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Kathleen A. Kron
Wake Forest University

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EXPLORING ALTERNATIVE SYSTEMS OF CLASSIFICATION

KATHLEEN A. KRON

*Department of Biology
Wake Forest University
Winston-Salem, NC 27109-7325*

ABSTRACT

Classification involves the development of a system of naming clades that can represent evolutionary relationships accurately and concisely. Using the acid-loving heath plants (Ericales) as an example, one can explore the application of different classification methods. The Linnean system of naming retains the traditional hierarchical framework (named ranks) and allows for the application of many currently used names. The “phylogenetic systematic” approach recommends the removal of an absolute hierarchy but allows retention of traditionally used endings such as -aceae. Historical usage of these names can lead to confusion when the names are used within a discussion or text, especially when a cladogram is not presented at the same time. Another method is suggested that removes the Linnean endings and adds the same ending (*ina*) to all clade names. This effectively eliminates absolute rank and clearly indicates that the group name represents a clade. The names used in this method and the “phylogenetic systematic” method do not indicate relative rank. Numbering systems and indentation are two ways in which relative rank has been conveyed. Indented lists have been the preferred method, often in combination with suffixes that indicate absolute rank. If absolute rank is eliminated, relative rank can still be reflected by indentation as in the “phylogenetic systematic” method. Relative rank can be conveyed by always presenting a cladogram in conjunction with a classification. In practice, relative rank is also effectively communicated within the context of discussion, thus a precise system of indicating relative rank within a formal classification may not be necessary.

Key words: classification of Ericaceae, Linnean classification, phylogenetic classification, rank, universal ending.

INTRODUCTION

Classification involves the development of a system of naming natural groups that can represent evolutionary relationships accurately and concisely. Traditional explanations of classification often merge the activities of grouping and ranking in the process of naming entities (e.g., Radford 1986). Recent discussions in the literature have pointed out the need for the distinction between grouping and ranking (deQueiroz and Donoghue 1988), and for reevaluating the procedure for the naming of groups (deQueiroz 1988, 1992; deQueiroz and Gauthier 1990, 1992; Bryant 1994). The effect of the discussions of naming clades is that a distinction between naming and ranking is made. While traditional practice has assumed the necessity of the application of the Linnean hierarchy in constructing classifications (see also ICBN), some workers also have recognized that application of the hierarchy with its requirements of named ranks can result in a number of practical problems (Wiley 1981; de Queiroz and Gauthier 1990, 1992). However, this sometimes was noted not as a flaw in the Linnean system, but as a weak point in the argument for a strictly cladistic classification (e.g., Cronquist 1981). Depending on the pattern of relationships, two related difficulties are prominent: numbers of names and proliferation of ranks. The tradition of exhaustive subsidiary categories also inflates the num-

ber of names and ranks in a cladistic classification (deQueiroz and Gauthier 1992). This paper explores some alternatives to the Linnean hierarchical system using the heath plants (Ericales) as an example. A new classification of the Ericales is not being presented at this time. All clade or taxon names in this paper merely are for demonstrative purposes and have no nomenclatural priority or weight. The following parameters under which comparison of alternative classifications is made provide a baseline from which the rest of the paper proceeds. First, all example classifications used name only strictly monophyletic groups. Second, all clades are named in each example to provide a consistent means of comparison among classifications. Third, all examples deal only with lineages above the species level. Finally, the phylogenetic relationships of the group are not discussed, rather this paper addresses some of the practical problems of converting a cladogram into a written classification.

METHODS

A phylogeny for the group of heath plants known as the Ericales (Cronquist 1981) indicates that the traditional families Ericaceae, Empetraceae, Monotropaceae, Pyrolaceae, and Epacridaceae all belong to the same clade (Anderberg 1992, 1993; Judd and Kron 1993; Kron and Chase 1993; Crayn, et. al. 1996; Kron

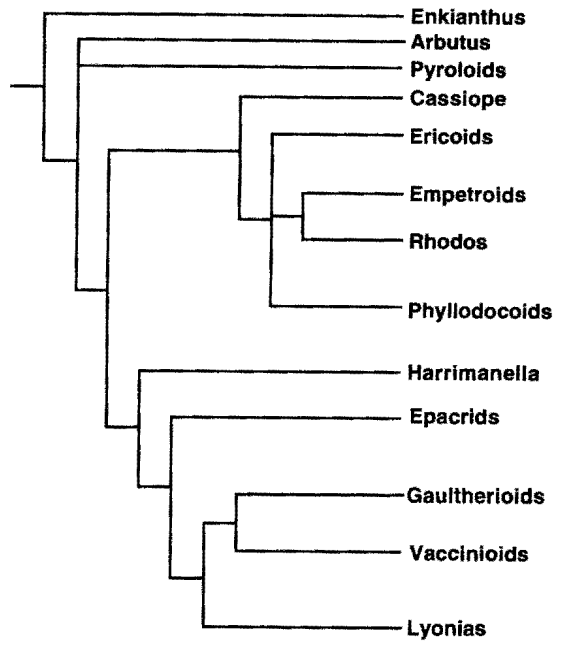
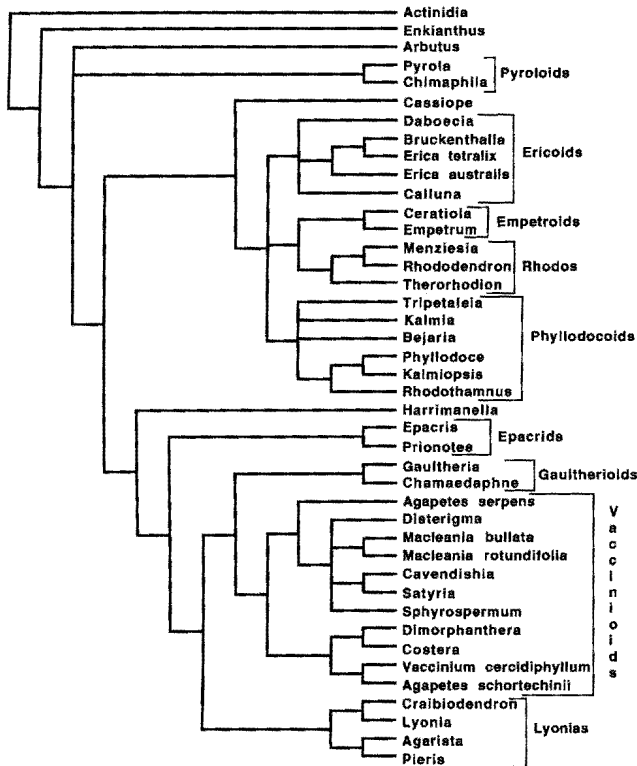


Fig. 2. Simplified cladogram of the ericads from Fig. 1. *Actinidia* has been removed and bracketed clades indicated in Fig. 1 used as terminals.

Fig. 1. Strict consensus of 84 most parsimonious trees from a parsimony analysis of *matK* sequence data (heuristic search, 1000 random replicates, TBR, MULPARS) using PAUP 3.1.1. (Swofford, 1993). Length = 1612, consistency index (CI) = 0.48, retention index (RI) = 0.63. Taxa in brackets are condensed into single representative clades in Fig. 2.

1996; Kron and King 1996). More specifically, the segregation of Empetraceae, Epacridaceae, Monotropaceae, and Pyrolaceae from the Ericaceae, makes the latter paraphyletic. Using this fairly well-supported set of relationships, one may question how one might change the classification to reflect the recent additional information. The tree from which the example classifications are constructed is shown in Fig. 1. This tree was produced from a recent sequence analysis of the chloroplast gene *matK*, but the general topology also is corroborated by results from morphology (Anderberg 1993; Judd and Kron 1993), *rbcL* (Kron and Chase 1993; Crayn et al. 1996; Kron and King 1996), and 18S (Kron 1996) data. In order to reduce the total number of names, and allow for comparison of multiple alternative classifications, this tree has been simplified. *Actinidia* (the outgroup) has been removed and only major clades have been depicted in Fig. 2.

DISCUSSION

Linnean Hierarchical Method

The Linnean system of naming retains the traditional hierarchical framework (named ranks) and allows for the use of many current names. Using this system,

one can classify the Ericales (Fig. 2) by using the modified Linnean system described in Wiley (1981). In this system the unresolved clades Ericoideae, Empetroideae, and Phyllodocoideae are all named at the same rank (Table 1). However, as can be seen in Table 1 the "familiar" names Ericaceae and Epacridaceae no longer have the same meaning in terms of the members of the group. In the classification in Table 1, Ericaceae

Table 1. Example classification using a modified Linnean method. Rank is assigned (left column). Name endings indicate rank.

Superorder	Ericanae
Order	Enkianthales
Order	Ericales
Suborder	Arbutineae
Suborder	Pyrolineae
Suborder	Rhodoreineae
Superfamily	Cassiopiineae
Family	Cassiopaceae
Family	Ericaceae
Subfamily	Ericoideae
Subfamily	Empetroideae
Tribe	Empetreae
Tribe	Rhodoreae
Subfamily	Phyllodocoideae
Superfamily	Harrimanelliineae
Family	Harrimanellaceae
Family	Epacridaceae
Subfamily	Epacridoideae
Subfamily	Vaccinioideae
Tribe	Vaccinieae
Subtribe	Gaultherinae
Subtribe	Vaccininae
Tribe	Lyoninae

Table 2. Example classification using a modified Linnean method with the nonchlorophyllous taxa and tropical blueberry clades added (underlined). Names required to change to accommodate the additional clades are in italics

<i>Subclass</i>	<i>Ericidae</i>
<i>Superorder</i>	<i>Enkianthanae</i>
<i>Superorder</i>	<i>Ericanae</i>
<i>Order</i>	<i>Arbutales</i>
<i>Order</i>	<i>Pyrolales</i>
<i>Superfamily</i>	<u>Pterosporiineae</u>
<i>Superfamily</i>	<u>Pryoliineae</u>
<i>Family</i>	<u>Monotropaceae</u>
<i>Family</i>	<u>Pyrolaceae</u>
<i>Order</i>	<i>Rhodorales</i>
<i>Suborder</i>	<i>Cassiopineae</i>
<i>Superfamily</i>	<i>Cassiopiineae</i>
<i>Superfamily</i>	<i>Ericaciineae</i>
<i>Family</i>	<i>Ericaceae</i>
<i>Family</i>	<i>Empetraceae</i>
<i>Tribe</i>	<i>Empetreae</i>
<i>Tribe</i>	<i>Rhodoreae</i>
<i>Family</i>	<i>Phyllodoceaceae</i>
<i>Suborder</i>	<i>Harrimanelliineae</i>
<i>Superfamily</i>	<i>Harrimanelliineae</i>
<i>Superfamily</i>	<i>Epacridiineae</i>
<i>Family</i>	<i>Epacridaceae</i>
<i>Family</i>	<i>Vacciniaceae</i>
<i>Subfamily</i>	<i>Vaccinioideae</i>
<i>Tribe</i>	<i>Gaultherae</i>
<i>Tribe</i>	<i>Vaccinieae</i>
<i>Subtribe</i>	<u>Costerinae</u>
<i>Subtribe</i>	<u>Sphyrosperminae</u>
<i>Subfamily</i>	<i>Lyonioideae</i>

are restricted to a small subset of traditionally defined Ericaceae (e.g., Cronquist 1981; Thorne 1992), and Epacridaceae include taxa that have previously been considered members of traditional Ericaceae. Another problem with the use of hierarchical names (Linnean) in this example is the proliferation of ranks. In this extremely simplified example the additional ranks of superorder and superfamily are required in order to name all clades (Table 1). Any clades subsequently added to this cladogram would necessitate renaming (i.e., adding and changing ranks) the clades, resulting in a "domino effect" (Table 2). In the example of Table 2 the addition of the nongreen clades to the classification requires the addition of the superfamily rank. This allows the use of the familiar name Monotropaceae, but its meaning has changed from previous classifications (Cronquist 1981). With the addition of the clades within the subtribe Vacciniinae (Table 1), virtually every name/rank must be changed to accommodate these new clades (Table 2). If the exhaustive subsidiary category method is used, or it is required that sister groups must have the same rank, the number of names and ranks would be even greater. Wiley (1981) has discussed the application and problems of using the Linnean system at some length. His sugges-

Table 3. Example classification using a modified Linnean method with the change in rank of the phyllodoceid clade (italicized).

<i>Superorder</i>	<i>Ericanae</i>
<i>Order</i>	<i>Enkianthales</i>
<i>Order</i>	<i>Ericales</i>
<i>Suborder</i>	<i>Arubtineae</i>
<i>Suborder</i>	<i>Pyrolineae</i>
<i>Superfamily</i>	<i>Pterosporiineae</i>
<i>Superfamily</i>	<i>Pyroliineae</i>
<i>Family</i>	<i>Monotropaceae</i>
<i>Family</i>	<i>Pyrolaceae</i>
<i>Suborder</i>	<i>Rhodorineae</i>
<i>Superfamily</i>	<i>Cassiopiineae</i>
<i>Family</i>	<i>Cassiopaceae</i>
<i>Family</i>	<i>Ericaceae</i>
<i>Subfamily</i>	<i>Ericoideae</i>
<i>Tribe</i>	<i>Ericaeae</i>
<i>Tribe</i>	<i>Phyllodoceae</i>
<i>Subfamily</i>	<i>Empetroideae</i>
<i>Tribe</i>	<i>Empetreae</i>
<i>Tribe</i>	<i>Rhodoreae</i>
<i>Superfamily</i>	<i>Harrimanelliineae</i>
<i>Family</i>	<i>Harrimanellaceae</i>
<i>Family</i>	<i>Epacridaceae</i>
<i>Subfamily</i>	<i>Epacridoideae</i>
<i>Subfamily</i>	<i>Vaccinioideae</i>
<i>Tribe</i>	<i>Vaccinieae</i>
<i>Subtribe</i>	<i>Gaultherinae</i>
<i>Subtribe</i>	<i>Vacciniinae</i>
<i>Tribe</i>	<i>Lyoniinae</i>

tions for modifying classifications include not naming all clades and relaxing the Hennigian criterion of assigning equal ranks to sister groups. Wiley (1981) recognizes that using the Linnean hierarchy is merely a convention rather than a biological necessity. He prefers to use it with some specific modifications. Even in the simplified example above, it is apparent that the Linnean hierarchical system of naming is not conducive to the addition of new phylogenetic information. Rather, even with some modifications (Wiley 1981), the Linnean system suffers from the problem of devising new ranks (names), and requires the application of unique suffixes to root names of taxa. Stability of taxon names is also a problem. If new information indicates that the clade named Phyllodoceae in Table 1 (subfamilial rank) is now sister to the clade Ericoideae, then the name Phyllodoceae must be changed to Phyllodoceae (tribal rank) even though the clade remains the same (Table 3).

Alternative Classification Systems

Numerical systems.—Although the Linnean system of classification is the most familiar (e.g., Takhtajan 1980; Cronquist 1981; Thorne 1992), other systems of classification have been proposed. The Linnean system was initiated prior to the general acceptance of evolution and cladistic methods. More recent alternative

Table 4. Example classification using the Hennig Numerical Method: numerical prefixes indicate rank, traditional Linnean suffixes retained.

1.0	Ericanae
1.1	Enkianthales
1.2	Ericales
1.2.1	Arbutineae
1.2.2	Pyrolineae
1.2.3	Rhodorieae
1.2.3.1	Cassiopiineae
1.2.3.1.1	Cassiopaceae
1.2.3.1.2	Ericaceae
1.2.3.1.2.1	Ericoideae
1.2.3.1.2.2	Empetroideae
1.2.3.1.2.2.1	Empetreae
1.2.3.1.2.2.2	Rhodoreae
1.2.3.1.3	Phyllodoceae
1.2.3.2	Harrimanelliineae
1.2.3.2.1	Harrimanellaceae
1.2.3.2.2	Epacridaceae
1.2.3.2.2.1	Epacridoideae
1.2.3.2.2.2	Vaccinioideae
1.2.3.2.2.2.1	Vaccinieae
1.2.3.2.2.2.1.1	Gaultherinae
1.2.3.2.2.2.1.2	Vaccininae
1.2.3.2.2.2.2	Lyonieae

classifications have operated under the assumptions of evolution and the necessity of recognizing strictly monophyletic groups. Among these alternatives are those of Hennig (1966, 1975), Hull (1966), and Farris (1976). Hennig's (1966) method is presented as numerical, although it uses traditional Linnean names and appends numerical prefixes to them (Table 4). In the example in Table 4, dots between the numbers indicate branching points. The actual numbers assigned would depend on where in the tree of life the classification began. Changes in rank, or the addition of clades clearly necessitates the renumbering of the classification. Depending on the position of the branches, these changes could be minimal or result in hierarchical changes at nearly every level. The method of Hull (1966) also is numerical ("phylogenetic numerclature") in that it assigns three numbers to a taxon name. The first number is the identification number. This number would be permanently associated with the taxon except in cases of synonymy and would be applied without regard to phylogenetic relationship. Hull (1966) does not elaborate on how the identification number would be assigned. The second number is the positional number, and is based on absolute ranks with numbers assigned to them. The positional number is a prefix to the identification number. Again, this number would depend on initial ranking of the group to be classified and the number could easily become very long. The phyletic number is added as a suffix to the identification number and is defined as "...the positional number of the taxon's lowest ranked immedi-

Table 5. Categories and modifying prefixes, and their assigned code numbers used to indicate rank. (modified after Farris 1976).

Categories	Modifying prefixes
10 Domain	Giga +4
9 Kingdom	Mega +3
8 Phylum	Hyper +2
7 Class	Super +1
6 Cohort	
5 Order	Sub -1
4 Family	Infra -2
3 Tribe	Micro -3
2 Genus	Pico -4
1 Species	

ately ancestral taxon." (Hull 1966). From a practical aspect this results in the phyletic number being the next most closely related, earlier branching, lowest rank taxon. For the example of Epacridaceae, the phyletic number would be the positional number assigned to *Harrimanella* (Fig. 2). In addition to these three numbers Hull (1966) intended for the continued use of traditional names. Thus, for the clade Epacridaceae the "phylogenetic numerclature method" would result in three numbers and a name: 1-2-3-2-2-1 Epacridaceae (878787) 1-2-3-2-2. From this example the numerical method of Hull appears full of practical difficulties. The identification number is redundant to the name. The positional number is essentially the same as the Hennigian numerical method (Hennig 1966; see also Rivas 1965). Even given that absolute rank could be determined, the juggling of three systems of numbers in addition to a name is cumbersome.

Farris (1976) introduced a system of classification that uses a combination of numbers and modifying prefixes to a predefined set of rank names (Table 5). The modifying prefixes could be used in any combination at every rank. Thus, problems of running out of ranks was avoided. In addition, each modifying prefix carries a "weight" and thus each taxon can be assigned a numerical value corresponding to its phylogenetic rank. In the example of the Ericales (Table 6) the name Ericaceae is maintained as a family that is equivalent to the Ericanae of Table 1. Farris's method allows the creation of new ranks as needed and each rank can be assigned a number. For the category "supersubfamily" the number would be 4 (family code) minus 0.1 (sub code) followed by 1 (super code). Thus supersubfamily Enkianthilanae would be assigned the number 3.91. If the nongreen clades are added to the classification (Table 7), no changes in ranks or names are required. The new categories superinfraclass and subsuperinfraclass are created to accommodate the nongreen clades. Although the method of combination of modifying prefixes solves the problem of creating new ranks, the development of new endings to root taxon names is not resolved. In addition, these cate-

Table 6. Example classification after Farris (1976). Modifying prefixes indicate rank (left column), names retain indication of rank also.

4.0	Family	Ericaceae
3.91	Supersubfamily	Enkianthilanae
3.91	Supersubfamily	Callunilanae
3.9	Subfamily	Arbutoideae
3.9	Subfamily	Pyroloideae
3.9	Subfamily	Ericoideae
3.8	Infrafamily	Cassiopaea
3.7	Microfamily	Ericacineae
3.7	Microfamily	Empetricineae
3.6	Picofamily	Empetridiinae
3.6	Picofamily	Rhodoriinae
3.7	Microfamily	Phyllodocidiinae
3.8	Infrafamily	Harrimanellaea
3.7	Microfamily	Epacricineae
3.6	Picofamily	Epacridiinae
3.6	Picofamily	Vaccinidiinae
3.59	Subpicofamily	Gaultherii
3.588	Infrasubpicofamily	Vaccinie
3.588	Infrasubpicofamily	Gaultherie
3.59	Subpicofamily	Lyonii

gory names and numbers are still tied to a Linnean hierarchical system. This is also true of the numerical methods of Hennig (1966) and Hull (1966). The use of numerical systems of classification could make names unnecessary if the numerical prefixes or codes could be consistently tied to a standardized absolute hierarchy, but this is highly unlikely. More significantly, codes or strings of numbers are not the best way to communicate a classification because they are difficult to verbalize or use in a written discussion (Wiley 1981). They are also nearly impossible to use in teaching systematics or biology in general. In the examples of Hennig (1966), Hull (1966), and Farris (1976) the combination of numbers and names merely complicate the construction of a classification and the numbers become essentially redundant to the names. Furthermore, all of these examples are still modifications of the Linnean hierarchical system.

The problems of assigning rank are several and have been discussed at length by de Queiroz and Gauthier (1992). Farris (1976) outlined four criteria for assigning rank 1) tradition, 2) number of species in a taxon, 3) amount of divergence, and 4) antiquity. Cladistic approaches to grouping and naming groups would consider only the fourth criterion as reliable in assigning rank. However, the age of divergence for most taxa is not known. Thus, the designation of absolute rank is essentially an arbitrary action. Most systematists have used category names to indicate relative rank. The differences are most notable at "higher" taxonomic categories such as subclass (Cronquist 1981) and superorder (Thorne 1992). In light of this problem, the value of assigning rank at all may be questioned. Griffiths (1973) has suggested that Linnean names for catego-

Table 7. Example classification after Farris (1976) with addition of the nonchlorophyllous clades (in italics).

4.0	Family	Ericaceae
3.91	Supersubfamily	Enkianthilanae
3.91	Supersubfamily	Callunilanae
3.9	Subfamily	Arbutoideae
3.9	Subfamily	Pyroloideae
3.81	<i>Suprainfracfamily</i>	<i>Pterospora</i>
3.81	<i>Superinfracfamily</i>	<i>Pyrolora</i>
3.809	<i>Subsuperinfracfamily</i>	<i>Monotropota</i>
3.809	<i>Subsuperinfracfamily</i>	<i>Pyrolota</i>
3.9	Subfamily	Ericoideae
3.8	Infrafamily	Cassiopaea
3.7	Microfamily	Ericacineae
3.7	Microfamily	Empetricineae
3.6	Picofamily	Empetridiinae
3.6	Picofamily	Rhodoriinae
3.7	Microfamily	Phyllodocidiinae
3.8	Infrafamily	Harrimanellaea
3.7	Microfamily	Epacricineae
3.6	Picofamily	Epacridiinae
3.6	Picofamily	Vaccinidiinae
3.59	Subpicofamily	Gaultherii
3.588	Infrasubpicofamily	Vaccinie
3.588	Infrasubpicofamily	Gaultherie
3.59	Subpicofamily	Lyonii

ries above the species level "might well be abandoned." Forey et al. (1992) discussed ranking in the use of indented lists, i.e., the position of the name on the page relative to other names used, "since it is not the rank that is important, only its position on the page." Forey et al. (1992) suggest one possible way to avoid running out of ranks is to just classify down to a certain level "leaving the diagram to convey the theory of relationship."

At this point it might be helpful to take a step back and ask several basic questions about systematics. Among the many suggested goals of systematics, the primary purpose is to discover the evolutionary history of life. Part of this discovery involves the reconstruction of phylogeny through the use of cladograms. Hennig (1975) notes that one other purpose of systematics is to convert the cladogram into a hierarchic system. This system is the classification. While, in theory, the conversion of a cladogram into a classification is "purely a formal operation" (Hennig, 1975), in practice, the operation becomes more complicated. The primary reason for this is incomplete knowledge. Systematists continue to discover new taxa, and new relationships among those taxa and previously known ones. What is the advantage of developing a "hierarchical system"? Hennig (1975) suggests the following: "...phylogenetic relationships can clearly be set out in a small space. . .," a "...written system allows for a quick and clear evaluation of the gaps in present knowledge of taxa of unknown relationships. . .," and one can "...reconstruct a cladogram from the classi-

fication." From the examples seen so far in this paper, the first and third advantages are somewhat debatable. A cladogram is actually a very concise way of representing relationships and if this is the case, then the necessity for being able to reconstruct a cladogram from the written classification is nullified. Gaps in the knowledge about taxa of unknown relationship can be seen in a written hierarchy, but should this be a major function of a classification? More specific questions are: Why pursue the assignment of rank in a classification if it is so problematic? What function does rank perform in a classification? If classification is to be a verbal or written form of communication of the phylogeny, then an indication of rank would allow one to specify which entities belong in a clade (i.e., relationship). Another way of thinking about this is that rank indicates levels of inclusiveness. This inclusiveness is initially communicated by a cladogram.

Phylogenetic systematic methods.—As an alternative to the Linnean hierarchical classification, de Queiroz and Gauthier (1990, 1992) have proposed a system that uses clade names (as opposed to names of classes). In this "phylogenetic systematic" approach the traditional endings are retained, yet have no hierarchical meaning. Relative rank is indicated by the indentation of clade names in the list. In their paper on phylogenetic taxonomy de Queiroz and Gauthier (1992) suggest that widely used names be preferred when naming 'crown clades.' They suggest that this will maintain nomenclatural stability. In the example of the Ericales (Table 8), widely used names such as Ericaceae, Epacridaceae, and Empetraceae have been retained. However, it is not possible to use them in a manner that includes the same taxa (or clades) as traditional usage. The Ericaceae in Table 8 include a small portion of the traditionally recognized Ericaceae (e.g., Cronquist 1981). If the name Ericaceae were to be used to include the *Enkianthus* clade, then it would also not coincide with traditional usage. In this example, only the Empetraceae include the same clades as traditional Empetraceae. The use of names that are still in the literature, yet have no meaning with regard to rank, can be confusing. For example, in the Ericales (Table 8) the clades Ericaceae and Empetraceae have the same "family level" ending familiar to systematists. However, under the phylogenetic systematic method, the clade Ericaceae is more inclusive than the clade Empetraceae, thus giving the impression of a family within a family. As a form of communication of relationships, clade names should be as unambiguous as possible. The continued use of "traditional" names may initially seem to increase stability; however, it already has been shown that the stability is in appearance only (Table 1, Linnean system), since the members of the named clades are different from pre-

Table 8. Example classification using the phylogenetic systematic method (de Queiroz and Gauthier 1992). Name endings do not indicate rank, indentation indicates relative rank. Widely used names are indicated in italics.

<i>Ericales</i>
Enkianthales
Ericanae
Arbutineae
Pyrolineae
Rhodorineae
Cassiopiineae
Cassiopaceae
Ericaceae
Ericoideae
Empetroideae
<i>Empetraceae</i>
Rhodoreae
Phyllodocoideae
Harrimanelliineae
Harrimanellaceae
<i>Lebetanthaceae</i>
<i>Epacridaceae</i>
Vaccinioideae
Vaccinieae
Gaultherinae
Vaccininae
Lyoninae

vious classifications, regardless of whether the same label is used.

A modification of the phylogenetic systematic method proposed by de Queiroz and Gauthier (1992) is to remove the Linnean endings and add the same suffix (*ina*) to all clade names (Table 9). The most significant advantage of using a universal ending is that it clearly indicates a new system of nomenclature. The phylogenetic systematic method as described by de Queiroz and Gauthier (1992) assumes that taxa in the system are named clades. Thus, by definition, named taxa in this system are monophyletic. This is in sharp contrast to the current Linnean-based system with many paraphyletic/polyphyletic groups that are formally recognized. The universal ending also clearly signals the elimination of Linnean categories. Retention of the widely used names (Linnean-based) in a new system of taxonomy only retains the ambiguity inherent in the Linnean hierarchical system as it is practiced by systematists today. The new universal ending can be used as clades are discovered, thus it will become increasingly clear which groups have been recently studied and which have not. Of course, in the future the issue of paraphyly vs. monophyly will only be a matter of historical interest in many groups (de Queiroz and Gauthier 1992).

The names used in the "phylogenetic systematic" method and the universal-ending modification do not indicate relative rank. As discussed above, numbering systems and indentation are two ways in which relative

Table 9. Example classification using the phylogenetic systematic method (de Queiroz and Gauthier 1992) and the universal ending (*ina*). Rank is indicated by indentation. Nonchlorophyllous and tropical blueberry clades are in italics.

Ericalina
Enkianthina
Arbuarctina
Arbutina
Pyrolina
<i>Pterosporina</i>
<i>Pyrolina</i>
<i>Monotropina</i>
<i>Chimaphilina</i>
Ericina
Bruckenthalina
Cassiopina
Callunina
Phillipina
Rhodorina
Empetrina
Rhododendrina
Phyllodocina
Pentachondrina
Harrimanellina
Lebetanthina
Epacridina
Gaultherina
Costerina
Pernettyina
Vaccinina
<i>Costerina</i>
<i>Sphryospermina</i>
Lyonina

rank has been conveyed. While it is possible to devise a combination of numerical prefixes with indentation and universal endings, relative rank can be conveyed by always presenting a cladogram in conjunction with a classification. Numerical methods are logical, but as can be seen in the above examples, they are not conducive to verbal communication. Indented lists are more flexible in accommodating changes in known relationships and the addition of new clades. However, once the name is removed from the list (i.e., included in a written or verbal discussion) its relative rank is less obvious. In practice, relative rank is usually effectively communicated within the context of discussion. At first consideration it may seem that valuable information is lost when named ranks are not used. However, in practice the rank of a taxon communicates very little about it. Consider the taxa Asteraceae, Actinidiaceae, and Ericaceae. All taxa are at the "family" level; however, there are thousands of species in Asteraceae (Bremer 1994), nearly 3000 in Ericaceae (Stevens 1971), but only about 350 species in Actinidiaceae (Willis 1973). In Asteraceae the ovary is always inferior, in Actinidiaceae the ovary is superior, but in Ericaceae ovary position varies from superior to inferior. Among these taxa Asteraceae are likely a more

recently derived lineage than Actinidiaceae or Ericaceae. Therefore, rank does not contain information regarding number of taxa, age, or amount of diversity.

Relative rank does convey relationship. However, the current system offers little to communicate relationship to someone who is not an expert in a particular group. The evidence for this can be seen in the practice of including the more inclusive taxon name in parentheses after a less inclusive name in the titles of journal articles (e.g., Styphelieae [Epacridaceae]). This is because Styphelieae means little to someone who has not worked with epacrids. Whether Styphelieae is called a tribe or not designated at some absolute rank is not important (e.g., use of universal ending: Styphelina [Epacridina]). What is important is that it is part of the epacrid clade. This relationship can easily be included in the context of the discussion and reinforced by the inclusion of a cladogram with the classification. Thus a precise system of indicating relative rank within a formal classification may not be necessary.

In summary, the Linnean hierarchical method is not conducive to the incorporation of new phylogenetic information and constrains the application of evolutionary principles to systematic nomenclature. One of the most severe constraints is that of assigning rank to named taxa. Numerical methods have been suggested as a means of providing unlimited categories, but are still essentially based on a Linnean system of names. In addition, these numerical methods are awkward and not easily conveyed in verbal or written communication. The phylogenetic systematic method eliminates rank as part of the name of a taxon and indicates relative rank by the use of indented lists. However, the Linnean-based names (with the now-meaningless rank endings) are retained. This introduces ambiguity into an otherwise very straightforward system. On the other hand, the use of a universal ending for all clades (*ina*) clearly indicates the change to a phylogenetic system. It eliminates the problem of ranking, its concomitant problem of devising new endings, and (of secondary importance) provides a means of tracking which groups have been recently studied.

Systematics is possibly one of the oldest of scientific endeavors. Over the centuries its practice has changed little despite the Darwinian "revolution" (Stevens 1984; de Queiroz and Gauthier 1990, 1992). A repeated call to "stability" has perhaps been responsible for discouraging the development of a system of classification that reflects evolutionary history (relatedness based on ancestry) and is flexible enough to accommodate a continual influx of new information. There are two kinds of change ahead for systematics. The first is the development of a new system of nomenclatural rules that are driven by evolutionary principles, rather than by tradition. This is perhaps the most dif-

ficult change. The second type of change is that of a continual influx of new information. This kind of change is what makes systematics an active and fascinating field of study. A taxonomy such as the modified phylogenetic system proposed would provide a concise means of communicating phylogenetic relationships when presented in conjunction with a cladogram.

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