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The systematics of arbuscular mycorrhizal fungi in relation to current approaches to biological classification

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Summary. During the past 30 years, numerous philosophical and procedural discussions have focused on the principles and methods of biological classification. From this have emerged three schools, phenetics, cladistics, and phyletics, each with its own theory of relationships, and its own set of explicit algorithms. At the same time, numerous studies on the economically important arbuscular mycorrhizal fungi have been completed. Some explicit approaches to classification have been made with higher fungi, and cladistic work has just begun on the vesicular arbuscular mycorrhizal (VAM) fungi. Thus it is now appropriate to examine the current status of the systematics of arbuscular mycorrhizal fungi and make suggestions for future work. The highest priority is to establish more refined circumscription of taxa at the lower levels of the hierarchy and to communicate these data and concepts to practicing physiologists, ecologists, etc., so that more rapid progress can be made in these areas. The limits of diversity of the group worldwide should be sought. A standardized identification manual (or atlas) would be most useful. Macromolecular studies are needed to help determine the close relatives of the VAM fungi as well as their interrelationships at the specific and generic levels. Continued emphasis needs to be placed on ontogenetic studies and their impact on variation in characters and states for taxonomic purposes. New quantitative classification approaches need to be used within the group, including phenetics and phyletics. Biogeographic concerns can then be addressed after the taxonomic issues have been more fully settled.

Key words: Vesicular arbuscular mycorrhizal fungi - Cladistics - Phyletics - Phenetics - Sytematics

Introduction

During the past 30 years, there has been a vigorous reexamination of the philosophy and methods of biological classification (Stuessy 1990). Systematists are now struggling to incorporate these new ideas into practical work, as well as to understand their philosophical and evolutionary importance. Systematics of mycorrhizal fungi has also moved at a rapid pace in recent years, and the vesicular arbuscular mycorrhizal (VAM) fungi have received particular attention (e.g., Morton 1988, 1990a, b; Morton and Benny 1990). Because of the great economic importance of these organisms, it might be helpful to consider the approaches being used in the systematics of these fungi in the context of broader changes taking place in systematics as a whole.

The purpose of this paper, therefore, is to: (1) present an overview of the three approaches to biological classification that are in current use (phenetics, cladistics, and phyletics); (2) summarize briefly the approaches to classification that are being used with other fungi; (3) review the present classification of arbuscular mycorrhizal fungi; and (4) offer suggestions regarding the systematics of arbuscular mycorrhizal fungi, with some priorities for consideration.

Different approaches to biological classification

Before discussing the different specific approaches to biological classification, a few general comments may be helpful. Systematics involves three distinct areas (Fig. 1): taxonomy, the study of phylogeny, and the study of the processes of evolution. Because systematics deals with the study of "the kinds and diversity of organisms and of any and all relationships among them" (Simpson 1961), it deals with all sorts of time, space, and form relationships, from the populational to the ecosystem level. An important part of systematics is taxonomy, which is involved with the principles and methods of classification. Classification can be viewed as consisting of two separate processes (Fig. 2): grouping and ranking. Grouping has received particular attention from practitioners, especially with regard to selection of characters, their description and measurement, and exactly how they are compared to yield the groups or taxa. Ranking has always been a difficult is-

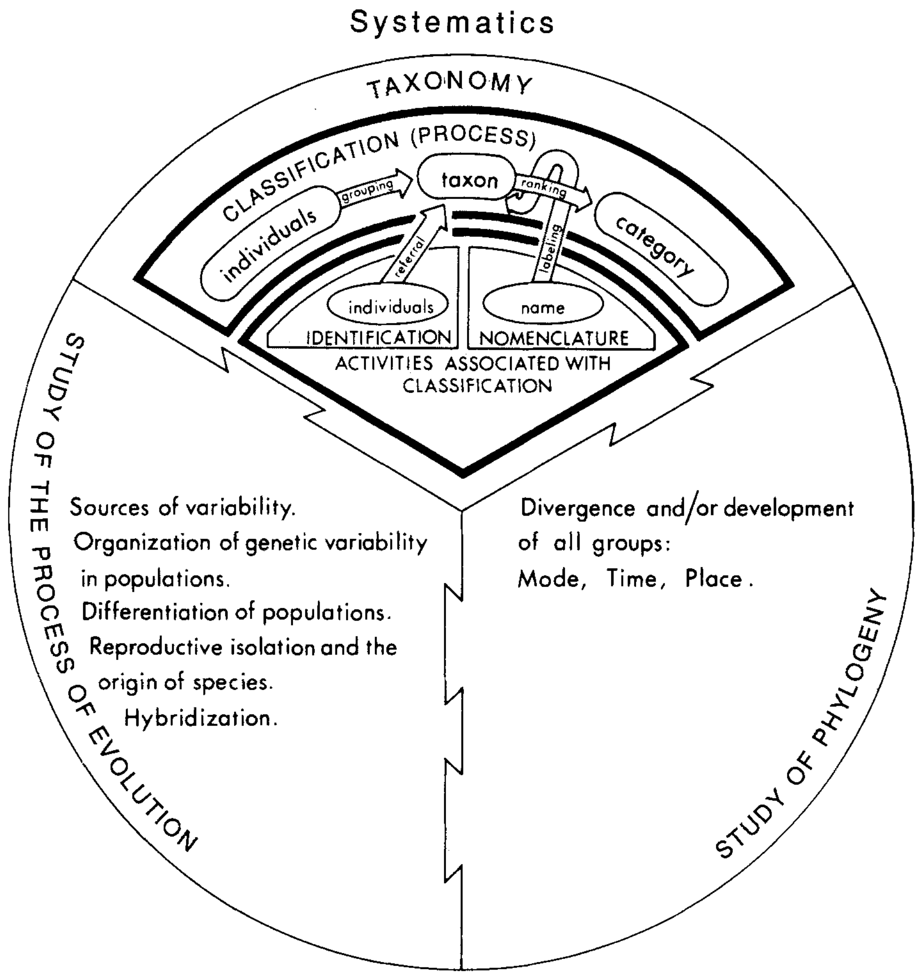

Fig. 1. Diagram of conceptual and procedural relationships among and within areas of systematics. From Stuessy (1979, p 622)

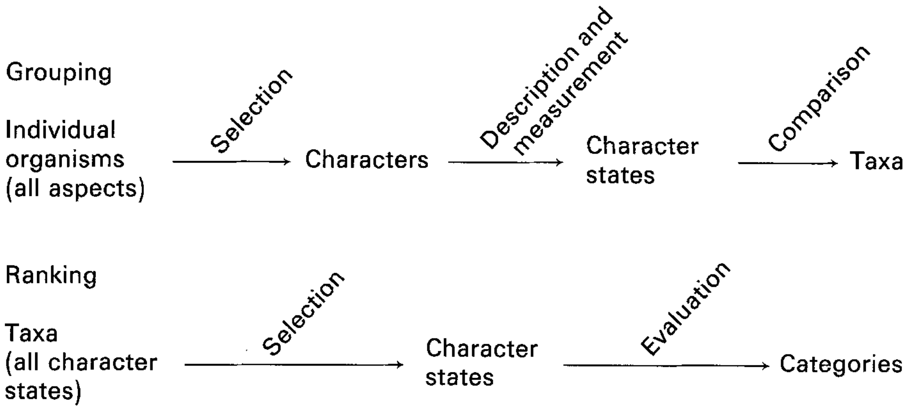

Fig. 2. Representation of the two primary operations of classification. From Stuessy (1979, p 623)

sue, with which all three schools of classification have struggled, largely without success. A brief discussion of each of the schools of classification [phenetics, cladistics, and phyletics (= evolutionary classification)] follows.

The phyletic (or evolutionary) approach to organismic classification, which began as a natural system during the Renaissance period, was elaborated and refined during the eighteenth century, and finally took on a modern phylogenetic perspective after Darwin's theory of evolution (Darwin 1859). This type of classification attempted to recognize groups resulting from the evolutionary process, and it relied upon experience and judgement for effective implementation. Classifications produced this way were highly predictive, with emphasis on branching patterns of evolution as well as divergence within lineages. Most of the systems of classification that we are using at different levels in the hierarchy in both plants and animals are still of this nature.

Although the phyletic approach to classification has worked well, a number of people in the late 1950s and early 1960s began to wonder whether there might not be a better way. In particular, difficulties arose because in many groups the fossil records are weak, and it was hard to determine which features of the organisms were evolutionarily significant. Workers reasoned (e.g. Sokal

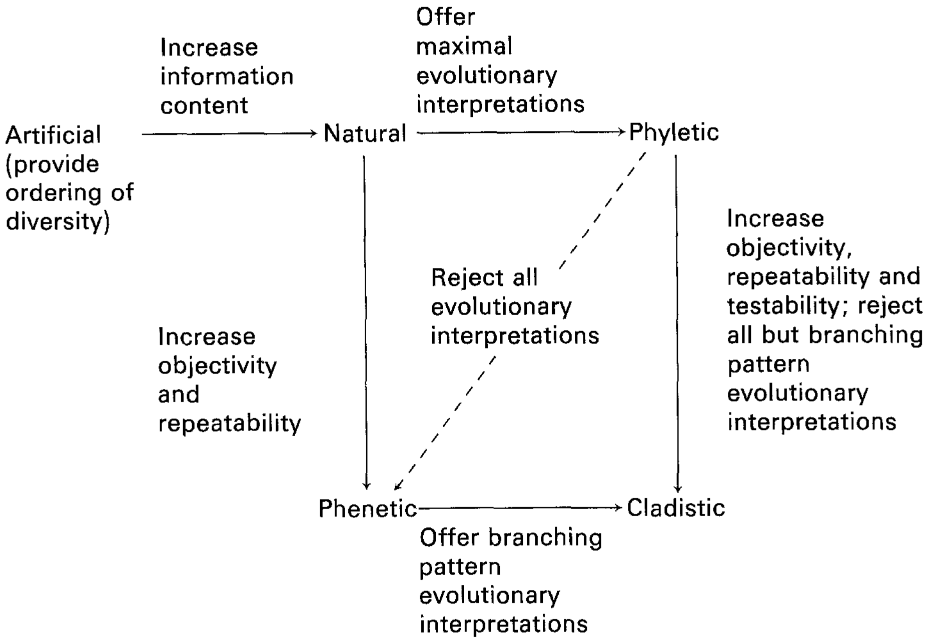

Fig. 3. Diagram showing major approaches to biological classification and the perceived needs that influenced their development. *Dashed lines* represent less significant influences. From Stuessy (1990, p 136)

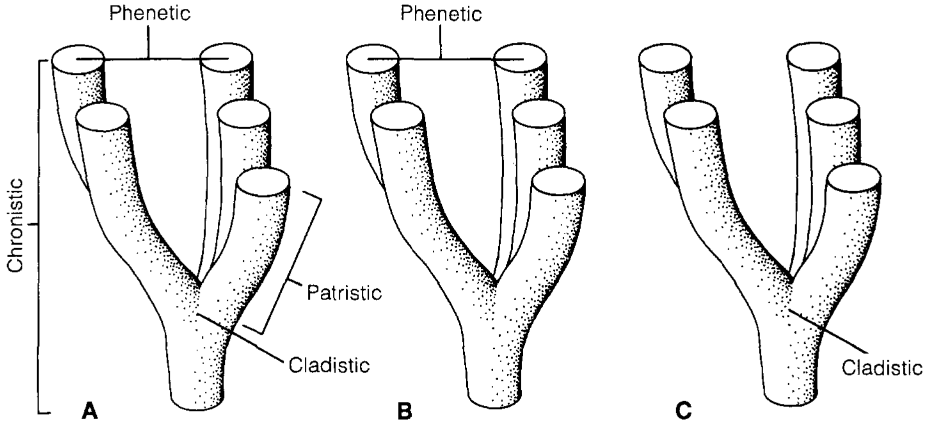

Fig. 4A–C. Kinds of information about phylogeny obtained and utilized in phyletic (**A**), phenetic (**B**), and cladistic (**C**) approaches to classification. From Stuessy (1990, p 141)

and Sneath 1963; Sneath and Sokal 1973) that the best assessment of relationships among taxa would be achieved by selecting a large number of characters, describing and measuring these in an objective fashion, giving them equal weight and comparing them numerically (usually with the help of a computer). Adherents of this school called it numerical taxonomy, but it has since been labeled phenetics. This approach to classification has been tested in various contexts for the past 30 years and its positive and negative aspects are reasonably clear (Stuessy 1990).

Many workers, although pleased by the repeatable and more objective nature of phenetics, were bothered by the omission of evolutionary considerations. They argued that it should be possible to make decisions on primitive and derived character states in such a fashion that a branching diagram could be developed that would reflect evolutionary relationships and would also retain the advantages of explicitness and repeatability of phenetics. These workers suggested the selection of characters believed to have high evolutionary value, the polarization of character states into primitive or derived conditions, and the construction of groups based on the maximum number of shared derived states (or synapomorphies). This approach is called cladistics. A number of people have been involved with its development, notably Hennig (e.g. 1966) and Nelson (1971; Nelson and Platnick 1981). These and other workers rejected phenetics and believed that by carefully selecting characters with high evolutionary content and making careful decisions about directionality of character states, a reasonably accurate evolutionarily based classification should result. The relationship of the three major approaches and the perceived needs that influenced their development are shown in Fig. 3.

More recently, a number of workers (e.g., Estabrook 1986; Hall 1988, 1992; Stuessy 1987, 1990) have been interested in providing more information about evolutionary relationships in a classification, but utilizing the positive aspects of objectivity and repeatability from phenetics and cladistics. Clearly the phyletic approach has more to offer in terms of more fully describing the hypothetical phylogeny (Fig. 4). At the present time, there are quantitative measures of phenetic and cladistic relationships, and patristic dimensions can also be derived directly from cladistic analysis. The absolute

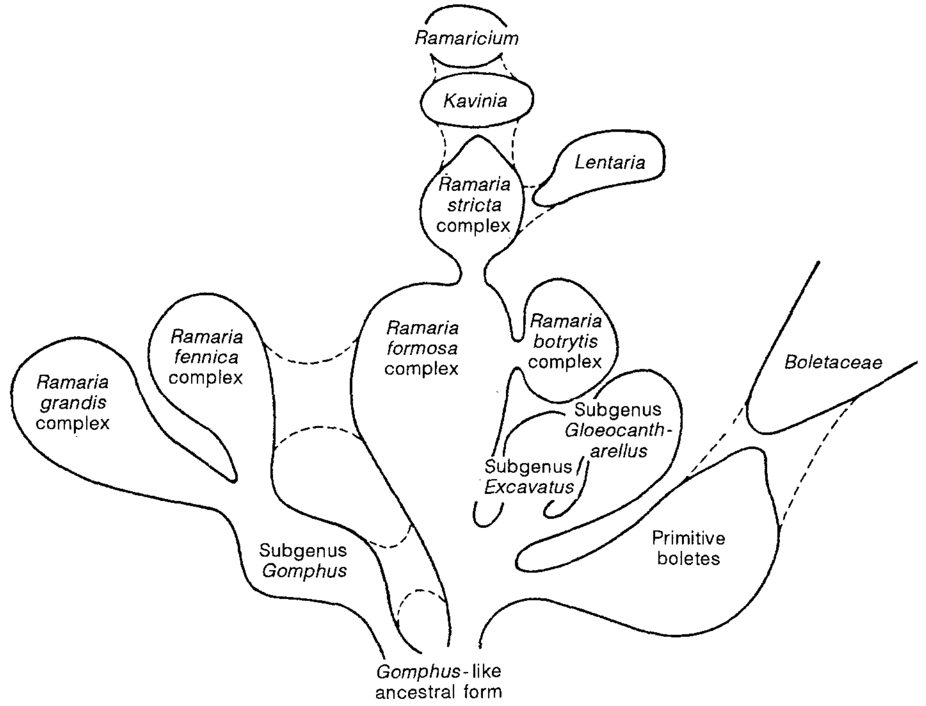

Fig. 5. Proposed phylogeny of the Gomphaceae. From Petersen (1971, p 368)

time dimension has not been considered relevant in either of the other two approaches but has always been considered important in phyletics, because the absolute time of divergence may suggest a particular ranking. The challenge at hand, therefore, is to provide a quantitative measure of all the relationships contained in phylogeny and to use this as a basis for constructing the classification. Future discussions will focus on how this information can best be captured and used to develop a hierarchical system, and what weights the different dimensions of phylogeny should have to give the most predictive classification for a particular group.

Classification approaches used in other fungal groups

Studies done on the higher fungi have largely been of the intuitive phyletic type. Many outstanding classifications have been provided which have established initial hypotheses of relationships. The study of the Gomphaceae by Petersen (1971) is an excellent example (Fig. 5). As with most intuitively generated phylograms, the axes of such diagrams are not entirely clear, and it is difficult to know exactly what information is being communicated. Nonetheless, it is still a good visual summary of relationships that can be used for many purposes. Because of the small number of systematic mycologists on the world scene, and because of the large numbers of fungi which have yet to be investigated at even the most rudimentary level, this by itself is a strong argument for continued intuitive studies with the greatest dispatch possible.

However, a number of phenetic and cladistic studies have also been done with higher fungi. For example, cluster analysis (a type of phenetics) has been carried out among genera and species of the tribe Ixechineae of the Boletaceae by Wolfe (1984; Fig. 6). The higher the level of similarity, the more closely related the taxa are regarded as being. Vilgalys (1986) completed a number of different studies in *Collybia* sect. *Levipedes* (Basidiomycetes). The relationships among ten of these species were portrayed by principal coordinate analysis (Fig. 7). In this type of technique the major axes of variation are determined among the characters used for the taxa and they are plotted in factor space. The distance from

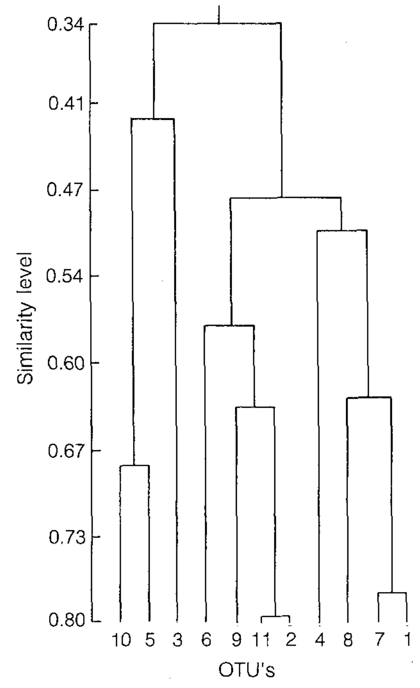

Fig. 6. Phenogram of the genera and species of tribe Ixechineae. From Wolfe (1984, p 141). OTU, Operational taxonomic unit (or taxon)

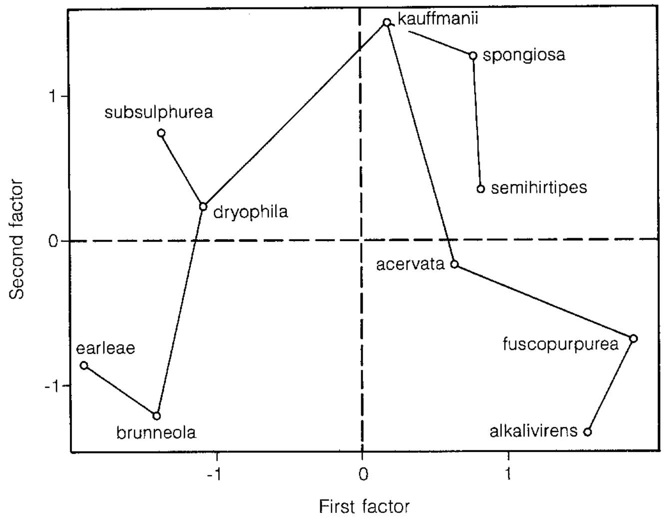

Fig. 7. Principal coordinate plot of first two factors for ten species of *Collybia*. Lines between taxa represent a minimum spanning tree. From Vilgalys (1986, p 229)

one taxon to another gives an indication of their relationship. A minimum spanning tree can also be superimposed over the principal coordinate plot, which is a distance measure that links the most closely related taxa (Fig. 7).

Cladistic analyses have also been done, but not as extensively. One of the earlier examples also comes from Petersen (1971), in which he used a Wagner groundplan/divergence diagram for species of *Gomphus* (Basidiomycetes; Fig. 8). A more conventional cladogram for indicating cladistic relationships, again among species of *Collybia* (Vilgalys 1986), is shown in Fig. 9. Although there are no doubt many other recent studies of a quantitative nature that could be used for illustration, the main point is that there have already been different approaches to classification within the higher fungi over the past two decades.

Present classification of arbuscular mycorrhizal fungi

The classification of arbuscular mycorrhizal fungi was first presented in modern terms by Gerdemann and Trappe (1974, 1975). Because of the cryptic nature of these soil fungi, classification has been problematic. Seven genera were included in the family Endogonaceae (Table 1): *Acaulospora*, *Endogone*, *Gigaspora*, *Glaziella*, *Glomus*, *Modicella*, and *Sclerocystis*. Ames and Schneider (1979) added the genus *Entrophosphora*, and Walker and Sanders (1986) added *Scutellospora*. *Glaziella* and *Modicella* were transferred out of the Endogonaceae and into Ascomycetes by Gibson et al. (1986) and Mortierellaceae (Zygomycetes) by Trappe and Schenck (1982), respectively.

This generic composition was the current status of arbuscular mycorrhizal fungi until more recent studies by Morton and colleagues (1988, 1990a, b; Morton and Benny 1990). In 1988, Morton exhaustively documented the characters and states that had been used to delimit and assess relationships among arbuscular mycorrhizal fungi. This foundation was followed by a cladistic analysis of these taxa and characters which yielded cladograms relating the six genera (*Acaulospora*, *Entrophosphora*, *Gigaspora*, *Glomus*, *Sclerocystis*, and *Scutellospora*) to each other in a quantitative fashion. There followed a formal, revised classification (Morton and Benny 1990) in which a new order, Glomales, was proposed to include all of the soil fungi that formed arbuscles and obligate mutualistic associations with terrestrial plants. Within this order they recognized two suborders (Fig. 10), Glomineae and Gigasporineae, with the former containing Glomaceae (*Glomus* and *Sclerocystis*) and Acaulosporaceae (*Acaulospora* and *Entrophospora*) and the latter the single Gigasporaceae (*Gigaspora* and *Scutellospora*). The main distinctions are that Glomineae contains both arbuscular and vesicular organisms, whereas the Gigasporineae are only arbuscular. Within the Glomineae, the two families are distinguished by a number of features but particularly the apical formation of chlamydospores from fertile hyphae in the Glomaceae and their formation from within the "neck" of a sporiferous saccule in the Acaulosporaceae.

Suggestions regarding systematics of arbuscular mycorrhizal fungi: some priorities for consideration

It is presumptuous for an outsider to attempt observations on the status of systematics of arbuscular mycorr-

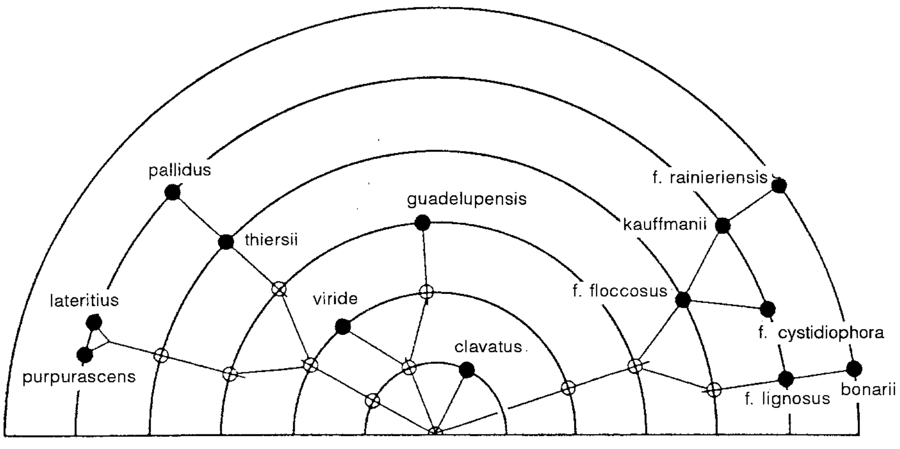

Fig. 8. Wagner groundplan/divergence cladogram for *Gomphus* species – *Clavariadelphus* ancestor. From Petersen (1971, p 366)

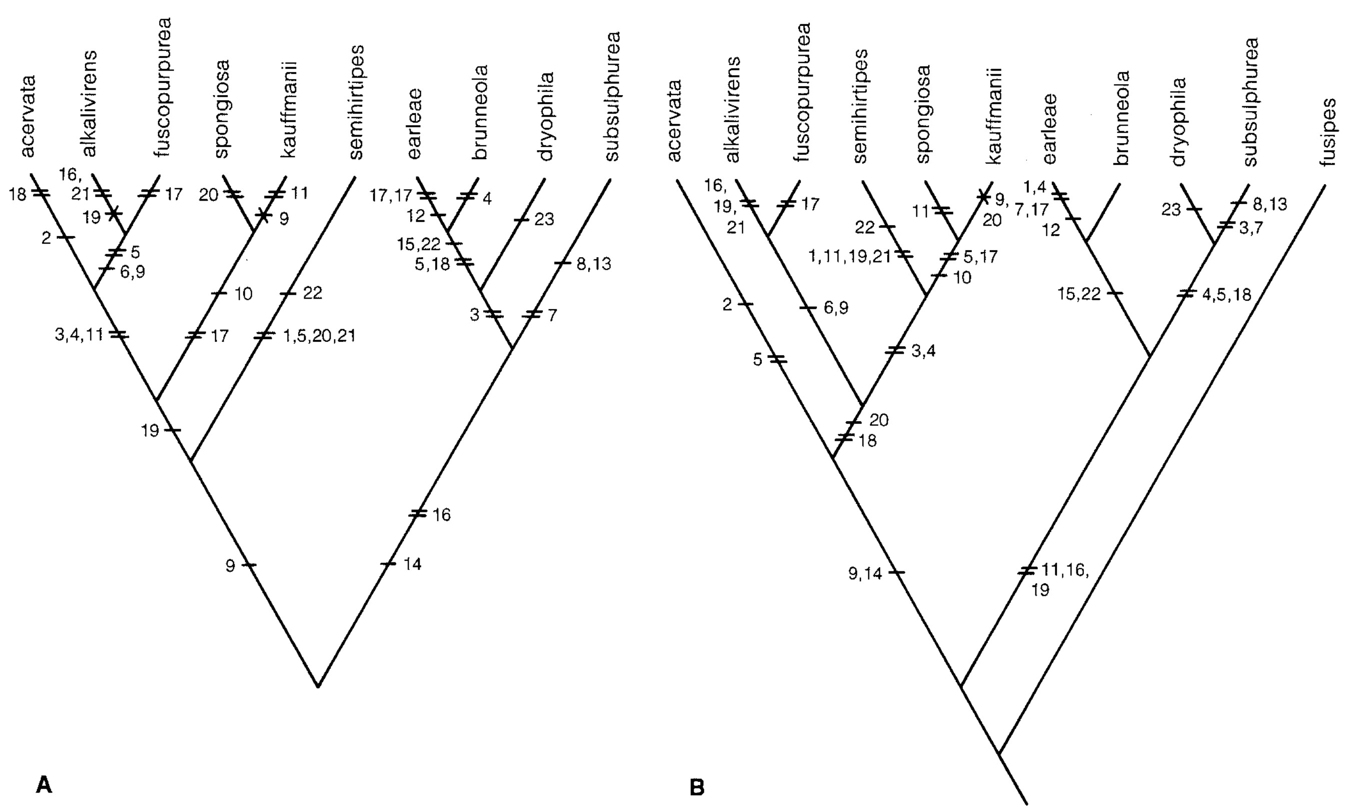

Fig. 9A, B. Wagner trees showing cladistic relationships among species of *Collybia*. Numbers represent character state changes. *Single lines* indicate synapomorphies, *double lines* parallelism, *x* a reversal. **A** Tree produced using only in-group taxa, rooted at either midpoint of greatest patristic distance or by designating most common character states as primitive. **B** Tree rooted by outgroup analysis using section *Striipedes* as outgroup. From Vilgalys (1986, p 230)

Table 1. Genera of Endogonaceae with a summary of their characteristics [from Gerdemann and Trappe (1975)]

Genera	Fruiting	Kind of spores	Spore germination	Type of mycorrhiza
Endogone	Sporocarps	Zygospores[a]	Unknown	Ectomycorrhiza or unknown
Gigaspora	Single spores	Azygospores?[b]	Through wall	Arbuscular[c]
Acaulospora	Single spores	Azygospores?	Through wall	Vesicular-arbuscular
Glomus	Sporocarps and single spores	Chlamydospores	Regrowth of attached hyphae	Vesicular-arbuscular
Sclerocystis	Sporocarps[d]	Chlamydospores	Regrowth of attached hyphae?	Vesicular-arbuscular
Glaziella	Sporocarps	Chlamydospores	Unknown	Unknown
Modicella	Sporocarps	Sporangiospores	Through wall	Unknown

[a] Sporangial stages uncertain

[b] *Gigaspora* species produce soil-borne vesicles on coiled hyphae that may represent vestigial sporangial stages

[c] Vesicles formed within roots have been reported for *G. calospora* (Furlan and Fortin 1973)

[d] Spores arranged in a single orderly layer

hizal fungi, let alone to offer suggestions on priorities for further research. Nonetheless, on the chance that a disinterested party may hit upon some ideas of value, I offer the following comments.

First priority

Because ecologists and physiologists of arbuscular mycorrhizal fungi need to know what their taxa are, the development of a more workable set of taxa at the specific, infraspecific, or strain level is urgently needed. To achieve this goal, a number of separate points might be considered.

The full number of arbuscular mycorrhizal taxa must be determined. It is hard to talk about relationships when many of the taxa are still unknown; in fact, for accurate assessments of evolutionary relationships it is nearly impossible. New taxa are still being described, and there are now more than 126 species recognized (Morton 1988). Much more exploration and pot culturing is needed to look for new diversity, particularly in tropical areas and in the southern hemisphere.

The terminology regarding characters and states for the Endogenales must be standardized. It is obvious that some of the structures, such as the azygospores, have vague definitions. A working group might be established to consider this issue and to develop standard

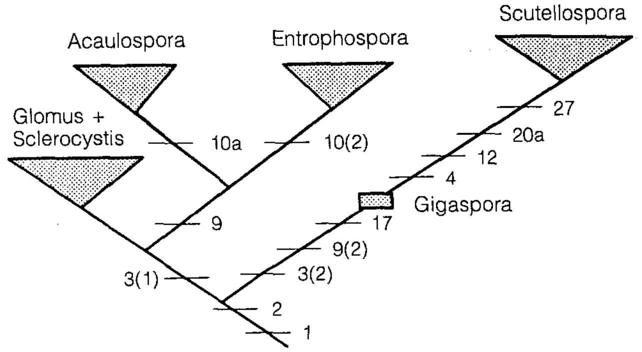

Fig. 10. Cladogram based on Hennigian argumentation analysis, which shows synapomorphies defining descendant monophyletic groups of arbuscular mycorrhizal fungi. From Morton (1990b, p 198)

descriptors of spore types, standard color codes, and so on. In this way new taxa can be relegated to their proper position more quickly and means for identification can be more precise.

The range of environmental variation of characters and states must be better understood. This involves not only the relationship to soil and climate but also host variation patterns. Some excellent studies have already been completed in this direction (e.g., Abbot and Robson 1979; Morton 1988), but more work is needed. Axenic and nonaxenic cultures of hosts and fungi should be done under varying conditions. Also there is a need for geographically oriented studies with many samples, for example involving contour analysis (Adams 1974) or spatial autocorrelation (e.g., Sokal and Oden 1978a, b), to look for trends in character state changes over broad areas.

Some agreement in the community should be achieved on what the basic level of classification of arbuscular mycorrhizal fungi should be. That is to say, what really is a useful species concept and how should it be defined? As these fungi really do appear to be asexual, is the term "species" really appropriate at all? Terms exist for asexual units in angiosperms such as "apomicton", "microspecies", and so on. Is the term "clone" a useful one? In angiosperms it refers to all genetically identical individuals coming from one parent. At the very least it would be useful to know what sorts of minimal character state differences are necessary for a new taxon to be delimited.

In view of the lack of biological data on populations and isolating mechanisms, it might be useful to adopt a purely phenetic species concept (e.g., Sokal and Crovello 1970). This is basically all one can do in dealing with asexual species, and morphological characters might be emphasized that have obvious value for the purpose of identification by other workers. Other techniques and types of characters, however, might prove to be especially diagnostic and additionally useful (e.g., Aldwell et al. 1983).

Second priority

There is a great need for macromolecular studies (using mitochondrial and/or nuclear DNA) to provide a more predictive framework of relationships as a stimulus for other studies. It is particularly important to understand the relationships among the genera of arbuscular mycorrhizal fungi, and between these and other zygomycotina. Only after problems at the specific level have been solved does it make sense to look at infrageneric relationships in detail. Work on these two levels can continue in parallel and be refined reciprocally as time goes on. It is important to stress the significance of voucher specimens here, both in pot culture and pickled. Close communication among workers attempting macromolecular studies should be maintained so as not to waste efforts in looking at the same taxa. Different genes should be examined and numerous restriction enzymes used. The power of such an approach cannot be underestimated; we have seen very great dividends from studies of the sunflower family (Compositae) by Jansen and colleagues (e.g., Jansen and Palmer 1987, 1988; Jansen et al. 1990).

For macromolecular studies to be effective, there is a need to determine the outgroups of arbuscular mycorrhizal fungi so that the sequences can be rooted. This will also provide a clearer perspective on the classification of the familial, subordinal and ordinal levels from the degree of difference to other previously classified fungal groups. Another concern might be the possibility of gene transfer from host to fungus. Is there any evidence that this has happened at all, and if so, what effects could that have had on the characters and states that the fungi now possess?

Third priority

Based on results from the two priorities discussed above, there will be a need to readdress the classification and phylogeny of the arbuscular mycorrhizal fungi in an explicit fashion. More developmental (ontogenetic) studies are needed to determine the homologies of the characters and states. More culture studies are needed in order to determine the variation and plasticity of important characters such as wall composition. Phenetic studies are needed at all levels but in particular at the specific or infraspecific levels. We do need more refined cladistic studies in view of the results from everything previously mentioned. The work done by Morton and colleagues is excellent (e.g., Morton 1990b), and it does represent a step in the right direction. More analyses are needed, however, with additional, more carefully refined data. In my opinion, the most predictive classification will result from explicit phyletics (Stuessy 1987), which is based not only on the branching pattern but the degree of differentiation within the group.

It will be important to understand which of the families of VAM fungi are viewed as most primitive evolutionarily. The work of Morton (1990b) has shown three major lines within the Glomales, but it is not at all clear which is most primitive. Because of the patristic distance separating *Gigaspora* from its immediate ancestor, it might be more advanced than many of the species within *Glomus* which are cladistically more derived but patristically less so. The fossil record shows that there are VAM fungi that appear to be *Glomus*-like (Stubblefield et al. 1987b) or *Sclerocystis*-like (Stubblefield et al. 1987a). The important thing about these fossil findings is that the vesicular arbuscular mycorrhizal condition existed early in Triassic times. Macroevolutionary ideas that would deal with long-term evolutionary events of phylogeny can only be determined accurately after a more precise phylogeny of the group itself is at hand. Having the fossil data is most important for setting at least a minimum age of evolution for the entire group.

Fourth priority

It is important to develop refined views on speciation and processes of populational level evolutionary phenomena. This is most difficult in asexual organisms, and it might be worth confirming whether or not these are truly asexual fungi. Isozymes might be useful here as well as ribosomal DNA. How much variation is there in a natural population, or within a clone, and are they really as genetically uniform as we think? If they are truly asexual, and if there is no gene exchange from the host, then one should expect uniformity within these so-called clones or species. This could be tested directly.

Fifth priority

When all of the other data are finally in hand, then one can develop a meaningful biogeographic framework for the group. Obviously, ideas on dispersal must be developed, for little has been said about how they apparently move around. Likewise, because the group is apparently so old, the importance of drifting continents must be taken into consideration as well as the distributions of the hosts themselves. Although there appear to be only weak associations with particular host angiosperms (Trappe 1987), some correlations do exist, and these could be explored within a biogeographic context. There are a number of different methods of biogeography including those that are basically phenetic, others that are cladistic, and traditional dispersalist and newer vicariance approaches. The same kinds of re-evaluations are taking place now in methods of biogeography that have been occurring in recent decades in classification (e.g., Myers and Giller 1988).

Conclusion

The systematics of arbuscular mycorrhizal fungi is in a most exciting phase. Workers in the field have brought together the available information and have catalogued the existing diversity in an outstanding fashion. Because of the economic value of these organisms, it is imperative that strong efforts be mounted now to focus directly on additional systematic issues in this group. The establishment of a series of workshops or focused working groups, perhaps through support from appropriate funding agencies, might be one mechanism for bringing community attention to these issues. From the point of view of an outsider, it has been a pleasure to come to know these organisms in more detail, to meet some of the workers personally, and to share the excitement of a rapidly developing field with so many options and alternatives.

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