Higher fungi genera : their holomorphic content

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Higher Fungi Genera: Their holomorphic content

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"If all fungi can be compared through their nucleic acids and placed on a single phylogenetic tree, do we need to maintain the Deuteromycetes?" (Bruns et al., 1991).

We are concerned with the fungal genus and how it is influenced by the answer to this contemporary question. The problem is one of combining into one system the two widely used systems of fungal taxonomy. The concept of the first major level of species groups, the genus, will be affected by combining into one "whole fungus" system the extant dual systems of fungal classification and nomenclature maintained as the Eumycota and the Deuteromycota. The observation by Luttrell (1977) that the morphological characters uniting fungal species into natural groups may not be traditional nor obvious ones has additional significance. The ability to demonstrate kinship of "true" species in the Ascomycetes and Basidiomycetes and the "form" species in the Deuteromycetes with molecular techniques now allows their egalitarian status.

All fungus forms were considered as autonomous species before the recognition of pleomorphy (Hennebert, 1971). The unified classification system integrated the classes Coniomycetes and Hyphomycetes for conidial forms with sexual character based orders such as the Gasteromycetes and Hymenomycetes (Fries, 1821-1832). The observation of ..."dissociated parts of a species composed of several elements." by Tulasne (1851) initiated the concept of fungal pleomorphy and its application to classification with a dual system, one for fungi with sexual reproduction and and one for those in which sexual reproduction was assumed to be unexpressed. Tulasne's thesis received support from de Bary's (1854) demonstration of a sexual state in the life cycle of *Aspergillus glaucus;* subsequent refinements were made by Gilkinet (1875) and de Bary (1887). The dual classification system for fungi was initiated by Saccardo (1877, 1882) with the separation from the Ascomycetes and Basidiomycetes of conidial forms as Coniomycetes, Hyphomycetes and Mycelia Sterilia in the form class Deuteromycetes.

Combination of Ascomycetes and Basidiomycetes with Deuteromycetes into one classification system requires a critical review of taxonomic practice that has developed since Fries and its fundamental modification theorized from Tulasne's observations. Foremost is the question of the extreme priority given to morphological characters that express the sexual process leading to the formation of the ascus and the basidium.

The nuclei of some fungal spores are the products of meiosis and others are the products of mitosis. In the life cycle of the "whole fungus", one may find several reproductive modes: 1) no spores, 2) meiospores, 3) mitospores, or 4) both meio- and mitospores. For ethnological as well as biologically practical reasons, the production of meiotic spores have been the historical source of the most important characters for higher fungus classification (Reynolds, 1987). The results are a taxonomic paradigm of only one type of holomorph and the related single type holomorphic genus.

These historical morphology-based concepts are now being tested with additional analyses from a molecular perspective; a case can be made for a concept of the polyholomorphic genus, one comprising meiotic, mitotic and pleomorphic holomorphs.

A. The universal holomorph: an artifact of historical necessity (Figure 1A).

The universal holomorph view of the "whole fungus" is that every fungus has (1) inherent morphological expression of attributes such as the ascus and the basidium that are correlated with meiosis, and (2) the potential for expression of additional, ameiotic reproductive traits.

Hennebert and Weresub (1977) cemented the paradigm that true fungi must be meiotic by defining the "whole fungus" (the holomorph) as containing a meiotic spore morph (the teleomorph). The holomorph comprised two forms, one strictly a meiotic state and the other having meiotic and mitotic states. While the fungus with only a meiotic morph was considered "whole", the fungus with only a mitotic morph (the anamorph) was merely a part of the "whole fungus" anatomy. All anamorphs were assumed to be in opposition to extant or as-yet-undiscovered teleomorphs. There was no doctrinal provision for a mitotic holomorph.

The universal holomorph paradigm was formulated during international discussion leading to a revision of the ICBN, Article 59, entitled, "The names of pleomorphic fungi" (Hennebert and Weresub, 1977). The practice of applying this concept to all taxonomic levels of ascomycete and basidiomycete fungi is assured by the ambiguous language of Article 59 (Reynolds and Taylor, 1991b). In fact, Article 59 can be read to the contrary to apply in a narrow sense to only the species, but not to supraspecific taxa.

Given the historical importance of meiotic characters it became necessary to separately classify fungi lacking them. The reproductively diverse higher fungi were classified in two systems, one system of the Eumycota and another for the Deuteromycota. The struggle to recognize phylogenetic relationships from analysis of morphological characters was recognized by Samuels and Seifert (1987). "The use of individual [morphological] characters in classification of [mitotic] fungi has left us with a taxonomic system that, by and large, has little predictive value." Another of their statements of morphological focus can be rephrased in the viewpoint of this article. In order to achieve a natural system of classification of the fungi imperfecti, the characters shared among closely related holomorphs must be identified.

We contend that the universal holomorph paradigm has inadvertent widespread application in classification and nomenclature of ascomycetous and basidiomycetous fungi (Reynolds & Taylor, 1991b, 1992). The widespread practice is evidenced in several ways.

1) A survey of taxonomic journals for the past decade including ACTA MYCOLOGIA, BULLETIN DE LA SOCIETE MYCOLOGIQUE DE FRANCE, CANADIAN JOURNAL OF BOTANY, CESKA MYKOLOGIE, CIENCIAS BIOLOGICAS, INDEX OF FUNGI, MYCOLOGIA, MYCOPATHOLOGIA, MYCOSYSTEMA, MYCOTAXON, MYCOLOGICAL RESEARCH, NORDIC JOURNAL OF BOTANY, NOVA HEDWIGIA, PERSOONIA, REVISTA MEXICANA DE MICOLOGIA, STUDIES IN MYCOLOGY, SYDOWIA.

All names of new ascomycete and basidiomycete species and genera were based on a designated or implied holomorph if the meiotic state was present in the type. Mitotic fungi were called "anamorphs" and their types were labeled anamorphic types, as were the names on which the names were associated. No mitotic holomorph was the basis of a specific or generic taxon.

2). Systema Ascomycetum.

The "Outline of the ascomycetes" compiled by O. E. Eriksson and D. Hawksworth is offered as a "classification of orders, families and genera of the ascomycetes." All taxa recognized are based on meiotic state species.

3). Names in current use.

The "names in current use" list is the basis of the effort to change the International Code of Botanical Nomenclature to afford specially protected nomenclatural status for names so as to reduce name changes due to the priority rule and misapplication of types (Hawksworth and Greuter, 1989). We add another potential problem resulting from the codification of this list to those pointed out by Gams (1991).

A list of several hundred names is being proposed under the heading Deuteromycetes. These names are presumed anamorphic names. No pleomorphic life cycle has been demonstrated for a large number; if given protected status in the code as anticipated, the mitotic holomorphs will be nomenclatorally legislated as the anamorphic state of pleomorphic holomorphs without evidence of any pleomorphic states.

B. The polyholomorphic genus: a natural taxon (Figure 1B).

In additional to the historical primacy given meiotic characters, there are two other hurdles to naming and classifying meiotic and mitotic fungi together: 1) The thought that successful fungi must have sexual reproduction, albeit cryptic, because asexual organisms were evolutionary dead ends (Kendrick, 1979); 2) The practical necessity of identifying the many, important mitotic fungi (Reynolds and Taylor, 1992). These hurdles may be illusory. Although asexual organisms may be dead ends over extremely long periods of time (Wagner, 1970), molecular evolutionary studies of closely related fungal genera have revealed molecular phyletic branches of mitotic species with divergences as old as those of their meiotic relatives (Guadet et al., 1989; Taylor et al, 1990). While not underestimating the importance of meiotic recombination, these observations suggest that parasexuality, and the action of selection on the huge numbers of mitotic propagules that fungi produce, can promote the evolution of asexual fungi at rates comparable to those of their close meiotic relatives. Experimental support for this view can be found in a recent review of fungal population genetics (Tibayrenc et al. 1991). The authors maintain that some fungi with documented sexual states have population structures expected of clonally reproducing organisms, while *Candida albicans*, with no known sexual state, has a population structure consistant with sexual recombination.

Investigation of nucleic acid characters has led to phylogenetic trees that combine fungi having meiotic spore states with those that are strictly mitotic. Furthermore, it has been demonstrated that nucleic acid characters may form part or all of the type element for a fungal species (Reynolds and Taylor, 1991a) in practical terms and under the International Code of Botanical Nomenclature. Nucleic acid characters are ubiquitous and are not dependent on the reproductive morphology of the fungus. The independence and universality of nucleic acid characters provides a practical means of classifying all fungi in one system, to be facilitated by the abolition, modification or reinterpretation of ICBN's Article 59 (Reynolds and Taylor, 1991b). At the species level, the resolution of the universal holomorph paradigm into its component meiotic and pleomorphic holomorphs is required. A third, new type of holomorph, the mitotic holomorph completes the contemporary recognition of the "whole fungus" in all its manifestations.

The merger of two classification systems effects the admission of all three holomorphs into a natural taxon. The generic concept then becomes one of polyholomorphic content.

Three basic types of holomorphs can be recognized on the basis of life cycle expression of morphological characters (Müller, page 264 in Kendrick,1979; Reynolds and Taylor, 1991b, 1992). 1) the meiotic holomorph with sexual reproduction characters. 2) The mitotic holomorph with mitotic reproduction characters. 3) The pleomorphic holomorph with characters expressed in the life cycle from both meiotic (teleomorph) and mitotic (anamorph) reproduction. The pleomorphic holomorph variants are: 1) teleomorph plus teleomorph (Hennen et al., 1984); 2) teleomorph plus anamorph (Müller, 1981); 3) teleomorph plus more than one anamorph (Carmichael, 1981); and 4) more than one anamorph (Hennebert, 1987). Each of these holomorphs can serve as the basis of a species and as such comprise the genus (Figure 2).

C. The monoholomorphic genus: a dual system taxon (Figure 1A).

Currently defined genera in the Ascomycetes and Basidiomycetes are based on the concept of only one, universal holomorph, i.e. monoholomorphic. No distinction is made between meiotic state morphs and the mitotic state is unaccounted for as a "whole fungus" in its own right. Admission to the "true" or "botanical" taxa requires morphological evidence of sexual reproduction. Placement in the form, or anatomical, taxon Deuteromycota was considered a temporary measure, and optional, until meiotic spores could be discovered.

Universal holomorph species and supraspecific taxa are based on a holomorphic misrepresentation. The monoholomorphic genus embodies two holomorphs, the meiotic holomorph and the pleomorphic holomorph. As with the subsumed mitotic morph, the meiotic holomorph is said to retain the potential of mitotic expression and indeed is a potential teleomorphic partner for the requisite anamorph-in-waiting. Yet, the meiotic morph is acceptable as a basis of the monoholomorphic taxon because of the expressed sexuality.

The mitotic fungus with more than one reproductive expression in its life cycle has received only recent attention in taxonomic literature. This type of monoholomorphic fungus has been treated as a problematic deuteromycete and called the pleoanamorph and the synanamorph (Hennebert, 1987).

D. The polyholomorphic example: morphological and molecular (Figure 1).

Potential monophyletic genera can be recognized on the basis of morphological characters alone. The comparison of shared characters in the several holomorphs of a polyholomorphic genus is the basis of comparison, rather than a comparison of monoholomorphic species primarily collected in a taxon on the basis of sexual characters. Depending on the evidence at hand, the predictive genus could be based on homologous reproductive states, as well as other supportive evidence from nonmorphological observations. Thus, predictions such as those of Ramírez (1985) are rendered moot: "Perhaps someday we may find that all species of *Penicillium* are actually 'perfect'."

D.1 The morphological character prediction.

The following examples of one system classification prediction are based on studies in the Capnodiaceae. A prediction of associated dual system taxa was made by Hughes (1976) with the proposal of the Capnodiaceae sensu stricto utilizing the concept of the universal pleomorphic taxon. Monographic revision of taxa in both groups has been done by Reynolds (1993). Two genera, *Capnodium* and *Leptoxyphium* , are recognized on the basis of similarity of reproductive structures and life cycle events in the component species.

The genus *Capnodium* example (Figure 3).

Four species comprise the genus *Capnodium* in one system of classification. Taxon 1, the type species, and species 4 have a pleomorphic holomorphic content with both teleomorphic and anamorphic (shaded) synonyms listed . Species 2 has a mitotic holomorph content. Species 3 is based on a meiotic holomorph.

The genus *Leptoxyphium* example (Figure 4).

In this example, a genus of mitotic species (1-3) comprises the original Spegazzini taxon. A pleomorphic holomorph species (4) was recently discovered and the life cycle link of a *Leptoxyphium* anamorph and a teleomorph that is unlike others in the Capnodiaceae has been demonstrated.

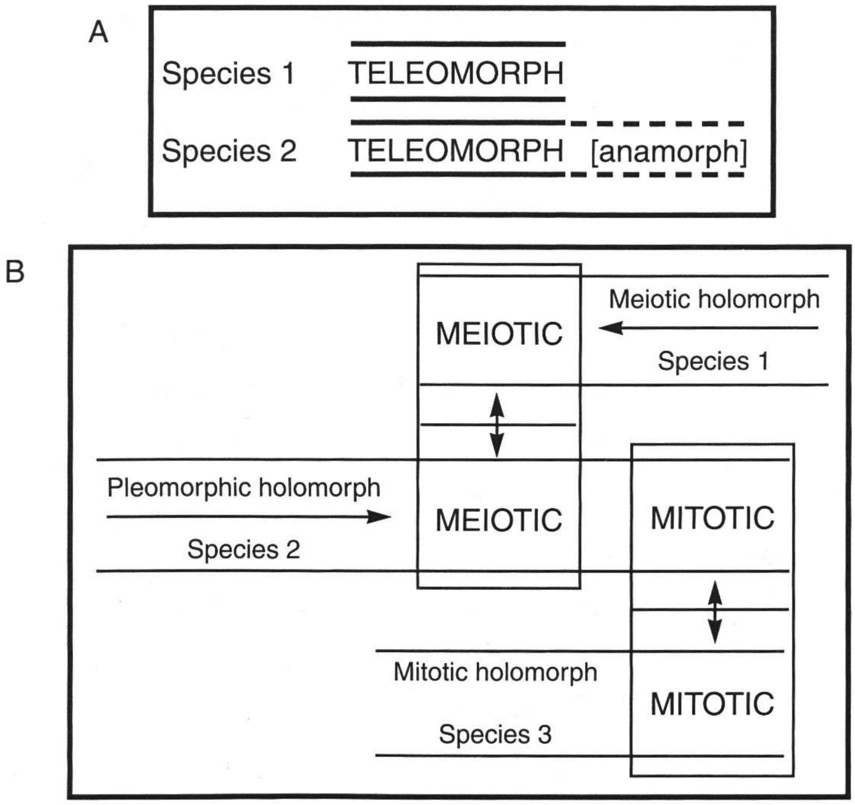

Figure 1: A comparison of three species classified in the dual system and in one system. **A**. The disposition of three species in the monoholomorphic classification system of Hennebert/Weresub. The Ascomycota genus (dark-lined box) comprises Species 1, known only from a sexual morph, and species 2, for which a teleomorph and an anamorph are known. Deuteromycota Species 3 is a form species, with the reproductive state designated the anamorph. The morphological expression of sexual morph characters is required for admission to the ascomycete genus.
B. The Ascomycota genus comprises all three species; Species 1 is based on a meiotic holomorph, Species 2 on a pleomorphic holomorph and Species 3 on a mitotic holomorph. The relationships between the species can be predicted by shared morphological characters such as the expression of sexual morph characters or the mitotic morph.

D.2 The molecular character confirmation.

The use of one generic name for a taxon of related meiotic and mitotic species was first broached by Raper (1957) on a morphology-character basis for *Aspergillus* and *Penicillium.* Our hypothetical molecular data examples are drawn from studies of selected species in the genus Talaromyces (Taylor et al., 1990), whose anamorphic morphs resemble those of the form genus *Penicillium* subgenus *Biverticillium* (Pitt, 1979; Stolk and Sampson, 1972).

	Meiotic	Mitotic	Pleo 1	Pleo 2	Pleo 3	Pleo 4
1	x					
2		x				
3	x		x	x	x	x
4	x		x	x	x	
5	x		x	x		
6	x		x			
7	x			x	x	x
8	x				x	x
9	x					x
10	x		x			x
11	x			x		
12	x			x	x	
13	x				x	
14	x		x		x	x
15	x		x	x		x
16		x	x	x	x	x
17		x	x	x	x	
18		x	x	x		
19		x	x			
20		x		x	x	x
21		x			x	x
22		x				x
23		x	x			x
24		x		x		
25		x		x	x	
26		x			x	
27		x	x		x	x
28		X	x	x		x
29			x	x	X	X
30			x	x	X	
31			x	X		
32			X			
33				x	x	x
34					X	x
35						x
36			x			x
37				x		
38				X	x	
39					x	
40			x		X	x
41			x	X		x

Figure 2: Polymorphic Content of Genera.

All combinations of species holomorph types that could comprise the polymorphic content of a genus are tabulated. Meiotic = meiotic holomorph species; mitotic = mitotic holomorph species; Pleo = pleomorphic holomorph species variants: 1 teleomorph + teleomorph, 2 teleomorph = one anamorph, 3 teleomorph + more thanone anamorph, 4 more than one anamorph.

***Capnodium* Montagne 1849**

1. C. salicinum Montagne 1849
   = Fumagospora capnodioides Arnaud 1911

2. C. anonae Patouillard 1904

3. C. cistophila (Fries) comb. nov.
   = Antennaria cistophila Fries
   = Capnodium cistophila Marie
   = Fumagospora cistophila Batista & Ciferri 1963

4. C. gaultheriae (Batista, Vital & Ciferri) comb. nov.
   = Fumagospora gaultheriae Batista, Vital & Ciferri

5. C. dematum (V. M. Miller & Bonar) Reynolds 1989
   = Phaeosaccardinula dematum V. M. Miller & Bonar 1941
   = C. baccharidis Batista & Ciferri 1963
   = Leptocapnodium krameri Batista & Ciferri 1963
   = Phaeoxyphella fisheri Batista 1963
   = Phaeoxyphella morotoni Batista & Ciferri 1963
   = Phaeoxyphella walteri Batista, Nascimento & Ciferri 1963

Figure 3: The Genus Capnodium, predictions from morphological data.
Five species are recognized. The shaded taxa are based on mitotic holomorphs. Species 1,3 and 5 are based on pleomorphic holomorphs. Species 2 is based on a meiotic holomorph, Species 4 is based on a mitotic holomorph.

Although we are using recognized species, we want to emphasize the hypothetical nature of this example; it is intended only to illustrate nomenclatoral options associated with classifying mitotic and pleomorphic holomorphs in one system.

Leptoxyphium Spegazzini 1918 emend.
= Caldariomyces Woronichin 1926
= Megaloxyphium Ciferri, Batista & Nascimento 1956
= Astragoxyphium Batista, Nascimento & Ciferri 1963

1. L. graminum (Patouillard) Spegazzini 1918
   = Capnodium graminum Patouillard 1897
   = Podoxyphium indicum Sharma, Mukerje & Behara 1973
2. L. axillatum (Cooke) Hughes 1976
   = Capnodium axillatum Cooke 1878
   = Polychaeton axillatum (Cooke) O. Kunze 1891
   = Astragoxyphium catalpae Batista & Ciferri 1963
3. L. ophidioglossum (Ciferri, Batista & Nascimento) Hughes 1976
   = Megaloxyphium ophidioglossum Ciferri, Batista & Nascimento 1956

4. Leptoxyphium litoralis sp. nov.

Figure 4: The Genus Leptoxyphium, predictions from morphological data. Four species are recognized. A new pleomorphic species (shaded), L. litoralis, is added to a genus with three mitotic holomorph species.

The dual classification of species used in the molecular study
(t) = teleomorph, (a) = anamorph.

Genus *Talaromyces*	
Section Talaromyces	
Series Flavi	
1. *T. flavus* (t)	*Penicillium dangeardii* (a)
2. *T. striatus* (t)	*P. lineatum* (a)
Series Lutei	
4. *T. luteus* (t)	*P. udagawae* (a)
Series Trachyspermi	
5. *T. mimosinum* (t)	*P. mimosinum* (a)
6. *T. intermedium* (t)	*P. intermedium* (a)
7. *T. trachyspermus* (t)	*P. lehmanii* (a)
Series Purpureus	
8. *T. purpureus* (t)	*P. purpureum* (a)
Series Thermophilus	
9. *T. thermophilus* (t)	*P. dupontii* (a)
Form Subgenus Biverticillium	
Form Section Simplicium	
Form Series Miniolutea	
	12. *P. minioluteum* (a)
	13. *P. funiculosum* (a)
	14. *P. purpurogenum* (a)
Form Series Islandica	
	15. *P. islandicum* (a)
	16. *P. variabile* (a)

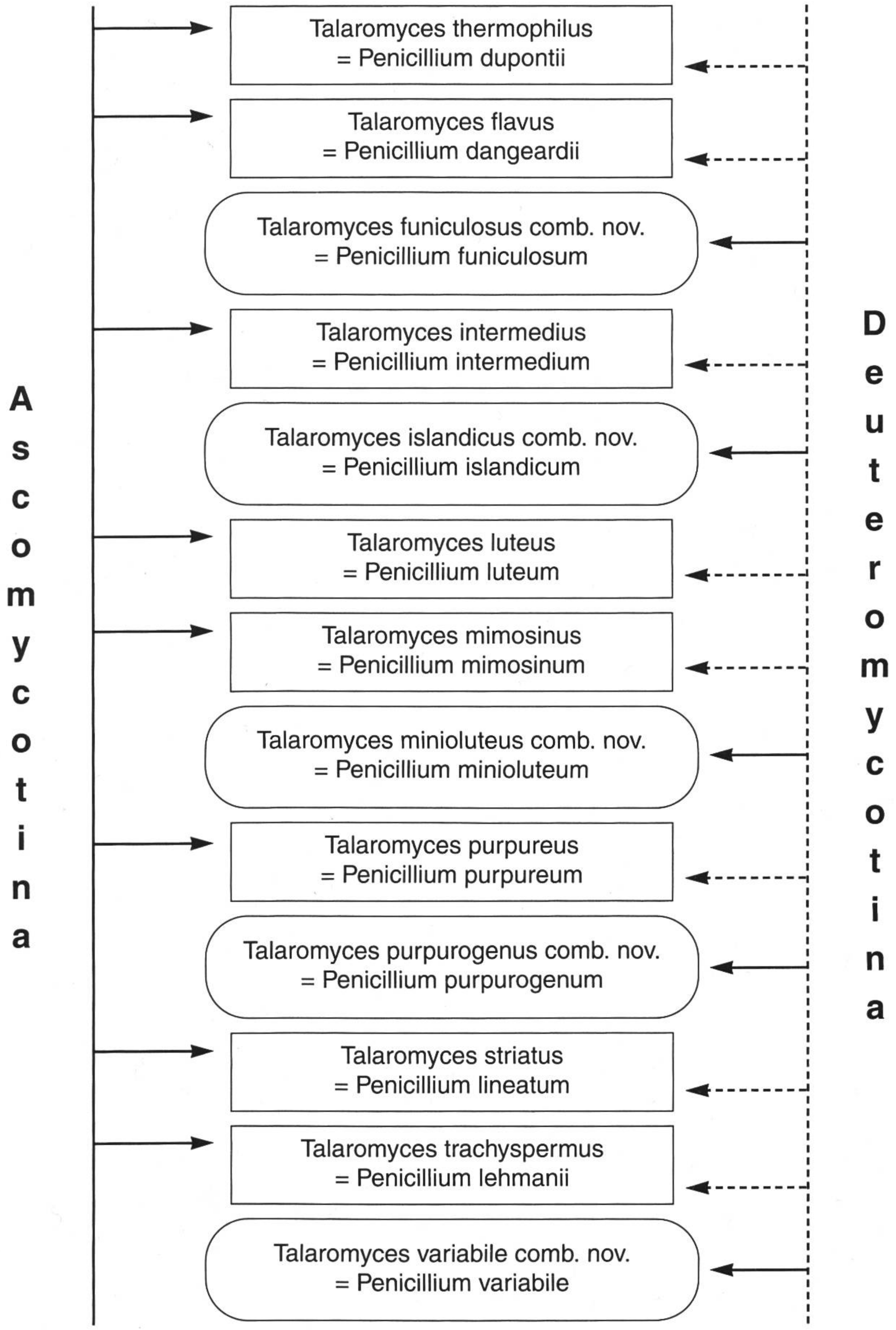

Figure 5: ***Talaromyces*** **and** ***Penicillium*** **subgenus** ***Biverticillium*** **placed in the same genus as** ***Talaromyces*** **emend.**

An extrapolation to one system classification from these representative species now in a dual system provides the following options. None of these options, unfortunately, are completely satisfactory because it is not possible to commemorate all relationships and differences with one choice of names. However, all options achieve the integration of all fungi into one system.

Option 1: Place all the species of *Talaromyces* and *Penicillium* in the Eumycota, but maintain the names existing in the dual system.

Eumycota
Talaromyces, Penicillium subgenus *Biverticillium*

Here, names would not have to be changed, but neither would they convey the current information about relationships. The users of these data would have to remember the phylogenetic relationships of individual taxa in addition to the classification. In fact, the names could be misleading. For example, species in *Penicillium* subgenus *Biverticillium* are likely to be more closely related to species in the genus *Talaromyces* than they are to species in other subgenera of *Penicillium* .

Option 2: Place *Talaromyces* and *Penicillium* subgenus *Biverticillium* in the same genus.

Eumycota *Talaromyces* emend.

Species in *Penicillium* subgenus *Biverticillium* would be moved to the genus *Talaromyces.* The name *Penicillium* would still be applied to species in the subgenus *Penicillium* which encompasses the type species, *P. expansum.* It would be clear that species formerly in *Penicillium* subgenus *Biverticillium* were closely related to species in *Talaromyces.*

Discovery of meiotic spore states would be commemorated by simply emending the description. However, the morphological distinction observed between mitotic spore morphs of *Talaromyces* and *Penicillium* subgenus *Biverticillium* (Pitt,1988) would not be recognized.

Option 3. Place species in *Penicillium* subgenus *Biverticillium* which are phylogenetically related to *Talaromyces* in a new genus in the Eumycota.

Eumycota
Talaromyces
Novomyces gen. nov. = *Penicillium* subgenus *Biverticillium*

Talaromyces would be unchanged, and species in *Penicillium* subgenus *Biverticillium* could be transferred to a new accommodating genus, *Novomyces.* Users would have to remember the close relationship between *Talaromyces* and *Novomyces,* but the differences between *Penicillium* subgenus *Biverticillium* and both the other subgenera of *Penicillium,* and the mitotic spore morphs of *Talaromyces* would be recognized.

E. The polyholomorphic genus content: naming the kinship system.

The basic unit in the traditional method for naming the kinship system is the Linnean binomen; the "whole fungus" name consists of a generic and a specific epithet. In a classification based on natural groups, related species are first recognized at the generic level.

The kinship system of the pleomorphic holomorph has been explored within the context of the Linnean binominal name. The simplest method to demonstrate the relatedness of the teleomorph and an anamorph is to use only one name for the species with a description including the characters of all pleomorphic expression. An alternative method was utilized in three variations. They are exemplary of the use of a or three part name, the trinominal rather than the binomial, to describe a pleomorphic kinship system.

The first variation is examplified by the work of the Commonwealth Mycological Institute mycologist, M. B. Ellis. He cited the anamorph as a state of the teleomorph, using only the generic epithet of the anamorph (Ellis, 1958). *Clasterosporium* state of *Asterodothis solaris* (Kalchbrenner & Cooke) Theissen.

Later usage incorporated the citation of synonyms. For example, the initial citation of the mitotic holomorph [sensu Reynolds and Taylor] or the anamorph [sensu Hennebert and Weresub, 1977] *Periconia igniaria* Mason & M. B. Ellis (Mason and Ellis, 1953) was later and cited as a pleomorphic holomorph (Ellis, 1971):

Periconia state of *Didymosphaeria igniaria* Booth
= *P. igniaria* Mason & M. B. Ellis

Some trinominals were cited with several binominal synonyms.

The trinominal was used several ways in the citation of the name of the type species of a mitotic genus (Ellis, 1971)

Sarcinella Saccardo
Type species: *Sarcinella* state of *Schiffnerula pulchra* (Sacc.) Petrak
= *S. heterospora* Sacc.
Dematophora Hartig
Type species: *Dematophora necatrix* Hartig
[= *Dematophora* state of *Rosellinia necatrix* (Hartig) Berl. ex Prill.]
Botrytis Micheli ex Fries
Lectotype species: *Botrytis cinerea* Pers. ex Pers., conidial

Sclerotinia fuckeliana (de Bary) Fuckel

This synonomy was followed by a description of:

Botrytis state of *Sclerotinia fuckeliana* (de Bary) Fuckel
= *B. cinerea* Pers. ex Pers.

The Ellis trinominal was an attempt to recognize the "whole fungus." The Linnean binominal simply acquired a form-genus name without the form-species epithet.

A second variation of the trinominal can be traced from the work of Hughes (1958). An attempt to cross reference the multiple mitotic states of a life cycle was made following the Ellis model; the generic name of the mitotic form species was associated with the binominal of an ascomycetous species. The *Sarcinella* example given above also illustrates this naming attempt. This kinship system was dubbed the "Cross-reference names for pleoanamorphic fungi" (Carmichael, 1979). A recommendation was that the name of the first described anamorph should receive priority and any later anamorph of the same fungus would be referred to it by a generic name in the cross reference. An example similar by Hennebert (1971) to the above mentioned *Sarcinella* trinominal was cited to justify Latinization. Weresub (1979) substituted the abbreviation "anam." [meaning anamorph] in lieu of the abbreviation "stat." [meaning status].

Hennebert (1987) admitted that the "method is of interest for avoiding the creation of names but the kind of resulting trinominal is subject to twice as many possible revisions as a single binominal, because of the implied organic connections between morphs."

A third variation of the use of the trinominal name is by Punithalingam (1969). This variation approached the polyholomorphic taxon concept advanced here. The application made use of a pleomorphic species and a mitotic species. A new genus, *Hyalotiopsis,* was described in the Sphaeropsidales. In the Latin description, the typus was cited as "Status conidialis Massariae indicae Punithalingam." No description was provided for the new trinominal except by implication of the generic data. A second species was added to the new genus as the binominal *Hyalotiopsis subramanianii* (Agnihothrudu) Punithalingam. It was noted that the basionym, *Hyalotiella subramanianii* Agnihothrudu, was previously published (1969. Proc. Indian Acad. Sci., Sect. B, 70:xx [sic]).

The Punithalingam point of view, however, is still that of the universal holomorph; the binominal nomenclature was used for a species concept incorporating a sexual state. Other species of Massariae based on meiotic holomorphs were not considered for inclusion in the *Hyalotiopsis* kinship system. The new genus was created as a deuteromycete taxon rather than as a "whole fungus" taxon.

At most, the trinominal documents the intersection of the botanical and form system of classification outlined by Hennebert and Weresub (1977). As used so far the trinominal mainly serves the pleomorphic holomorph.

The trinominal recognizes, as anamorph, the connection between the mitotic and the meiotic states of a pleomorph. For these fungi the trinominal can be used to collect the pleomorphs sharing a particular anamorph in the way that higher taxa, e.g. families, collect lower taxa, e.g. genera. The trinominal, however, does not serve the mitotic holomorph at all well because it cannot accommodatethe naming of the mitotic holomorphs as an independent taxa. The tripartite name still represents the dual system of classification that places the mitotic morph in the Deuteromycotina. The Hughes example illustrates that a trinominal with interchangeable names for a mitotic holomorph with more than one mitotic state invites confusion. The major problem is that the phylogenetic relationships of the mitotic morph to a pleomorphic or meiotic holomorphs are still obscured.

The trinominal experiment, used mainly in late 1950s through the 1970s, does provide some insight into the postulation of general guidelines for the construction of binominal alternatives to naming a kinship system.

1. Each unit of the kinship system should be regarded as a distinct phylogenetic unit.
2. Maximum information content should be equally retained about all members of the kinship system.
3. The naming system should interface well with the traditional binominal nomenclature.
4. The naming system should have predictive value for relationships with closely as well as somewhat distantly related taxa.
5. A change in a species designation from a meiotic holomorph or a mitotic holomorph to a pleomorphic holomorph with additional knowledge should be accommodated with a minimum of disruption.

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