped basidiomycetous anamorphs which may well display similar parallelism or convergence with ascomycetous anamorphs. But these cases will be the exception rather than the rule. I do not think that arguments of possible polyphyly can reasonably be advanced to defend many of the segregate genera produced in recent years.

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