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Integrating phylogenetic analysis and classification in fungi

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Abstract: The central goal of taxonomic mycology is to create classifications that communicate understanding of fungal phylogeny. To insure that taxonomy reflects up-to-date phylogenetic hypotheses, there must be efficient mechanisms for translating phylogenetic trees into classifications. The current taxonomic system, which is based on the hierarchy of Linnaean ranks and the International Code of Botanical Nomenclature, is unsatisfactory for this purpose. One problem with the current taxonomic system is that a large number of ranks are necessary to classify complex phylogenetic trees. Rank proliferation creates a tension between the desire to name clades and the need to keep the number of ranks manageable. In addition, ranked classifications are quite sensitive to minor changes in tree topology, and are therefore unstable. The instability of ranked tree-based classifications encourages systematists to defer naming strongly supported clades if their internal structure or higher-level relationships are not well resolved. Thus, the current taxonomic system impedes progress toward a phylogenetic classification of fungi. As an alternative to the current taxonomic system, de Queiroz and Gauthier developed a system of "phylogenetic taxonomy," which explicitly defines taxon names as designating clades, and which does not use taxonomic ranks. Eliminating the concept of rank promotes nomenclatural stability because the names of taxa are not sensitive to changes in their position in the tree relative to other taxa. As published fungal phylogenies grow in size and number, the problems of rank proliferation and nomenclatural instability caused by the current taxonomic system will become more severe. Serious consideration should be given to replacing the Code with a rankless system based on phylogenetic taxonomy. Although at this time there is no alternative to the Code, it is likely that detailed proposals for rankless codes of nomenclature will be developed in the next few years.

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INTRODUCTION

The primary goal of taxonomic mycology is to create classifications of fungi that reflect their evolutionary relationships. Thanks to recent advances in phylogenetic theory and molecular techniques, knowledge of fungal phylogeny is increasing rapidly. Nevertheless, taxonomic changes may not be keeping pace with progress in phylogenetic reconstruction. This is a serious concern because phylogenetically accurate taxonomy is an underpinning of all biological disciplines, and is one of the most tangible products of systematic research. To insure that taxonomy reflects the most up-to-date phylogenetic hypotheses, there must be efficient mechanisms for translating phylogenetic trees into classifications. The purpose of this essay is to discuss such mechanisms, with the ultimate aim of promoting the integration of phylogenetic analysis and classification in fungi.

PHYLOGENY AND TAXONOMY

Phylogenetics disconnected from classification in fungi.—Although phylogenetic inference and classification are conceptually linked in modern systematics, in practice they are essentially independent operations; phylogenetic inference involves the discovery of evolutionary relationships among organisms, whereas classification involves the representation of groups of organisms by a system of words. A review of recent issues of Mycologia confirms that in practice there is a strong dichotomy between fungal phylogenetics and fungal classification. We surveyed 110 papers grouped under the headings "Molecular Evolution" and "Systematics" that appeared in Mycologia vols. 86–88 (1994–1996). Papers were scored for presence of a phylogenetic analysis, presence of a formal taxonomic proposal resulting in the recognition of a new or modified taxon (such as a diagnosis, transfer, or change of rank), and the type of data that was generated (TABLE I). Twenty-seven papers included a phylogenetic analysis (23 based on molecular data), but only 6 of these also included a formal taxonomic proposal. In contrast, 80 papers included a

TABLE I. Papers containing phylogenetic analyses and taxonomic proposals published under "Molecular Evolution" and "Systematics" in Mycologia, vols. 86–88, 1994–1996

	Type of data generated in study			
	Molecules[a]	Morphology[b]	Molecules and morphology	All studies
Total	27	92	10	110
Phylogenetic analysis[c]	23	4	0	27
Taxonomic proposal	7	78	5	80
Analysis and proposal	5	1	0	6

[a] Nucleic acid sequences, RFLPs, and protein electrophoresis data.

[b] Ultrastructure, anatomy, and macromorphology.

[c] Parsimony, maximum likelihood, and phenetic analyses.

formal taxonomic proposal (78 based on morphological characters), but no phylogenetic analysis. Overall, only six out of 110 papers included both a phylogenetic analysis and a formal taxonomic proposal. Thus, it appears that phylogenetic analyses are having relatively little impact on the development of fungal classifications.

To understand why so few fungal phylogenetic studies result in formal taxonomic proposals, we consulted authors of the 21 Mycologia (1994–1996) papers that included phylogenetic analyses, but not taxonomic proposals. Although the results are anecdotal and the sample size is small (16 responses, available on request from DSH), several general themes emerged repeatedly: (i) Fungal phylogeneticists are very interested in seeing the results of their studies translated into taxonomy, which is not surprising considering that classifications could be the most enduring and influential products of phylogenetic research. (ii) Although phylogenetic analyses supported an existing classification in several cases, most analyses suggested that taxonomic changes are necessary. (iii) Phylogeneticists interpret their work cautiously, often citing the need for increased taxonomic sampling, as well as analysis of independent molecular or morphological data sets. (iv) Nevertheless, most authors also indicated a high degree of confidence in at least some aspects of their results, which is borne out by inspection of bootstrap analyses. Of the 12 analyses that used the bootstrap, all but one found one or more branches supported at 95% or above. These observations suggest that the primary barrier to the conversion of phylogenetic trees into classifications is lack of confidence in phylogenetic hypotheses, due in large part to incomplete taxon sampling. Nevertheless, the fact that many robustly supported clades are going unnamed suggests that there are also methodological (or psychological) barriers to translating trees into classifications.

Methods for phylogenetic classifications: general considerations.—Before selecting a method for translating trees into classifications, it is necessary to decide what information classifications should represent. Our position is that biological classifications should reflect only phylogenetic relationships, and that therefore only monophyletic groups should be given formal taxonomic names. We reject systems that attempt to reflect degrees of similarity among taxa, in addition to their phylogenetic relationships, and which therefore sanction the naming of paraphyletic groups (Brummitt, 1996). The literature on this subject is extensive and will not be reviewed here (Hennig, 1966; Wiley, 1981). Very briefly, we prefer classification systems that strictly reflect phylogeny because these do not entail arbitrary decisions about degrees of similarity, and because they are unambiguous with respect to the meaning of taxonomic names (i.e., all names refer to hypothesized clades).

Having decided that the goal of classification is to communicate information about phylogeny, we may consider criteria by which methods of classification can be judged: (i) Classifications should not be misleading about the phylogeny of the organisms they represent. (ii) Methods of classification should efficiently promote the translation of phylogenetic hypotheses into classifications. That is to say, once a monophyletic group has been discovered by a systematist, it should be possible to name it quickly and simply. (iii) Classifications should be stable. Nevertheless, classifications must be able to change to reflect advances in understanding. Therefore, methods of classification should accommodate changes in phylogenetic hypotheses with minimal perturbation of systems of names. Conversely, methods of classification should not promote changes in names in the absence of changes in phylogenetic hypotheses. An example of this kind of change would include a change in the rank of a taxon without a change in its hypothesized phylogeny (de Queiroz and Gauthier, 1992).

The current taxonomic system.—The current taxonomic system for fungi is based on the Linnaean ranked hierarchy of taxonomic categories, applied according to the rules of the International Code of Botanical Nomenclature (Greuter et al., 1994; hereafter, the Code). Under the Code, taxon names are defined in terms of a rank assignment and type specimen (for taxa up to family, or higher if the name is based on a generic name). A descriptive list of characters (for

some groups this must be in Latin), an illustration (for some groups), and publication by "effective" means are required for a name to be legitimate and valid under the Code.

In the current system, there are seven primary ranks, from species to kingdom. The Code states that "Further ranks may also be intercalated or added, provided that confusion or error is not thereby introduced" (Art. 4.3), but the relative order of ranks may not be altered (Art. 5.1). Rank assignments are central in determining synonymy and priority. Names are considered synonyms only if they are at the same rank, and the oldest validly published name of a taxon takes priority over other names, but "in no case does a name have priority outside of the rank in which it is published" (Art. 11.2).

The Linnaean hierarchy and the Code have no basis in evolutionary theory (de Queiroz and Gauthier, 1994). Indeed, according to the Preamble of the Code (p. 1) "The purpose of giving a name to a taxonomic group is not to indicate its characters or history, but to supply a means of referring to it and to indicate its taxonomic rank." Nevertheless, a central tenet of modern systematics is that classifications should reflect historical phylogenetic relationships. Therefore, in constructing classifications, taxonomists face two separate challenges: obeying the Code, and communicating phylogenetic hypotheses. As we will show, these goals often conflict.

The difficulty of following the Code while constructing a phylogenetically accurate classification is particularly evident when dealing with the discovery that a group is paraphyletic (de Queiroz and Gauthier, 1992, 1994). This is illustrated by the recent study by Norman and Egger (1996) on relationships of the ascomycete genera *Plicaria* and *Peziza*. In this study (Norman and Egger, 1996, Figs. 12 and 13), *Plicaria* was shown to be a monophyletic group that is nested within *Peziza*, which is therefore paraphyletic (FIG. 1A). Faced with this situation, there are two choices under the current system: either the entire *Peziza*-plus-*Plicaria* clade can be recognized as a single genus (FIG. 1B), or additional genera can be

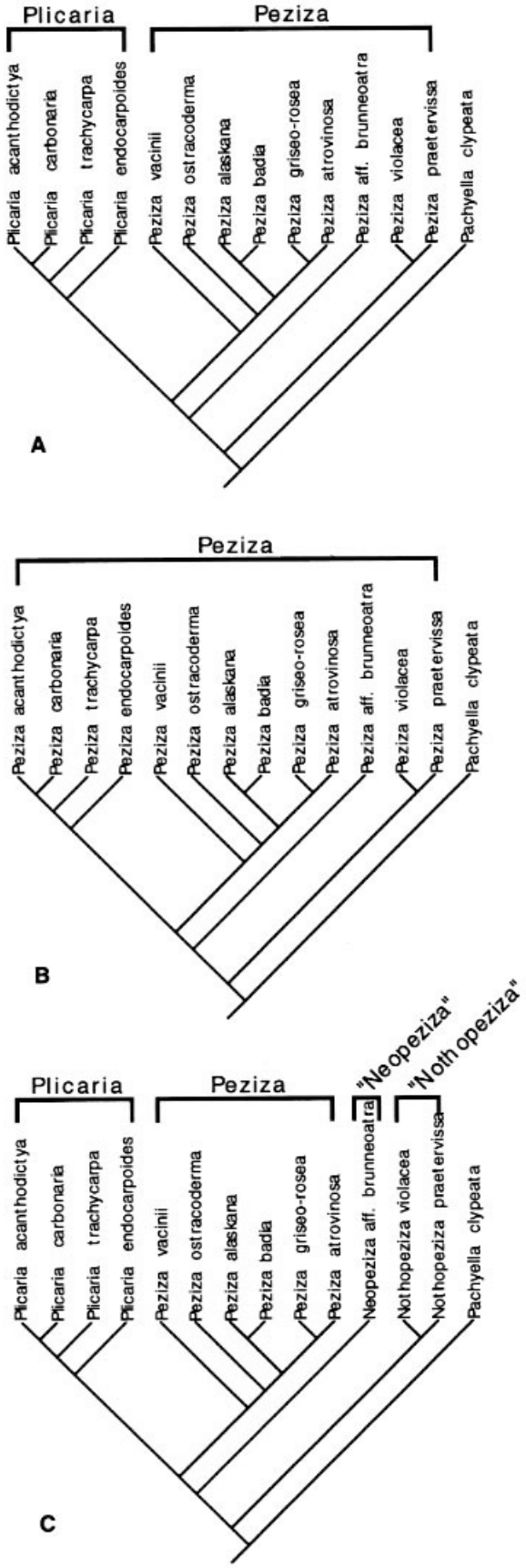

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FIG. 1. Phylogenetic relationships and classification options for *Plicaria* and *Peziza* under the current taxonomic system, based on an analysis by Norman and Egger (1996). A. *Plicaria* is nested within *Peziza*, which is paraphyletic. B. *Plicaria* is "lumped" into *Peziza*, which, as the older generic name, has taxonomic priority. C. *Plicaria* is retained as a genus and *Peziza* is "split" into multiple monophyletic genera. The names in quotation marks are used for the sake of argument only and are not formally proposed here.

named (FIG. 1C). If the entire clade is to be recognized as a single genus, then nomenclatural priority dictates that it be called *Peziza* (FIG. 1B). Under this scenario, the clade formerly known as *Plicaria* would have to be renamed, or else go without a name, even though its monophyly was upheld. Because priority is tied to rank, there is no guarantee that this clade (having been reduced to an infrageneric category) would even continue to have *Plicaria* as part of its name. Changing the name of *Plicaria* would create a discontinuity in the taxonomic literature, making it difficult for later researchers to find information about these fungi.

If instead, the *Peziza*-plus-*Plicaria* clade were to be split into multiple genera the species formerly known as *Peziza* would have to be placed in at least three genera (FIG. 1C). This approach would preserve the name *Plicaria*, but some of the species formerly placed in *Peziza* would be transferred into other genera, which again would cause a loss of nomenclatural continuity.

Additional challenges arise when complex phylogenetic hypotheses are translated into classifications with taxa at multiple ranks. Hennig (1966) suggested that the Linnaean hierarchy could be applied in a manner that is consistent with phylogeny if (i) only monophyletic groups are recognized as taxa, and (ii) sister taxa are given equal rank. Hennig also suggested that taxonomic ranks be defined in terms of absolute age of origin. Although this idea makes sense in theory, it has widely been ignored for practical reasons. In fungi, using age to determine rank would be especially problematical owing to the poor fossil record.

One obvious problem with the Hennigian approach to Linnaean classification is that a large number of ranks would be required to classify a complex tree. The number of ranks needed to name every clade in a fully dichotomized tree is equal to the maximum number of nodes that can be traversed in a direct path from the root of the tree to one of its terminal taxa. For example, if the *Peziza-Plicaria* clade was classified as a single genus, a minimum of eight ranks (in this case including "sub-subseries") would be required to classify every node. An indented list showing the classification would look like this (in all examples the names used are for demonstrative purposes only):

genus Pachyella
  Pachyella clypeata
genus Peziza
  subgenus 1
    Peziza violacea
    Peziza praetervissa
  subgenus 2
    section 1
      Peziza aff. brunneoatra
    section 2
      subsection 1
        series 1
          Peziza vacinii
        series 2
          subseries 1
            Peziza ostracoderma
          subseries 2
            sub-subseries 1
              Peziza alaskana
              Peziza badia
            sub-subseries 2
              Peziza griseo-rosea
              Peziza atrovinosa
      subsection 2
        series 3
          Peziza endocarpoides
        series 4
          subseries 3
            Peziza trachycarpa
          subseries 4
            Peziza carbonaria
            Peziza acanthodictya

To get a rough idea of how many ranks it might take to classify all fungi, consider that (i) it would take approximately 30 ranks (from genus up) to classify every clade in the 500-taxon *rbc*L seed plant phylogeny published by Chase et al. (1993), and (ii) there may be as many as 1.5 million species of fungi (Hawksworth, 1991). Ironically, a fully resolved phylogeny of all fungi, which is the ultimate goal of fungal systematics, would be a nightmare for classification under the current taxonomic system.

One way to solve the problem of rank proliferation would be to let many clades go unnamed. Indeed, Art. 4.3 of the Code (which prohibits creating so many ranks that "confusion" results) would seem to mandate this approach. In other words, one could compensate for the inability of the current taxonomic system to represent complex trees by accepting a reduced level of phylogenetic precision in classification. This would be unfortunate because it would deprive systematists of one of the most effective ways to communicate understanding of phylogeny, which is to give names to clades. Naming clades makes it possible to highlight clades with particular attributes, and it empowers studies in cognate disciplines, such as biogeography and paleontology. Although we may never understand phylogeny so well that we could name every clade of fungi, giving up the option of naming every clade we might wish to name would signal a clear failure of the taxonomic system, the

goal of which should be to facilitate rather than discourage the naming of clades.

To reduce the number of ranks necessary to classify phylogenetic trees, Nelson (1974) suggested that clades in asymmetrical ("pectinate") portions of trees could be assigned the same rank and listed in a sequence that reflects their position in the tree. If users understand that the sequencing convention is being employed, then they will be able to infer the complete structure of the tree from the list of taxa alone. Sequencing was incorporated by Wiley (1979, 1981) as part of his "Annotated Linnaean Classification" system, which was designed to facilitate phylogenetic classification using the Linnaean hierarchy. In the *Plicaria-Peziza* example, a minimum of three sequenced ranks would be needed to classify all clades, as follows:

genus Pachyella
  Pachyella clypeata
genus Peziza
  subgenus 1
    Peziza violacea
    Peziza praetervissa
  subgenus 2
    Peziza aff. brunneoatra
  subgenus 3
    section 1
      Peziza vacinii
    section 2
      Peziza ostracoderma
    section 3
      Peziza alaskana
      Peziza badia
    section 4
      Peziza griseo-rosea
      Peziza atrovinosa
  subgenus 4
    Peziza endocarpoides
  subgenus 5
    Peziza trachycarpa
  subgenus 6
    Peziza carbonaria
    Peziza acanthodictya

It is important to appreciate that the apparent efficiency in rank usage of the sequencing convention comes only at the expense of deciding not to name some individual clades. For example, in the sequenced *Peziza-Plicaria* classification, the clade that includes the species formerly classified in *Plicaria* is unnamed. If the clade formerly known as *Plicaria* were to receive a name, it would require the addition of one more rank to the system. Thus, there is a trade-off between phylogenetic precision and proliferation of ranks.

A problem that is related to the proliferation of ranks is the proliferation of redundant names that results from the use of mandatory ranks (de Queiroz and Gauthier, 1992). Under the current system, every organism is assignable to a taxon in each of seven primary ranks from species to kingdom. This requirement creates redundant names for higher taxa that have few subordinate taxa. For example, the basidiomycete order Heterogastridiales contains one family (Heterogastridiaceae), one genus (*Heterogastridium*), and one species (*H. pycnidioideum,* Oberwinkler et al., 1990). Each of these taxa contains the same organisms as the taxon at the next higher or lower rank in the series, and therefore conveys no additional information about relationships. The proliferation of redundant names is exacerbated by the common practice of using exhaustive subsidiary ranks (de Queiroz and Gauthier, 1992), although this is not mandated above the genus level by the Code (cf. Cantino et al., 1997).

A weakness of both Hennigian and sequenced Linnaean phylogenetic classifications is that they are quite sensitive to rearrangements in tree topology. Under either system, the ranks of taxa, and hence their names, depend on their position in the tree relative to other taxa. Therefore, a minor change in tree topology can cause a cascading series of rank and name changes (the addition or deletion of a taxon could have the same effect). This is illustrated with reference to the recent analysis of truffles and related epigeous ascomycetes by O'Donnell et al. (1997). In this study, two trees were presented based on parsimony and neighbor-joining (NJ) analyses of combined 18S and 25S rDNA sequences (O'Donnell et al., 1997, Figs. 2, 3; FIG. 2). By comparing the classifications that would be derived from the two trees, we can see how ranked classifications change in response to changes in phylogenetic hypotheses. Using the Hennigian approach, every clade in the parsimony tree can be classified using eight ranks, with genera as terminal taxa and orders as the highest rank. A total of 29 suprageneric taxa are needed, which takes into account the fact that three redundant, mandatory taxa (families) are mandated by the Code (FIG. 2A). In the NJ tree, 32 suprageneric taxa would be needed, including two redundant taxa that are mandated by the Code (FIG. 2B). Seventeen out of the 21 suprageneric clades (i.e., clades containing two or more genera) in the parsimony tree (81%) are also supported as monophyletic in the NJ tree, which indicates that there is a high degree of topological congruence between the two trees. Nevertheless, only 9 suprageneric clades in the parsimony tree (43%) are both monophyletic and equal in rank in the NJ tree. Eight suprageneric clades in the parsimony tree that are also supported as monophyletic

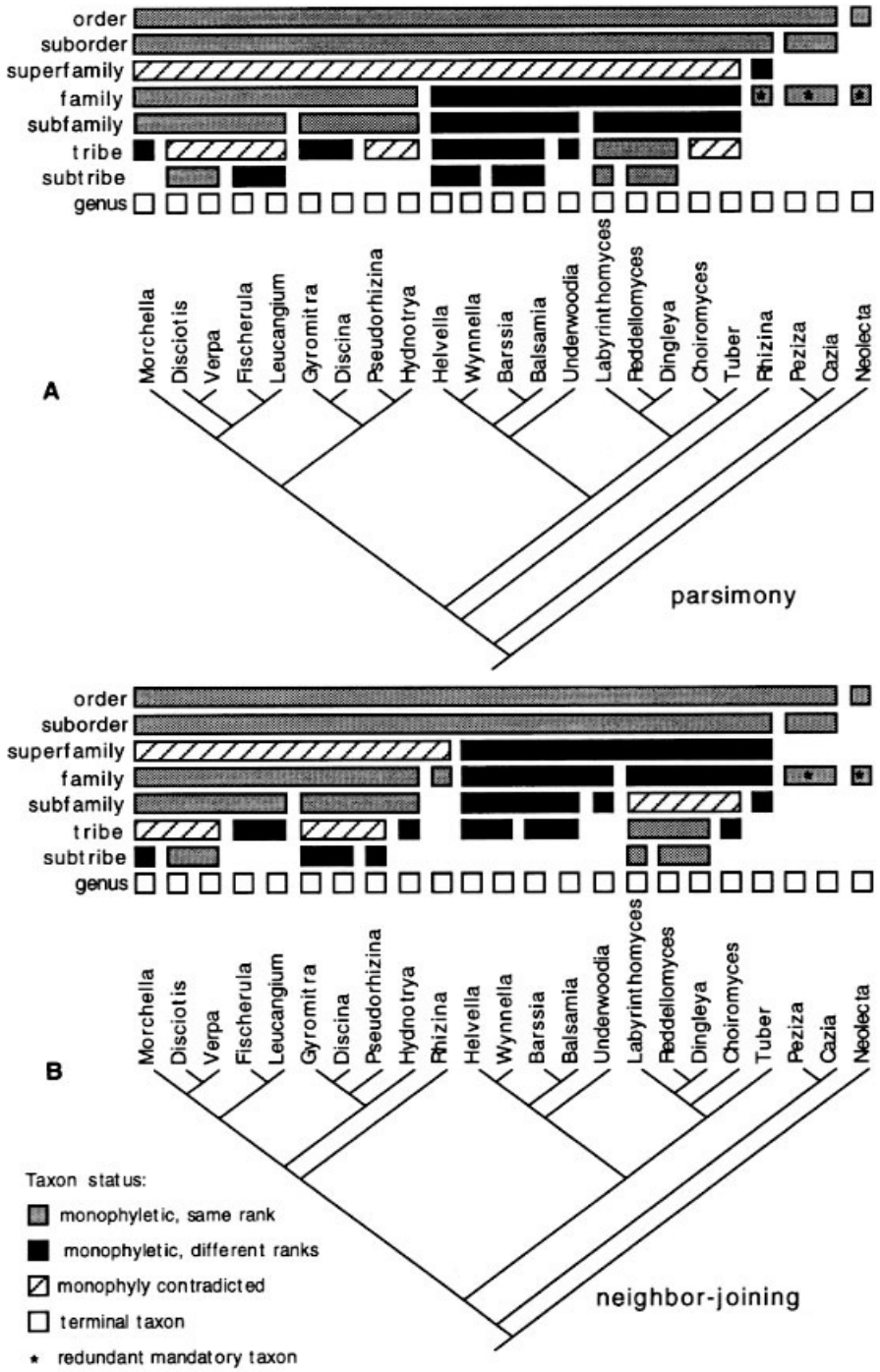

FIG. 2. Hennigian classifications of truffles and epigeous ascomycete relationships based on trees from O'Donnell et al. (1997; some taxa have been pruned to simplify the example). A. Tree inferred using parsimony. B. Tree inferred with neighbor-joining. Eight ranks are needed to classify every node in both trees. Shaded blocks above trees correspond to named clades. Black and gray blocks indicate taxa that are supported as monophyletic in both trees. Black blocks indicate taxa that are placed at different ranks in the two trees, and which therefore would have different names. Gray blocks indicate taxa that have the same rank in both trees. Classifications do not follow the convention of exhaustive subsidiary ranks (Cantino et al., 1997). Some redundant taxa are mandated by the Hennigian convention of placing sister taxa at equal rank (e.g., the superfamily containing only *Rhizina*, FIG. 1A); others are mandated by the *Code* (e.g., the family containing only *Neolecta* FIG. 1A and B).

in the NJ tree would have to be given different names if the NJ tree was used to revise the classification. For some clades this might require only a change in the suffix, but again there is no guarantee that the same basionym would be valid and have priority at the new rank.

Phylogenetic taxonomy.—Recognizing the limits of the Linnaean system, de Queiroz and Gauthier (1992, 1994) developed a system of "phylogenetic taxonomy" to suggest how the rules of biological nomenclature could be reformulated with evolution as the central organizing principle. The major innovations of phylogenetic taxonomy are that taxon names are defined strictly in terms of evolutionary history, and that ranks are not used. (A further discussion of the principles and nomenclatural implications of phylogenetic taxonomy can be found in R. K. Brummitt, 1996, Quite happy with the present code, thank you, http://www.inform.umd.edu/PBIO/nomcl/brum.html; Cantino et al., 1997; de Queiroz, 1997; K. de Queiroz, 1996, A phylogenetic approach to biological nomenclature as an alternative to the Linnaean systems in current use, http://www.inform.umd.edu/PBIO/nomcl/dequ.html; de Queiroz and Gauthier, 1992, 1994; Kron, 1997; Lee, 1996; Lidén and Oxelman, 1996; Schander and Thollesson, 1995; Sundberg and Pleijel, 1994.)

Definition of taxon names in terms of evolutionary history is a key principle of phylogenetic taxonomy. Under the current system the names of taxa are defined in terms of a rank and a type specimen. Under phylogenetic taxonomy the names of taxa are defined strictly in terms of common descent. Several kinds of phylogenetic definitions of taxon names were described by de Queiroz and Gauthier (1992, 1994). For example, "node-based" definitions of taxon names take the form "the most recent common ancestor of taxon A and taxon B, and all of its descendants." Thus, a node-based definition of *Plicaria* could be "the most recent common ancestor of *P. acanthodictya* and *P. endocarpoides* and all of its descendants" (FIG. 1). Regardless of the type of phylogenetic definition that is employed, the important point is that taxon names are defined as the names of clades. This has implications for the concept of synonymy; under phylogenetic taxonomy, names are synonymous only if they refer to the same clade (de Queiroz and Gauthier, 1992). The concept of priority is also affected; under phylogenetic taxonomy, priority would be given to the earliest name given to a particular clade.

The most conspicuous difference between phylogenetic taxonomy and the current system is the absence of ranks. Under phylogenetic taxonomy taxa

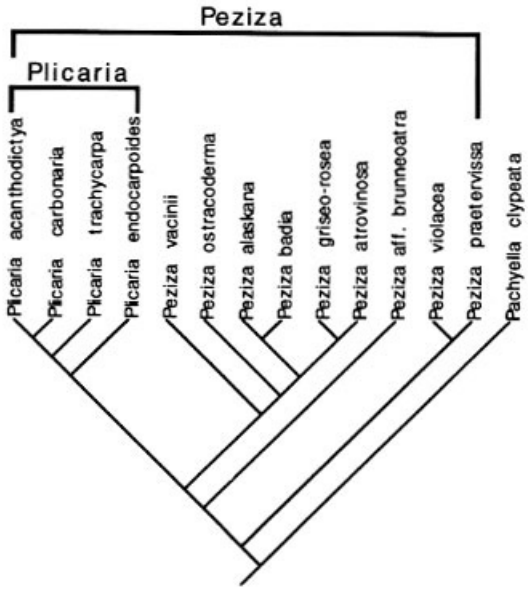

FIG. 3. Phylogeny and classification of *Peziza* and *Plicaria* under phylogenetic taxonomy, based on an analysis by Norman and Egger (1996). *Peziza* and *Plicaria* are unranked taxa. *Plicaria* is nested within *Peziza*.

are named, but they are not assigned to Linnaean categories. Preexisting taxonomic names with suffixes originally denoting rank (e.g., Tulasnellales) could be used in phylogenetic taxonomy, but they would cease to have any meaning in terms of rank. Because suffixes no longer signify ranks, it would be perfectly admissible to have a taxon with a name ending with "-ales" nested within a more inclusive clade with a name ending with "-aceae." A modification suggested by Kron (1997) would be to replace all existing suffixes with a new suffix (such as "-ina") to signify that taxa are unranked.

Eliminating ranks simplifies taxonomy and promotes nomenclatural stability. This can be illustrated with the *Peziza-Plicaria* example. As discussed previously, under the current system, the fact that the genus *Plicaria* is nested within the genus *Peziza* requires either that *Plicaria* be eliminated as a generic name, or that *Peziza* be divided into at least three genera (FIG. 1). Either way, there would be a loss of continuity in names. In a phylogenetic taxonomy, *Plicaria* and *Peziza* would be unranked. Therefore, there would be no obstacle to retaining *Plicaria* in its original sense and modifying *Peziza* so that it includes *Plicaria* (FIG. 3). This would promote continuity of names because all the species formerly recognized in *Plicaria* would still be in *Plicaria*, just as all species formerly in *Peziza* would still be in *Peziza*. The only change in taxon membership would be that all species of *Plicaria* would simultaneously be members of *Peziza*. Because the names *Plicaria* and *Peziza* refer

to different clades (one nested in the other), they are not synonyms in the phylogenetic system.

The example from O'Donnell et al. (1997) also illustrates how phylogenetic taxonomy contributes to nomenclatural stability in spite of changing ideas about phylogenetic relationships. In that study, two topologically similar trees were presented (FIG. 2). Using the Hennigian approach to classification under the current taxonomic system, the two trees would require that different names be used for eight clades that are supported as monophyletic in both trees but that are not assigned the same rank. Under phylogenetic taxonomy there are no ranks and so there would be no need to change the names of the clades whose monophyly is uncontested. The only names that might have to change would be the names that apply to clades that are not supported as monophyletic in both trees. Phylogenetic taxonomy promotes stability because the name of a taxon is insensitive to changes in its position in the tree relative to other taxa.

DISCUSSION

As the preceding examples illustrate, the current taxonomic system leaves much to be desired. The problem of rank proliferation creates a tension between the desire to name clades and the need to keep the number of ranks manageable. Furthermore, names in ranked phylogenetic classifications are sensitive to minor changes in tree topology, and are therefore unstable.

The instability of ranked classifications creates taxonomic confusion, and, even more importantly, may slow the rate at which phylogenetic discoveries are formalized in classifications. Because minor rearrangements in tree topology can cause a cascading series of rank and name changes, systematists are understandably reluctant to name individual clades if the overall topology is poorly resolved. Nevertheless, in current phylogenetic research there is a strong tendency to evaluate putative monophyletic groups clade-by-clade, using node-based measures of robustness (such as the bootstrap), or by comparing trees derived from independent data sets. Consequently, noteworthy phylogenetic discoveries are often made one clade at a time. For the sake of producing up-to-date, phylogenetically accurate taxonomies, it is desirable that strongly supported clades receive names as quickly as possible, even if their higher-order relationships or internal topology are still unresolved. The current system encourages systematists to defer making formal taxonomic proposals until the overall phylogeny is well resolved and a "complete" classification can be proposed. In this way, the current rank-based taxonomic system impedes progress toward a phylogenetic classification of fungi because it insures that there will be a lag of indefinite duration between the discovery of a clade and its formal recognition.

Ranks not only slow progress toward a phylogenetic classification, they can also obscure the results of prior phylogenetic studies. This is because use of the current system to make phylogeny-based classifications can result in the unnaming or renaming of groups whose monophyly is uncontested (de Queiroz and Gauthier, 1994). For example, if *Plicaria* were subsumed into *Peziza* (FIG. 1B) then the name indicating that this clade exists would be lost or changed. If the goal of systematics is to discover and give names to monophyletic groups, then a taxonomic system that can require the unnaming or renaming of monophyletic groups is counterproductive.

The major problems facing phylogenetic classification under the current system are all related to ranks, which suggests that we should abandon rank-based taxonomy. What desirable features of taxonomy would be lost if we eliminated ranks? A common argument in favor of ranks is that they allow efficient communication, although the nomenclatural instability caused by ranks certainly reduces taxonomic efficiency, as does the redundancy resulting from the use of mandatory categories. Nevertheless, the Linnaean ranks form a nested hierarchy, which suggests that the ranks of taxa could convey information about their phylogenetic relationships and relative ages. This is true only in a limited range of situations, however. For example, we can infer the nested relationship of *Amanita* and Amanitaceae from their suffixes and the common basionym. Outside of such cases, ranks alone convey no information about which taxa are nested within one another (de Queiroz and Gauthier, 1992). Other information, from a tree or an indented list, is needed to infer relationships. For example, simply knowing that *Limacella* is a genus and that Amanitaceae is a family does not tell one anything about the relationships of these taxa, other than that Amanitaceae is not nested in *Limacella*.

Ranks not only lack significant information content, they can be positively misleading (Doyle and Donoghue, 1993). This is because placing taxa at the same rank seems to imply that they are roughly equivalent in age, or in diversity or disparity, which may or may not be true. Therefore, relying on ranks to make predictions about such properties of taxa can result in error. For example, it would be dangerous to assume that a particular molecular region that provides phylogenetic resolution among the species of one genus will be informative in another genus (cf., Kohn, 1992; Taylor et al., 1990). Similarly, just because one

family contains a thousand species and another contains a hundred species does not mean that the rate of diversification is higher in the more speciose family (it could be the opposite). Although most evolutionary biologists probably view ranks with caution, other users may not be so sophisticated. Getting rid of ranks altogether would eliminate a potential source of confusion.

CONCLUSIONS

The Preface (p. XV) of the Code states that "The Code is a living and adapting body of law and as long as it keeps evolving in tune with changing needs and new challenges it will keep its authority and strength." As we have demonstrated, the current system does not meet the needs of phylogenetic classification. A number of recently discovered clades have been given only informal, unranked names (e.g., eudicots, archiascomycetes), which suggests that the authority of the Code is already eroding (or that some workers are going to great lengths to circumvent the Code). This is troubling because a broadly accepted code of nomenclature is necessary to insure the uniform application of names.

As published fungal phylogenies grow in size and number, the problems of rank proliferation and nomenclatural instability caused by the current system will become more severe. If the Code is to retain its authority, it must become compatible with phylogenetic classification. It might be possible to integrate rankless classification into the current system gradually. One step in this direction would be the addition of a new unranked category to the Code that could be used with no effect on the ranks of other taxa. Allowing unranked taxa would facilitate the formal recognition of newly discovered clades by eliminating undesirable name changes resulting from changes in rank assignments. Another option, which deserves serious consideration, would be to replace the current Code with a new code that implements the principles of phylogenetic taxonomy. At this time there is not an alternative phylogenetic code, but it is likely that detailed proposals for rankless nomenclatural systems will emerge in the next few years. We hope that this essay will encourage mycologists to critically evaluate the alternatives, and perhaps join in the development of a new phylogenetic code of biological nomenclature.

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LITERATURE CITED

Brummitt, R. K. 1996. In defense of paraphyletic taxa. Pp. 371–384. *In*: *The biodiversity of African plants*. Eds., L. J. G. van der Maesen, X. M. Van Der Burgt, and J. M. Van Medenbach De Rooy. Kluwer Academic Publishers, Dordrecht, Netherlands.

Cantino, P. D., R. G. Olmstead, and S. J. Wagstaff. 1997. A comparison of phylogenetic nomenclature with the current system: a botanical case study. *Syst. Biol.* 46: 313–331.

Chase, M. W., and 40 others. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc*L. *Ann. Missouri Bot. Gard.* 80: 528–548.

de Queiroz, K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso* 15: 125-144.

———, and J. Gauthier. 1992. Phylogenetic taxonomy. *Annu. Rev. Ecol. Syst.* 23: 449–480.

———, and ———. 1994. Toward a phylogenetic system of biological nomenclature. *TREE* 9: 27–31.

Doyle, J. A., and M. J. Donoghue. 1993. Phylogenies and angiosperm diversification. *Paleobiology* 19: 141–167.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane, and J. McNeill. 1994. *International code of botanical nomenclature* (*Tokyo Code*). Koeltz Scientific Books, Königstein, Germany. 389 pp.

Hawksworth, D. L. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycol. Res.* 95: 641–655.

Hennig, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana. 263 pp.

Kohn, L. M. 1992. Developing new characters for fungal systematics: an experimental approach for determining the rank of resolution. *Mycologia* 84: 139–153.

Kron, K. A. 1997. Exploring alternative systems of classification. *Aliso* 15: 105–112.

Lee, M. S. Y. 1996. The phylogenetic approach to biological taxonomy: practical aspects. *Zool. Scr.* 25: 187–190.

Lidén, M., and B. Oxelman. 1996. Do we need "phylogenetic taxonomy"? *Zool. Scr.* 25: 183–185.

Nelson, G. J. 1974. Classification as an expression of phylogenetic relationships. *Syst. Zool.* 22: 344–359.

Norman, J. E., and K. N. Egger. 1996. Phylogeny of the genus *Plicaria* and its relationship to *Peziza* inferred from ribosomal DNA sequence analysis. *Mycologia* 88: 986–995.

Oberwinkler, F. O., R. Bauer, and R. J. Bandoni. 1990. Heterogastridiales: a new order of basidiomycetes. *Mycologia* 82: 48–58.

O'Donnell, K. O., E. Cigelnik, N. S. Weber, and J. M. Trappe. 1997. Phylogenetic relationships among ascomycetous truffles and the true and false morels inferred from 18S and 25S ribosomal DNA sequence analysis. *Mycologia* 89: 48–65.

Schander, C., and M. Thollesson. 1995. Phylogenetic taxonomy—some comments. *Zool. Scr.* 24: 263–268.

Sundberg, P., and F. Pleijel. 1994. Phylogenetic classification and the definition of taxon names. *Zool. Scr.* 23: 19–25.

Taylor, J. W., T. D. Bruns, and T. J. White. 1990. Can the amount of molecular divergence define species and genera: comparison of Sordariales and Agaricales? P. 343. *In: Fourth International Mycological Congress Abstracts*. Eds., A. Reisinger and A. Bresinsky. University of Regensburg, Regensburg, Germany.

Wiley, E. O. 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Syst. Zool.* 28: 308–337.

———. 1981. *Phylogenetics. The theory and practice of phylogenetic systematics*. John Wiley and Sons, New York. 439 pp.