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# Genera in the Agaricales: Advances and Retreats in the Search for a Natural System.

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**Summary:** The historical development of the genus concept in the Agaricales is reviewed. Evolutionary theory did not exert much influence on the factual content of the classification of the Agaricales; and even the justification of the classification did hardly change. The two mostly used classifications of the Agaricales are based on a mixture of both phylogenetic and phenetic considerations. Many genera of the Agaricales, which have been newly described in the last decades, are based on insufficient criteria for generic delimitation. This generification must be considered a retrograde step in the construction of a natural system of the Agaricales. Cladistic methods are sound principles to arrive at a natural classification. Application of cladistic methodology in the Agaricales is beset with many difficulties, e.g. the lack of a sufficient number of characters, uncertainty with regard to possible outgroups, lack of robustness, lack of truly synapomorphous characters, etc. For these reasons a direct translation of cladograms into a classification will yield an unstable system and hence diminish the utility of classifications for practical purposes. As long as cladistic methods will not result in stable classifications, the introduction of new genera should not be encouraged. A traditional eclectic classification seems therefore the best option for the time being. A consistent application of phylogenetic methods will ultimately result in a classification that is not of much use for mycofloristic practice, and will most likely result in giving up the Agaricales as a holophyletic group. The Agaricales, as now circumscribed, will turn out to be either paraphyletic or polyphyletic.

**Zusammenfassung:** Die historische Entwicklung des Gattungskonzeptes innerhalb der Agaricales wird zusammengefaßt. Die Evolutionstheorie hat den tatsächlichen Inhalt der Klassifikation der Agaricales kaum beeinflußt; auch die Rechtfertigung der Klassifikation hat sich kaum geändert. Die zwei meistverwendeten Systeme der Agariales sind auf einem Gemisch phylogenetischer und phänetischer Überlegungen aufgebaut. Die meisten Gattungen, die in der letzten Dekade neu geschaffen wurden, basieren auf ungenügenden Kriterien für Gattungsabgrenzung. Diese "Generifikation" bildet einen Schritt rückwärts im Aufbau eines natürlichen Systems der Agaricales. Kladistische Methoden sind besser geeignet für eine natürliche Einteilung. Die Verwendung kladistischer Methodologie innerhalb der Agaricales hat aber viele Schwierigkeiten, z.B. das Fehlen einer ausreichenden Zahl von Merkmalen, Unklarheit bezüglich möglicher Aussengruppen, Fehlen von Robustheit, Fehlen wirklich synapomorpher Merkmale, usw. Eine direkte Übersetzung eines Kladograms in eine Klassifikation wird deshalb ein instabiles System schaffen, und die praktische Verwendbarkeit der Klassifikation herabsetzen. Solange die kladistischen Methoden keine

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stabile Klassifikation hervorbringen, sollten keine neuen Gattungen geschaffen werden. Eine traditionelle Klassifikation scheint mir deshalb gegenwärtig die beste Möglichkeit. Eine konsistente Anwendung phylogenetischer Methoden wird schließlich eine Klassifikation hervorbringen, die für die mykofloristische Praxis eher weniger von Nutzen ist. Sie wird auch dazu führen, daß die Agaricales als holophyletische Gruppe aufgegeben werden müssen. Die Agaricales, wie sie jetzt aufgefaßt werden, sind höchstwahrscheinlich paraphyletisch oder sogar polyphyletisch.

## Introduction

Genera have a particular relevance in taxonomy as the genus concept is the second principal category in the systematic hierarchy that comes after the species. Probably more has been written about the concept of the genus than about any other rank above the species. But discussions on generic concepts are still much to be welcomed, especially as the genus concept is not extensively discussed in mycology.

In the most important works on the genera of the Agaricales (Kühner, 1980; Singer, 1975, 1986) not much attention is given to the question what genera are and how the genus category should be defined. If the genus is given any attention at all by mycologists, it is usually from a highly critical point of view. One is immediately reminded of the question "Do you believe in genera?" (Booth, 1978) or the picture of the "generic iceberg" (Kendrick, 1974) or the complaint about the "excessive multiplication" of genera (Romagnesi, 1977).

Discussions on genera are important from a practical point of view. First, we often start learning Agaricales by recognising the traditional genera. Even in the Agaricales, where a folk taxonomy hardly existed (Walters, 1986; Morris, 1988), most of the major genera seem to be some kind of folk genera. Second, genus names are part of the taxon's name (unlike family names) and for that reason genus names play a decisive role in information storage and retrieval.

Besides practical and conventional problems, there are a number of fundamental considerations about the genus concept, related to the existence of genera and the way we can identify them. It has sometimes been questioned whether individual genera (not the genus as a category, which is certainly conventional) exist objectively, independent of our ability to recognise them. I think that they do, in the same way that all holophyletic groups are considered to really exist (Löther, 1972; Wiley, 1981a). Holophyletic taxa are the passive products of speciation, splitting and subsequent formation of species, which really exist in nature. As a consequence holophyletic taxa are historical groups with an objective existence. This idea largely conforms to our intuition, as certain genera clearly give the impression of real existence. Romagnesi (1977) suggested that this is clear in genera like *Pluteus* Fr., *Volvariella* Speg, *Inocvbe* (Fr.) Fr., *Melanoleuca* Pat., and *Coprinus* Pers.; and that it also applies to monotypic genera like *Rhodotus* R. Maire (but see the cladistic problem with monotypic genera). I would probably therefore disagree with Bisby & Ainsworth (1943) who believed that "nature may make species, but man has made the genera".

## Historical sketch

It has repeatedly been said that the character does not make the genus. This expression can be found in the works of Linnaeus (1751), Fries (1838), Bentham (1861), and several other taxonomists. It was Darwin (1859) who realised that this expression had profound implications. He wrote: "such expressions as the famous one of Linnaeus ..... that the characters do not make the genus, but that the genus gives the characters, seem to imply that something more is included in our classification than mere resemblance. I believe ..... that propinquity of descent ....... is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classification".

Evolutionary thinking did scarcely influence the classification of the Agaricales, just as it had little impact on the classification of higher plants. Stevens (1984) concluded that evolutionary theory had no effect on taxonomic methodology, although it changed the way in which classifications were explained and justified.

Within the Agaricales most of the Friesian tribus survive in our present-day classification. This is the more surprising if we realise how artificial Fries's classification was and how his deductive and a priori method of logical division influenced his taxonomic work (Eriksson, 1962; Kuyper, l991a).

Fayod (1889) was one of the first mycologists to explicitly base his classification on evolutionary theory. He stated as the aim of his work the establishment of the phylogenetic affinities between the different groups of fungi. Singer (1936, 1942) also expressed his ideas on naturalness of a classification of the Agaricales. He stated that his classification was intended to be evolutionary. In his opinion genera (i) should differ in important characters, (ii) should show a hiatus with neighbouring and related genera, and (iii) should preferably be monophyletic or consist of parallel polyphyletic groups (but then the genus had to be a morphological and biological unity). This latter criterion was probably included because Singer (1942) considered the genus *Russula* Pers. polyphyletic. In later classifications, however, Singer deviated from this phylogenetic reasoning and he introduced a phenetic methodology in his classification of the Agaricales (Machol & Singer, 1972). This could be the reason for Kühner's statement (1980) that Singer seemed more interested in hiatuses (Singer, 1986 explicitly speaks of "hiatusbased taxonomy") between genera than in natural relationships.

In this paper I will both sketch how the genus concept has been and can be applied within the Agaricales. Additional quantitative data on a bias in generic concepts is published separately (Kuyper, l991b).

As a point of departure for the discussion I take it that genera should preferably be natural in the phylogenetic sense. This phylogenetic naturalness is often inferred from phenetic naturalness. Let me immediately add that naturalness has no implications with regard to homogeneity and size of genera. I will categorically state that considerations of utility, however important, are of less relevance than the fundamental problem of naturalness. Genera, which turn out to be unnatural, must be given up - and indeed have often been given up, if we look at the taxonomic history of old Friesian taxa like *Omphalina* Quél. (Kuyper, 1986a; but the genus *Gerronema* Sing. has now become the dustbin for the omphalinoid Tricholomataceae), *Armillaria* (Fr.) Kumm., and *Pholiota* (Fr.) Kumm.

## Principles of generic classification

If a generic classification is claimed to have a scientific basis, a theory of classification with sound principles is necessary. In my opinion evolutionary theory is the only candidate for such a scientific classification and for that reason a scientific classification is a phylogenetic classification. There are different methods for the incorporation of evolutionary principles in a classification. I object to the construction of so-called theory-free classifications (see Kendrick & Weresub, 1966 for corticioid fungi). The same objection applies to Bayesian analysis of generic affinities (Machol & Singer, 1972; Clémençon, 1976), a divisive method that also aims at representing phenetic resemblance instead of the branching process.

From a practical point of view, cladistically natural classifications seem to correspond fairly well with phenetically natural classifications (Kalkman, 1987; Kuyper, 1988), because recency of common origin is often related to the morphological gaps between neighbouring genera.

In this paper I will investigate in how far the criticism on current generic concepts in the Agaricales is correct. For that reason I will look at the taxonomic practice of the last ten years, in which many new genera of Agaricales have been described. Hopefully an evaluation of the strong and weak foundations of new genera will suggest us both the advances and the retreats we made on our search for a natural system.

## New genera in the Agaricales

The new genera of Agaricales that have been newly created ("generification") in the last 10-15 years can be categorised in four different groups:

1. generification by discovery
2. generification by homogenisation
3. generification by inflation
4. generification by cladistic analysis

### *Generification by discovery*

When new species are discovered that cannot be accomodated in existing genera, new, often monotypic genera are erected. This occurs both in tropical countries (*Callistodermatium* Sing., *Pegleromyces* Sing., *Janauaria* Sing., and *Clavomphalia* Horak), but even in Europe new genera are described that fit this category (*Stanglomyces* Raithelhuber and *Wielandomyces* Raithelhuber). In these latter two instances I stronly doubt whether they really represent good genera, as these taxa are insufficiently described and compared with existing genera. From the description alone the genus *Wielandomyces* seems a simple synonym of *Agrocybe* Fay.

### *Generification by homogenisation*

This procedure of generification is encountered if species are separated from existing genera on the basis of one aberrant and striking character. One is reminded of *Inocybella* Zerova (separated from *Inocybe* (Fr.) Fr. on account of spore characters; *Meqatricholoma* Kost, separated from *Tricholoma* (Fr.) Staude; *Rhodocybella*, separated from *Rhodocybe* R. Maire; *Dactylosporina* (Clémençon) Dörfelt, separated from *Xerula* R. Maire on account of echinate spores; *Singerocybe* Harm., separated from *Clitocybe* (Fr.) Staude on account of the peculiar intercalary elements in the pileipellis; *Mariaella* Sutara, separated from *Suillus* S. F. Gray on account of hymenophoral trama and fertile stipe covering; *Setulipes* Antonin, separated from *Marasmius* Fr. on account of the non-hymeniform pileipellis as cases in point. Unfortunately far less attention is given to the remainder of the genus and it is unclear and usually without arguments whether this remaining part of the genus is holophyletic.

This procedure seems widespread with species that have been transferred from genus to genus in the Agaricales. Examples include *Rickenella* Raithelhuber (its constituent species have been previously classified as

*Omphalina* Quél., *Mycena* (Pers.) Roussel, *Hemimycena* Sing., *Marasmiellus* Murrill, or *Gerronema* Sing.), *Cantharellopsis* Kuyp. (the type species has been considered a *Cantharellus* Adans.: Fr., *Hygrophoropsis* (Schroeter) R. Maire, *Gerronema* Sing., or *Leptoglossum* P. Karst.), *Gamundia* Raithelhuber (the species were previously classified as *Omphalina* Quél., *Clitocybe* (Fr.) Staude, *Rhodocybe* R. Maire, or *Fayodia* Kühner), and *Ossicaulis* Redhead & Ginns (the type species was previously classified as *Pleurotus* (Fr.) Kumm., *Clitocybe* (Fr.) Staude, or *Pleurocybella* Sing.; the difficulties in finding an acceptable generic disposition for it can be clearly seen in Singer (1986), where the name *Ossicaulis* Redhead & Ginns is accepted as a synonym of *Neoclitocybe* Sing., but the type species is accepted as a member of *Clitocybe* (Fr.) Staude). However, one should be aware that almost every large genus can contain borderline cases and that by making the genera more and more homogeneous the need for more and more segregate genera arise. Homogenisation is often accompanied by inflation (see below). It seems that homogeneity and naturalness have often been confused (Steenis, 1978).

This generification could lead to excessive splitting. One can, fairly safely in my opinion, predict that some species are candidates for the transfer to a new autonomous genus on the basis of this criterion, e.g. *Mycena rorida* (Scop.: Fr.) Quél. on the basis of the structure of the pileipellis, *Omphalina cyanophylla* (Fr.) Quél. on account of dextrinoid trama and absence of cystidia, *Omphalina grossula* (Pers.) Sing. on account of pileipellis and ecology (up to now classified as an *Omphalina* Quél., *Gerronema* Sing., *Aeruginospora* Höhn., and *Cuphophyllus* (Donk) M. Bon), *Pholiota oedipus* (Cooke) P. D. Orton, *Clitocybe puberula* Kuyp. on account of differentiated pileipellis and cheilocystidia, *Hygrophoropsis morqanii* (Peck) H. E. Bigelow on account of non-dextrinoid spores, and *Cortinarius pseudocrassus* Joss. ex P. D. Orton on account of its pleurocystidia.

Such genera are extremely problematic if they are characterised by a character which might be of a polyphyletic origin. This situation is encountered in *Coprinella* Zerova (a segregate of *Coprinus* Pers. with ornamented spores; but ornamented spores seems to have been arisen more than once, cf. Orton & Watling, 1979) and also in *Astrosporina* Schroeter (separated from *Inocybe* (Fr.) Fr. on account of angular and nodulose spores, cf. Kuyper, 1986b).

Some mycologists have thought that *Phytoconis* Bory (= *Botrydina* Bréb.) belongs to the same category, but I will show below that it belongs to the fourth category.

### Generification by inflation

The most obvious examples of generification by inflation can be found in the books by Kummer and Quélet where the tribus of the old genus *Agaricus* L. were all elevated to generic rank. We all got used to these genera, but we would now object to the next step in the inflation process, as was clear from the reception of a score of higher taxa of Basidiomycetes (Jülich, 1982).

Recent examples in the Agaricales include: *Microcollybia* Lennox and *Rhodocollybia* Sing., both segregated from *Collybia* (Fr.) Staude; *Pseudolyophyllum* (Raithelhuber) Raithelhuber, a segregate for species of *Clitocybe* (Fr.) Staude with a hygrophanous pileus; the acceptance of this group is even more difficult as it seems unlikely that this is a holophyletic group (Kuyper, unpublished data); *Hemipholiota* (Sing.) M. Bon, a segregate of *Pholiota,* to which *P. populnea* (Pers.: Fr.) Kuyp. & Tjall., *P. albocrenulata* (Peck) Sacc., and *P. oedipus* (Cooke) P.D. Orton are said to belong.

A somewhat different situation is encountered in *Entoloma* (Fr.) Kumm. At the same time a number of (new) taxa have been recognised on generic level (*Pouzarella* Mazzer, *Inopilus* Pegler, *Claudopus* (Fr.) Gillet: but that latter taxon is almost certainly polyphyletic!) and some of the classical taxa (e.g. *Eccilia* (Fr.) Quél., *Leptonia* (Fr.) Kumm., *Nolanea* (Fr.) Kumm.) have been given up. Apparently both lumping and splitting can occur as uncorrelated activities in the same systematic treatment.

An even more striking example of the consequences of generification by inflation concerns the Hygrophoraceae. Since almost a century this group has been conceived as a separate family. Although the members of this group are comparatively easy to recognise difficult to come (Romagnesi, 1977), it proved extremely up with reliable characters that justify separate family. The only two characters, viz. thick, waxy lamellae and long basidia in comparison with their length are (i) almost universally considered as primitive characters (and hence not suited for recognition of distinct groups, cf. Kühner, 1980; Oberwinkler, 1982; but Corner (1957) considered long basidia as a derived character) and (ii) allow for many exceptions both within and outside the group (see Bas, 1988). However, mainly because this group is considered as an autonomous family, the next logical step is to inflate the rank of the taxa below it. Kovalenko (1989) on the basis of earlier work by Herink has done that: he now recognises 7 genera in this group, viz. *Cuphophyllus* (Donk) M. Bon, *Neohygrocybe* Herink, *Pseudohygrocybe* (M. Bon) Kovalenko, *Hygrocybe* (Fr.) Kumm., *Gliophorus* Herink, *Camarophyllopsis* Herink (but the general resemblance -or even close relationship with *Dermoloma* (J. Lange) Herink- seems to have been unnoticed by him), and *Hygrophorus* Fr. There is in my opinion insufficient argument for recognition of Hygrophoraceae as a monophyletic group, and even pigment chemistry allows for several classifications (Bresinsky & Kronawitter, 1986) as these pigments are often lacking within this group and they also occur in some *Amanita* Pers. species. And the suggestion by Arnolds (1989) that Hygrophoreae and Hygrocybeae represent different tribus within the Tricholomataceae (hence implying that the Hygrophoraceae are even polyphyletic) has not been convincingly refuted.

Deflation is much rarer, although both Romagnesi (1977) and Kühner (1980) seem to favour this procedure. Interestingly Kühner (1980) simultaneously reduced the number of genera and increased the number of families. Again splitting and lumping can go hand in hand. Geesink (1984) has pointed out some problems with generic merging, the main one being that once the lumping snowball gets running, it can be extremely difficult to stop it. Stevens (1984) also pointed out that by generic merging problems are created, especially if unrelated species are incorrectly subsumed in a genus or family. However, *Flammula* (Fr.) Kummer is almost universally merged with *Pholiota* (Fr.) Kummer, although the newest trend is now to separate *Hemipholiota* (Sing.) M. Bon, providing a further example of simultaneous splitting and lumping. With *Pholiotina* Fay. and *Conocybe* Fay. both a wide and a narrow genus concept seem to coexist, stimulated - as one would almost be tempted to say - by the possibility of making new combinations in either genus and hénce obtaining nomenclatural immortality. The same problem of a dual taxonomy will probably occur in *Lyophyllum* P. Karst. and *Tephrocybe* Donk for some time to come. *Panus* Fr. and *Lentinus* Fr. have been merged by Pegler (1983), but recently Redhead & Ginns (1986) have split it again, partly on the basis of old characters but with the addition of the correlated character of the type of rot (white rot versus brown rot).

*Cortinarius* (Pers.) S.F. Gray seems -except for (sub)genus *Dermocybe* (Fr.) Wünsche- now almost universally deflated. Nobody would probably think of reintroducing *Myxacium* (Fr.) Kumm. as a separate genus. In fact many people would now recognise the artificial nature of this taxon, which consists in Europe of three independent groups, almost certainly without any clear phylogenetic affinity. Interestingly, *Leucocortinarius bulbiger* (A. & S.: Fr.) Sing., which comes in almost all characters so close to members of subgenus *Phlegmacium* (Fr.) Fr. that it can easily be confused with species of sect. Multiformes, is considered to belong in an autonomous genus, and Kühner (1980) considers this species only as extremely convergent with cortinarioid fungi.

### Generification by cladistic analysis

This last category of generification is based on a complete phylogenetic analysis of a certain complex and its subsequent translation in a consistent classification. This is the rarest way of making new genera, although it constitutes the only advance towards a natural system. Due to the scarcity of morphological and molecular characters one should, however, be extremely careful in finding an acceptable rank for the groups then recognised. Cladograms of fungal taxa usually show a low consistency index because of high convergence and large number of reversals (Bruns & Palmer, 1989), are not robust, and consensus trees are almost completely unresolved, and groups may be incompatible despite character compatibility, suggesting that such cladograms are likely to remain unstable and hardly predictive.

As an example I refer to my earlier work on the European omphalinoid Tricholomataceae (Kuyper, 1986a; cf Redhead & Kuyper, 1987). On the basis of this analysis it was most parsimonious to consider lichenisation within this group to have arisen only once and not twice, as had implicitly been assumed by almost all agaricologists. However, it does not strictly follow from this analysis that *Phytoconis* Bory must be separated from *Omphalina* Quél. on generic level. Recognition as a subgenus might have been equally acceptable. Our choice was made on the basis of the idea that genera should preferably have some minimal quality (see below).

There are several reasons for treating this analysis with caution, viz. (i) tropical species of *Gerronema* Sing. were not included; in fact the type species *G. melanomphax* Sing. turned out to have sarcodimitic tissues (Redhead, 1987) and the European taxa hitherto referred to this genus are most likely not congeneric with the tropical representatives of this genus; (ii) the European taxa, which were treated as members of *Gerronema* Sing. formed a very heterogeneous assemblage, which is almost certainly not holophyletic as can be seen from the group incompatibility despite character compatibility; (iii) the so-called derived series (*Arrhenia* Fr., *Leptoglossum* P. Karst., and *Phaeotellus* Kühner & Lamoure) were omitted. This has most likely also influenced the final outcome of the cladistic analysis. In fact, *Omphalina* Quél. was recognised as a paraphyletic group. We can only guess whether *Arrhenia* Fr. sensu lato, and *Arrhenia* Fr. plus *Omphalina* Quél. are holophyletic or not.

A similar analysis has been executed by Høiland (1987) for the European boletes. Not many taxonomic changes were proposed - probably because omission of all extra-European taxa made the cladogram of restricted applicability. It has generally been stated (Corner, 1972; Singer, 1981) that knowledge of the tropical boletes is an absolute prerequisite for a sound generic delimitation of the boletes. In how far this also applies to cladistic classification is not clear; it will probably depend on the origin of the boletes, whether the boletes form a polyphyletic (Heim, 1971; Pegler & Young, 1981) or holophyletic (Singer, 1981b; Bruns & Szaro, 1990) group, with either a temperate of tropical area of origin. There are also problems with Høiland's a priori transformation series of chemical constituents, which seems to make the cladogram not maximally parsimonious. We can be rather confident that parts of this cladogram are fairly robust, as analysis of molecular data showed a highly congruent cladogram (Bruns & Szaro, 1990). Bruns's studies also indicate that morphological evolution might proceed much faster than molecular evolution (Bruns & al., 1989), implying that gasteroid forms (e.g. *Gastroboletus* Lohwag (probably polyphyletic?) or *Gastrosuillus* Thiers) do not deserve any status at all. A similar problem of unequal rates of molecular and morphological evolution is probably encountered in *Leucocortinarius* Sing. (see above), in the relationship between *Chamonixia* Rolland and *Gyroporus* Quél. (Høiland, 1987) and *Laccaria* B. & Br. and *Hydnangium* Wallr., and in members of the so-called secotioid syndrome (Thiers, 1984).

The cladogram of *Inocybe* (Fr.) Fr; with regard to the species with metuloid cystidia is also not robust at all (especially with regard to the separation of species with smooth versus nodulose spores, and species with a pileocarpous versus stipitocarpous development) and that was a reason why I did not translate this cladogram into a classification, even on infrageneric level (Kuyper, 1986b). Another reason from refraining from a detailed infrageneric classification was that I had not studied the species with angular and nodulose spores.

Similar problems od consistency and robustness were encountered in a preliminary cladistic analysis of *Clitocybe* (Fr.) Staude and *Lepista* (Fr.) W.G. Smith (Kuyper, unpublished results), both on the basis of morphological characters and with addition of a few chemical characters. In this case too no robust cladograms could be constructed, and I am still unable to state with any confidence whether *Clitocybe* (Fr.) Staude and *Lepista* (Fr.) W.G. Smith sensu Singer (1986) are holophyletic, whether the emendations of Harmaja (1974, 1976, 1978) made *Clitocybe* (Fr.) Staude and *Lepista* (Fr.) W.G. Smith holophyletic (irrespective whether both should be recognised as independent genera or not), or whether *Lepista* (Fr.) W.G. Smith is a polyphyletic segregate of *Clitocybe* (Fr.) Staude (as Bigelow (1982) has suggested). It seems therefore useless to come up with a major revision of the (infra)generic taxonomy in this group, and the best way might be to maintain both genera in their present circumscription for conventional reasons.

## Value of generic characters

It has already been remarked in the introduction that the characters do not make the genera. It is well known amongst taxonomists that characters do not have an absolute value, but only a relative value, implying that characters, which can be used for generic segregation in one taxon, can only be used at (infra)specific level in another group. As an example I refer to the value of albinistic spores, which is recognised on generic (or even familial) rank in *Leucocortinarius bulbiger* (A. & S.: Fr.) Sing., on generic rank in *Hebelomina* R. Maire, on species rank in *Tubaria hololeuca* (Kühner) or *Suillus hololeucus* Pantidou, or not given any attention at all in *Inocybe* (Fr.) Fr.

It is, however, important to get some insight in the value of the characters that are used for generic delimitation. Singer (1975, 1986) provided an extensive discussion on the taxonomic value of different characters within the Agaricales.

In order to be useful for a cladistic classification, we have to look only to the derived character state, as groups, based on the common possession of the primitive character state, cannot be said to be natural. Unfortunately, it is not known with most characters what the primitive (plesiomorphous) and the derived (apomorphous) character state is. Outgroup comparison to determine character polarity is often difficult, as there is a large controversy among mycologists on direction of evolution within the basidiomycetes. The Agaricales have been derived from the Gasteromycetes (Singer, 1985) and vice versa (Heim, 1971); The Boletales have been derived from the Agaricales (Høiland, 1987) and vice versa (Pöder, 1984); and the white-spored Tricholomataceae have been derived from the brown-spored Cortinariaceae (Clémençon, 1977; Høiland, 1984) and vice versa (Kühner, 1980). With regard to the latter relationship it might be useful to point out that brown-spored taxa also occur in the Tricholomataceae (*Clitocybe benekei* H.E. Bigelow & A.H. Smith, *Ripartites* P. Karst.) and that pale-spored taxa also occur in the Cortinariaceae (*Pleurotellus* Fay., congeneric with *Crepidotus* (Fr.) Staude). White and brown spores also occur in the very closely related genera *Cystoderma* Fay. and *Phaeolepiota* Konr. & M. (Bas, 1988).

We therefore have to rely on much weaker arguments in order to determine character polarity within the Agaricales. A general survey of morphological, developmental, and chemical characters yielded some general criteria to determine character polarity (Kühner, 1980). But even with the help of these characters, our cladistic classifications are founded on a weak basis.

Truly synapomorphic characters, which can be used for generic delimitation, are extremely scarce within the Agaricales. The peculiar spore wall structure of *Entoloma* (Fr.) Kumm. and *Fayodia* Kühner sensu stricto, and the hymenial thickening of *Chrysomphalina* Clémençon are good synapomorphies for generic delimitation. Lichenisation within the Agaricales is almost certainly a good synapomorphy for *Phytoconis* Bory. But it would be difficult to come up with many more examples. There are, of course, some further examples on higher taxonomic levels, e.g. the heteromerous trama for the Russulaceae, the acrophysaloid hyphae in Amanitaceae plus Pluteaceae (if it is absent from *Floccularia luteovirens* (A. & S.: Fr.) and *Ripartitella rickenii* (Bohus) Sing.; these two species were considered congeneric by Singer (1975) but classified in different families in Singer (1986) and inverse hymenophoral trama for Pluteaceae.

Some other characters show synapomorphous tendencies (Cantino, 1982) or nonuniversal synapomorphies (Sluys, 1989), implying that they occur in most (but not all) taxa and never outside the group, e.g. nodulose hyaline spores with a large apiculus in *Mycenella* (J. Lange) Sing., strobilurins and oudemansins in Xerulaceae sensu Redhead (1987; if truly holophyletic?) and pulvinic acid derivatives in the Boletaceae.

Most characters that have been used for generic classification are not restricted to one taxon: they occur in several groups, where the character apparently originated convergently or in parallel. In some instances we can find a combination of such characters that is unique for a certain genus, e.g. the combination of smooth or nodulose brown spores with metuloid cystidia (*Inocybe* (Fr.) Fr. subgenus *Inocybe*; nodulose spores also occur in *Conocybe* Fay., metuloids also occur in *Galerina* Earle and *Crepidotus* (Fr.) Staude), the combination of metachromatic spores with carotenoids (*Haasiella* Kotl. & P.; carotenoids seem to have originated at least twice in the Agaricales, once in *Haasiella* Kotl. & P. plus *Chrysomphalina* Clémençon, once in *Phyllotopsis* Sing.; metachromatic spores also occur in the Agaricaceae), siderophilous basidia combined with a brown rot (*Hypsizygus* Sing.; siderophilous basidia can also be found in other members of the Lyophylleae and in *Termitomyces* R. Heim and *Entoloma* (Fr.) Kumm.; brown rot also occurs in *Ossicaulis* Redhead & Ginns and possibly in *Coprinus* Pers.), etc.

However, in the majority of genera we do not find such monothetic sets, but we see that the genera are based on polythetic sets: none of the characters is unique to the group, and not all species of this group show the complete set of characters. As an example I refer to the genus *Pholiota* (Fr.) Kumm., where the polythetic set consisting of (i) brown spores with a germ-pore, (ii) presence of chrysocystidia, and (iii) presence of styryl-pyrones is characteristic for this genus. Genera like *Collybia* (Fr.) Staude and *Mycena* (Pers.) Roussel seem also based on a polythetic set. In such cases it is extremely difficult to determine the value of individual characters as parallelisms cannot be easily recognised from apomorphies.

In such cases generic delimitation will almost certainly remain highly controversial. The best example in my opinion is to be found in the Strophariaceae, where hardly any agreement on generic delimitation seems to exist, as several species have been classified in *Psilocybe* (Fr.) Kumm., *Hypholoma* (Fr.) Kumm., and *Stropharia* (Fr.) Quél. Smith's suggestion that these genera should be merged is probably another indication of the hopelessness of arriving at a natural classification in this group (Smith, 1977). Maybe the recognition of genera like *Entoloma* and *Cortinarius* is evidence of the same difficulty.

This scarcity of truly unique characters within the Agaricales has probably lead to the gross overestimation of some unique characters, which were said to indicate natural relationships with fungal groups that were normally not considered related with the Agaricales. Redhead (1977) considered the sarcodimitic trama so unique that he supposed that the Xerulaceae evolved convergently with the Tricholomataceae from different ancestors. Oberwinkler (1976) considered *Verrucospora* Horak a member of the Thelephoraceae on the basis of spore structure and Kost (1990) has recently postulated a relationship between species of *Lyophyllum* P. Karst. and *Typhula* Fr. (although the joint possession of primitive characters was cited as evidence). On the basis of nematode-trapping capacity some species of *Pleurotus* (Fr.) Kumm., *Hohenbuehelia* Schulzer and *Resupinatus* S.F. Gray have been merged in one genus (Miller, 1986).

## Problems of ranking

Finally I wish to comment on the relationship between the cladistic analysis and the subsequent classification. Two problems are involved, one fundamental and one conventional (Kornet, 1988). The first problem refers to the translation of a cladogram into a classification. It has often been said that a cladogram must be consistent with a classification, which certainly implies that polyphyletic taxa are not admissible in the final classification. There seems to be disagreement about the acceptability of paraphyletic groups in the final classification.

Mayr (1974) has stated that he considered paraphyletic groups acceptable in a number of specified cases, but most present-day cladists (e.g. Wiley, 1981b) disagree. They have categorically stated that paraphyletic groups are absolutely inadmissible in a classification. Without going into detail with regard to the problem I wish to note, however, that application of that strict criterion will be very problematic in a classification of the Agaricales at least for the time being. This criterion will result in the inclusion of most socalled reduced series and gastroid forms (assuming that such forms are derived) in the same genus as the members with a lamellate or boletoid hymenophore. Such classifications will probably be inconvenient from a practical point of view and unstable for some time to come. For these reasons both Kuyper (1986a) and Høiland (1987) accepted paraphyletic groups.

The second problem refers to the ranking of the holophyletic groups. It has been largely a matter of convention which (holophyletic) groups should be recognised as genera. Practical considerations do of course play a role, as genera with a very high number of species are generally considered as undesirable, although most mycologists would see more difficulties than advantages in inflating the infrageneric taxa of *Cortinarius* (Pers.) S.F. Gray or *Entoloma* (Fr.) Kumm. But neither size of the holophyletic group, nor its absolute age (Hennig, 1982) are acceptable criteria for generic delimitation.

The search for synapomorphies, synapomorphic tendencies, or unique combinations of characters as evidence for holophyletic taxa might in some cases easily lead to extensive generic splitting (cf. Kuyper, 1986a). Some mycologists have felt that this is an undesirable side-effect of cladistics. However, the cladistic analysis of the European omphalinoid Tricholomataceae did not make it obligatory that *Phytoconis* Bory and *Omphalina* Quél. sensu stricto have to be recognised as autonomous genera. Recognition as different subgenera within the same genus might have been equally acceptable. The choice to recognise them as genera was not based on the assumption that lichenisation was such an important character that it must be used on generic level, but on the basis of the idea that genera should preferable have some minimal phylogenetic quality (Geesink, 1984). As the phylogenetic quality of the more inclusive group was difficult to assess, the generic splitting was an inevitable consequence. It is probably too early in my opinion to judge whether this classification has been completely successful, although I maintain that it is successful enough to continue it for some time.

## Conclusion

In the preceding pages I have given some summary views on problems with generic delimitation in the Agaricales (by itself a group which holophyly has never been demonstrated or even made plausible!).

I suggested that cladistic methods can form the way out of such problems. We must certainly not be so naive as to overestimate the impact of cladistic methods. And there are certainly good reasons to treat both our present-day cladograms with caution and to be suspicious of a direct translation of a cladogram into a classification. In order to improve this present status of cladistic analysis of the Agaricales we need good monographs. World monographs for the Agaricales are extremely rare, but even good regional and continental revisions are much too rare. We also badly need extensive character analysis. I indicated that our cladograms are not robust at all. As a consquence such cladograms are liable to much change after the addition of new species and/or new characters. We need therefore more morphological, developmental (both of the basidiocarp and of the spore wall), chemical, and molecular studies.

But with different methods we would probably discover that cladograms based on morphology and based on molecular data will not automatically be congruent, just as they conflict in other areas of taxonomy (Patterson, 1987). It will certainly take some time before we arrive at a reasonable compromise on the basis of an understanding of the relative rates of morphological and molecular evolution. Such an understanding will also allow us to incorporate the relevant reduced series and the gastroid forms in the natural system of the Agaricales. And it will also allow us to better understand the Agaricales as a group: even if it would ultimately mean giving up the Agaricales as a holophyletic group.

Unfortunately, even a minimal phylogenetic quality for the genera of the Agaricales can conflict with stability of generic concepts. In the meantime we should therefore refrain from proposing revolutionary alterations in the circumscriptions of the various genera of the Agaricales. Practical considerations and some minimal nomenclatural stability are simply too important to neglect.

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