
The problems of traditional and phylogenetic taxonomy of fungi

Vasilyeva LN^{1*} and Stephenson SL²

¹Institute of Biology and Soil Science, Far East Branch of the Russian Academy of Sciences, Vladivostok 690022, Russia, vasilyeva@biosoil.ru

²Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA, slsteph@uark.edu

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The current taxonomic system, based on the hierarchy of Linnaean ranks, is said to be unsatisfactory. Many people insist that the very concept of rank should be eliminated, and the current taxonomic system should be replaced with a rankless system based on phylogenetic taxonomy. However, it is not the elimination of the concept of rank but rather the correct ranking of characters that will promote stability in taxonomy. The first problem of both traditional and phylogenetic taxonomies is the chaotic employment of differences that leads to the segregation of groups which are not comparable in rank. A proper rank coordination could be carried out by the special weighting of differences among tentative groups. Groups become equal in rank when they are distinguished by state combinations of the same character set. The second problem of both traditional and phylogenetic taxonomies is the employment of internal polymorphism of genera and families for the re-unification of species into new taxa. This could be overcome if taxonomists take into consideration the law of homologous variation within closely related genera and families.

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*Corresponding author: Vasilyeva LN – e-mail – vasilyeva@biosoil.ru

Introduction

Already it has been 15 years since the statement was made that “in mycological taxonomy, the rift between traditional morphologists and molecular phylogeneticists remains unbridged” (Seifert et al. 1995: S760). In this opposition, the contrast seems to exist between morphology and phylogeny, as well as between the words ‘traditional’ and ‘molecular’. However, both morphology and molecules can serve phylogeny, and one meets with the real opposition between traditional and phylogenetic methodologies. Supposedly, “the current taxonomic system, based on the hierarchy of Linnaean ranks is not satisfactory” (Hibbett & Donoghue 1998: 347). On the one hand, this hierarchy seems to be unsatisfactory

because of few available ranks, whereas “a large number of ranks are necessary to classify complex phylogenetic trees” (l. c.). On the other hand, the phylogenetic taxonomists say that the very “concept of rank should be eliminated, and the current taxonomic system should be replaced with a *rankless system based on phylogenetic taxonomy*” (l. c., italics added). These two contradictory demands—many ranks vs. a rankless system—concern two different aspects of phylogenetic theory.

The notion of a ‘rankless system’ seems to be the consequence of a world view called the “great chain of being”. The latter held a central place in Western thought for centuries and saw the organic world as ordered in a *linear sequence* (Nee 2005). Such a sequence

does not entail the appearance of ranks, but modern evolutionary views suggest a hierarchical development of the biota. “When we depict evolutionary relationships in the form of a tree, we acknowledge that *genealogical relationships are hierarchical by nature*” (Spatafora & Blackwell 1994: 233, italics added).

It should be emphasized, however, that both world views do not exclude each other. Living or extinct *beings* do comprise a sequence, while *relationships* among organisms might be hierarchical. It is currently known that the original gene pool which once existed on the Earth split into smaller pools, and they are now called Bacteria, Archaea and Eucarya (Woese 2000). The differences among them are the oldest fundamental differences that can be recognized for living organisms and have persisted from their very appearance to the present day.

Later, the domain Eucarya was split into a number of kingdoms, and their differences—once again—remained to be the same during the further differentiation of Eucarya into smaller groups. While almost all animal phyla were established during the ‘Cambrian explosion’ (Marshall 2006), appearances of new groups during the ‘Ordovician radiation’ were manifested at lower taxonomic levels (Droser & Finnegan 2003). As a result, the organic world represents a *nested hierarchy* of groups (Fig. 1).

Thus, the same relationships exist among taxonomic groups at the same level through their evolution. These relationships could be expressed in differences that have appeared *in sequence* during the differentiation of the organic world. When Linnaeus first introduced the very fruitful idea of the hierarchical ordering, he unintentionally created a *taxonomic model of hierarchical evolution*. The Linnaean hierarchy conveys both the nesting of small groups within the larger ones and the distribution of characters among levels in accordance with their appearance in time.

The sequence of characters marking different levels is the *only evolutionary line* (‘natural scale’) in the hierarchical system, so there is no need to arrange organisms in a ‘chain of beings’ (i.e. the construction of system does not require the tracing of ancestors

and descendants). If one could establish the sequence of characters correctly, one would find the only structure that retains stability in the continuing process of change. Thereby, one would come to the most natural system reflecting the hierarchical evolution.

Therefore, it is not the elimination of the very concept of rank that “promotes nomenclatural stability” (Hibbett & Donoghue 1998: 347) but rather it is the proper *ranking of characters* for the groups being considered. The problem of ranking is the gist of taxonomy, although both traditional and phylogenetic taxonomy seem to have failed in resolving this problem. It is true that the current taxonomic system is not satisfactory, but this is *not* because it is based on the hierarchy of Linnaean ranks. Instead, the situation exists because there was no *method* for finding the place of a character in the hierarchy.

Even if taxonomists could have a kind of a ‘rough’ hierarchy on the basis that some characters cover more extensive groups than others, the choice of characters for group delimitation *at each level* is often haphazard. The chaotic employment of any ‘unique character’ leads to groups that are similar to ones in the ancient Chinese encyclopedia described by the famous Argentine writer Jorge Luis Borges. In that encyclopedia, animals were divided into many groups, including such examples as (1) belonging to the emperor, (2) embalmed, (3) fabulous, (4) stray dogs, (5) suckling pigs, (6) those that look like flies from a long way off, and so on.

Such a ‘classification’ is quite compatible with the practice of constructing a key for the identification of groups assigned to the same level (species, genera, or families). For example, the delimitation of genera in the family Capnodiaceae (Capnodiales, Ascomycota) goes as follows: *Trichomerium* differs from all other genera in having sessile fruit bodies, *Scorias* is characterized by a ‘stromatal habit’ of those fruit bodies, *Capnodium* possesses pigmented ascospores, *Limacinula* is based on the presence of thin-walled hyphae below the ascomata, while *Trichopeltheca* has no periphysoids (Reynolds 1986).

The dichotomous key for these genera is similar to a cladogram and is considered to represent ‘phylogenetic relationships’. In fact,

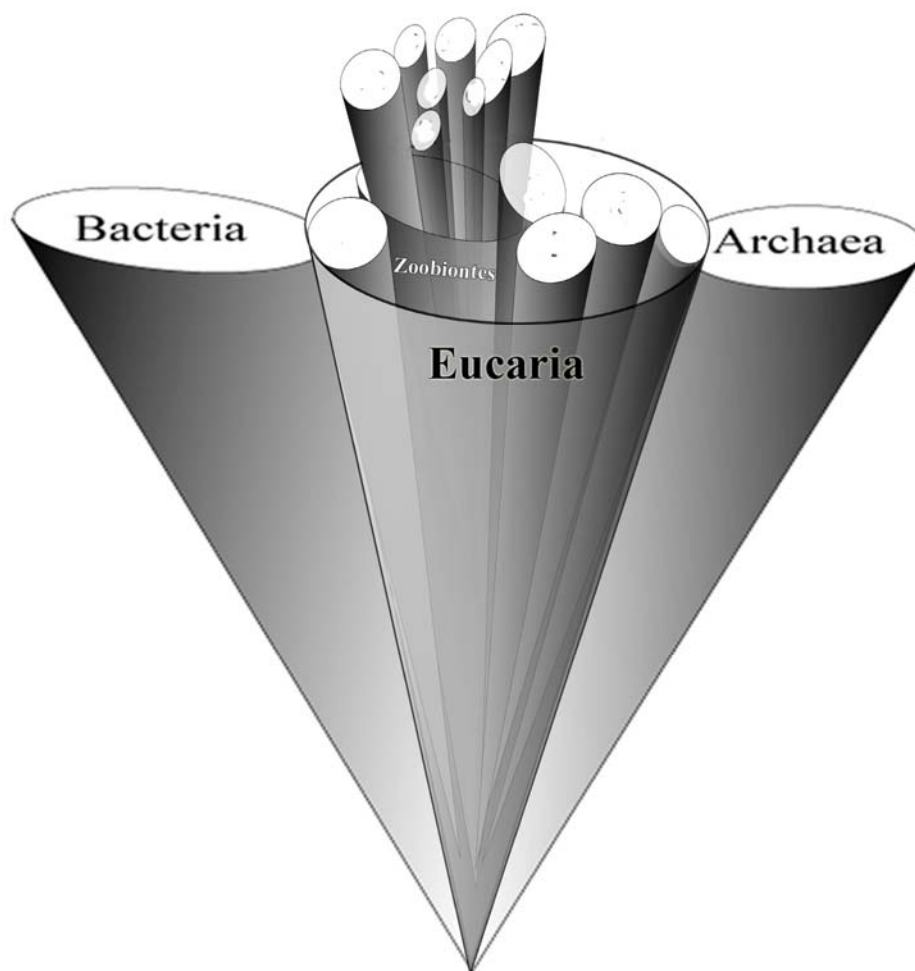


Fig. 1. The organic world depicted as a *nested hierarchy* of groups.

the first problem shared by traditional and phylogenetic taxonomy is the ‘principle of dichotomy’. The first *hierarchical* dichotomy could be found in Plato's dialogue *Sophiste*, although its invention is attributed to the neoplatonic philosopher Porphyry. The famous ‘Porphyrian tree’ is known to be a tree-like construction where points of branching are marked by the differences of successively smaller groups. However many dichotomies do not convey hierarchical relationships at all.

The keys of traditional taxonomy that are based on chaotic employment of ‘unique’ character states for the segregation of species or genera are clearly artificial but they, at least, do not aim at the ‘phylogeny reconstruction’. It is worse that phylogenetic taxonomy—using precisely the same approach to characters—proclaims that a ‘dichotomy principle’ is the only one which should be used to show the real and hierarchical relationships. This is why each point of branching in a cladogram is often

considered to correspond to a different level of hierarchy and also why phylogeneticists require “a large number of ranks... to classify complex phylogenetic trees” (Hibbett & Donoghue 1998: 347).

One can understand the key-like and artificial nature of many ‘phylogenetic trees’ from the statement that “over 12,000 equally parsimonious trees are possible for the 142 taxa” (Parmasto 1995: S843). Evidently, 12,000 different keys could be constructed, depending upon the choice of the first taxon which is pared off from all of the others, but the *true hierarchy of characters should be a single one*.

In the true hierarchy, many characters are equal in level, and our task is to find such character complexes. In his discussion of molecular characters and their significance for fungal systematics Hibbett (1992: 534) was quite right in stating that “molecular characters, though informative in many cases, are not the

‘Rosetta stone’ of systematics”; in fact, they are subject to many of the same problems as morphological characters, and “the characters themselves are only as good as the method of analysis”. In the section that follows, the *method of analysis* aiming at the *testing taxa for rank equality* will be discussed.

First, this method does not allow us to employ chaotic differences for the segregation of taxa of equal rank. It is based on the very old rule discussed already by Linnaeus, who used such words as ‘unique idea’ for a set of characters distinguishing genera in the natural order (*Philosophia Botanica*-187). That was his way of saying that taxonomic groups are *comparable in level*, or rank, only when they are defined by state combinations of the *same character set*. When this rule is applied in practice, taxa of the same level are usually arranged in the combinatorial—multidimensional - space of character states (Vasilyeva 1999).

One should not take *any* characters with states combining with each other. One should weight delimitative characters in accordance with the *frequency of their participation in delimitation*. When a taxonomist begins to study, for example, a family, he or she wants to know all genera that were placed into that family but cannot always estimate the differences between them properly. A good example is the family Gnomoniaceae (Diaporthales, Ascomycota). Different authors have assigned about 40 genera to this family and have made use of a number of distinguishing characters.

The most frequently used distinguishing character was the kind of spores, which delimits *Gnomoniella* (amerospores) *Apiognomonia* (apiospores), *Gnomonia* (didymospores) and *Ophiognomonia* (scoleospores) (Fig. 2). A second character often used for distinguishing genera in this family is the position of the elongated perithecial beak—it may be central or lateral as in *Apiognomonia* and *Apioplagiostoma*, *Gnomonia* and *Plagiostoma*, *Ophiognomonia* and *Pleuroceras*.

A third character used most frequently to describe new genera in this family is the kind of fruit body. The latter could be simple without any stromatic development, or such a stromatic development is present and referred

to as a clypeus. The presence or absence of a clypeus distinguishes *Gnomoniella* and *Mazzantia*, *Gnomonia* and *Melanopelta*, *Apioplagiostoma* and *Hypospilina*, *Pleuroceras* and *Linospora*. The further development of stromatic tissue leads to the appearance of a stromatic capsule that surrounds the fruit body. Moreover, this kind of fruit body combines with different kinds of spores, as is the case for *Mamianiella* (amerospores) and *Mamiania* (apiospores).

The Gnomoniaceae in two monographs (Barr 1978, Monod 1983) also includes the genus *Plagiosphaera*, which shares its place with *Pleuroceras* by having the same state combination of characters in question. One treatment (Barr 1978) distinguishes these genera on the basis that members of *Pleuroceras* occur on dead leaves of deciduous trees, whereas members of *Plagiosphaera* occur on herbaceous stalks. Such a difference does not allow us to consider these two taxa as separate genera, since many closely related genera, such as *Plagiostoma*, *Gnomonia* or *Gnomoniella* include members that occur both on leaves of trees and herbaceous stalks. As such, this character displays variability *inside* genera (element of the *internal polymorphism*) in this group and cannot be used to divide some other genera.

In the other treatment (Monod 1983), one can see that *Ophiognomonia* and *Pleuroceras* are distinguished from *Plagiosphaera* because these two genera lack paraphyses, as do all other members of the Gnomoniaceae. In such a case, *Plagiosphaera* should belong to a different order, since the presence or absence of paraphyses is of value at that high level. The removal of *Plagiosphaera* from the Gnomoniaceae would increase both the *naturalness of the family composition* and the *naturalness of character hierarchy*, since one false ‘generic’ character (occurrences on the leaves of deciduous trees or herbaceous stalks) became lower in level, whereas another character (presence or absence of paraphyses) used for genera delimitation appears to be higher in level.

A similar investigation of other situations in which two or more genera fall in the same place in accordance with the distribution along the most frequent delimitative characters

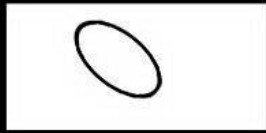
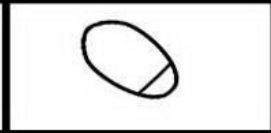
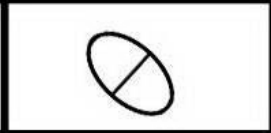
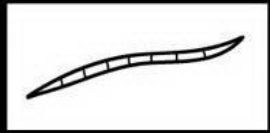
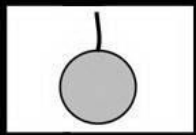
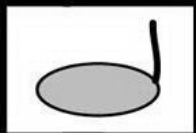
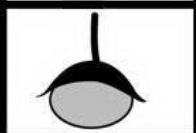
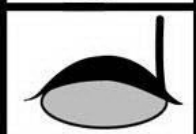
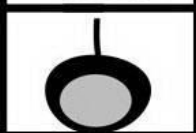
				
	Gnomoniella	Apiognomonina	Gnomonia	Ophiognomonina
		Apioplagiostoma	Plagiostoma	Pleuroceras Plagiosphaera
	Mazzantia		Melanopelta	
	Clypeoporthella	Hypospilina	Chalcosphaeria	Linospora
	Mamianiella Dicarpella	Mamiania	Mamiania alni	

Fig. 2. Characters that have been used to distinguish different genera in the family Gnomoniaceae.

allows us to go further in making the *existing system* more natural without eliminating the Linnaean ranks. Moreover, in addition to containing groups that are ranked properly in relation to each other, the natural system should be highly prognostic (de Hoog 1981).

Evidently, the empty places at each level can predict the possible—living, fossil, forthcoming, or yet unfound—organisms with certain character state combinations. Some expected combinations in the family Gnomoniaceae really do exist, but - without the method of *a posteriori* estimation of delimitative characters - these combinations are buried in wrong places. Thus, the genus *Chalcosphaeria* (didymospores + clypeus + lateral perithecial beaks) was described almost a century ago, but its name was reduced to synonyms of either *Plagiostoma* (Barr 1978) or *Hypospilina* (Monod 1983). Another example is *Mamiania alni* (didymospores + central beaks + stromatic capsule), which might deserve its own genus that is not yet described.

It might seem curious that the improvement of a character hierarchy is carried out with the help of combinatorial constructions. Some authors consider such constructions as a special kind of a system that

has a reticulate structure (de Hoog 1979) in opposition to a hierarchical system. However, the opposition is imaginary, since reticulations are particular phenomena at different levels of the hierarchy. What does really make a contrast is *reticulate* versus *dichotomous* arrangement of groups *at the same level*.

Since dichotomous constructions do not convey real phylogenetic relationships among groups of the same rank (see above), how might these groups originate? There is no need to talk about a special 'reticulate evolution', since they appear as the result of Darwinian 'indefinite' variation, which simply means that any character of an organism can change in a good or bad direction.

One can turn to a large group, for example a genus containing numerous species, and expect that one of the species combinations might be ancestral to some others. The species that differs from many others at least in one character is the most suitable candidate for an ancestor, and one can designate some of its characters by capital letters (ABCD). All of these characters can change simultaneously but in different descendants, and one can find descendant combinations such as aBCD, AbCD, ABcD, ABCd.

Now, if only one character changes in each case, any descendant shares with an ancestor almost the same genetic program and the ability to change in the same directions. Therefore, already the third generation of descendants might represent more diverse combinations (i.e., abCD, abcD, aBCd, AbcD, AbCd, ABcd, etc.). After all, a combination consisting of completely apomorphic states (abcd) might originate, and the combinatorial space constructed with the help of four changing characters will be completed with groups of the same level.

One should take into account that every such diversification includes one group that is characterized only by plesiomorphies and one group that possesses exclusively apomorphies. Character states of all other groups are mixtures of apomorphies and plesiomorphies in different proportions. This makes the second principle of phylogenetic theory, namely the ‘principle of synapomorphy’, invalid. Similar to the ‘dichotomy principle’, it merely creates heterogeneous groups and increases the artificiality of systems.

Except for cases in which synapomorphies are states of delimitative characters, they might occur in the *internal polymorphism* of closely related taxa. It is very important to keep in mind the extent to which such polymorphism can exist. For example, the two genera *Gnomonia* and *Plagiostoma* differ in the position of the perithecial beak (central or lateral) and are placed in different families by those authors who *overestimate* the level of this character (Barr 1978; Lumbsch & Huhndorf 2007). However, these genera have exactly the same internal polymorphism (i.e. repetitive characters that distinguish species within them).

Those repetitive characters are the basis of the law of *homologous variation* (Vavilov 1922), which tells us that the more complete the series of repetitive characters in two genera (or families), the more closely related these genera (or families) are. Therefore, the position of *Gnomonia* and *Plagiostoma* within the same family is supported by their similar internal polymorphism. Unfortunately, the “phylogenetic” approach is known for two blunders when that polymorphism is concerned.

What is it that phylogeneticists really do? They take *species*, for example from the genera *Gnomonia* and *Plagiostoma*, and involve them in phylogenetic analysis. The same features of these species could be apomorphic and plesiomorphic—at the *species level*—within both genera, but the employment of the ‘synapomorphy principle’ will unite ‘apomorphic species’ from two genera into a *new heterogeneous* group. Thereby, phylogeneticists make a change at the generic level by using species characters. There are even some drastic changes at much higher levels—one can look at the treatment of erysiphaceous fungi among the leotiid discomycetes (Lutzoni et al. 2004: 1457).

The second blunder of the phylogenetic approach is associated with the fact that characters of internal polymorphism *always outnumber* the few differences that exist between closely related genera or families. In molecular taxonomy, which provides many more characters than morphology, the characters of internal polymorphism become an overwhelming majority. Of course, species of many genera of the family Gnomoniaceae (and even the whole order Diaporthales) could appear near each other on a ‘molecular tree’ (Castlebury et al. 2002). There is nothing ‘phylogenetic’ in such an approach; it is a purely ‘numerical’ taxonomy which makes unifications on the basis of ‘overall similarity’ and even does not envisage the *testing* of tentative groups by weighting their delimitative characters.

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