A COMPARISON OF PHYLOGENETIC NOMENCLATURE WITH THE CURRENT SYSTEM: A BOTANICAL CASE STUDY

PHILIP D. CANTINO,1 RICHARD G. OLMSTEAD,2 AND STEVEN J. WAGSTAFF3

1Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701-2979, USA; E-mail: pcantino1@ohiou.edu
2Department of Botany, Box 355325, University of Washington, Seattle, Washington 98195-5325, USA; E-mail: olmstead@u.washington.edu
3Manaaki Whenua Landcare Research New Zealand, Ltd., P.O. Box 69, Lincoln 8152, New Zealand; E-mail: wagstaffs@landcare.cri.nz

Abstract.—The family Lamiaeaceae was used as a case study to compare our current system of nomenclature with a phylogenetic alternative proposed by de Queiroz and Gauthier (1992, Annu. Rev. Ecol. Syst. 23:449–480), with emphasis on nomenclatural stability and efficiency. Comparison of published cladistic analyses revealed 19 suprageneric clades within Lamiaeae that are supported well enough to merit naming, but many genera could not be placed with confidence in any inframafamilial taxon. Two phylogenetic classifications were prepared, one following current nomenclatural rules and conventions and the other following the phylogenetic system of nomenclature. A comparison of the classifications revealed examples of unstable and ambiguous names that resulted from employing current rules and conventions to name clades. Old names based on nomenclatural types of uncertain phylogenetic relationship and inframafamilial taxon names based on the type of the family are particularly prone to instability. The phylogenetic system appears to have fewer problems but may also lead to nomenclatural confusion if taxon names are defined carelessly. The current system produces less efficient classifications because the principle of exhaustive subsidiary taxa leads to inclusion of redundant names (monotypic taxa) when the classification is based on an asymmetrical cladogram. In contrast, the phylogenetic system contains no redundant names. We endorse the recommendation that the principle of exhaustive subsidiary taxa be abandoned. Phylogenetic definitions should be provided for taxon names whenever phylogenies are translated into classifications. The definitions should be accompanied by a list of synapomorphies and a statement of clade membership to facilitate subsequent provisional referral of newly studied species to supraspecific taxa. [Classification; Lamiaeaceae; nomenclature; phylogenetic systematics; phylogeny; taxonomy.]

In a recent series of papers, de Queiroz and Gauthier (1990, 1992, 1994) proposed fundamental changes in the naming of organisms. Their revolutionary ideas warrant widespread discussion and are beginning to receive attention from the systematics community (Bryant, 1994, 1996; Sundberg and Pleijel, 1994; Graybeal, 1995; Schander and Tholleson, 1995), but their proposals have not been examined in the context of the International Code of Botanical Nomenclature (ICBN; Greuter et al., 1994).

In explaining the need for a new system of nomenclature, de Queiroz and Gauthier (1992, 1994) made the following points. First, if a system of biological nomenclature is to serve its primary function of communication, it must provide taxon names that are explicit, universal, and stable. Second, as the tenet of evolution has become incorporated into the philosophical framework of systematics, species have become equated with population lineages, and higher taxa have become equated with clades. Thus, taxon names have implicit phylogenetic meanings, and biological nomenclature should provide clades with names that are explicit, universal, and stable. Third, the current system of nomenclature fails to meet these objectives because it is founded on pre-Darwinian principles. Currently, taxon names are defined in terms of nonevolutionary concepts: Linnaean categories (ranks) and nomenclatural types. When this nonevolutionary system is applied to taxa with implicit phylogenetic meanings, the result is nomenclatural ambiguity and instability.

Even under a nonphylogenetic interpretation of taxa, our current system fails to provide stable names whenever unification
and division (lumping and splitting) of taxa occur (de Queiroz and Gauthier, 1994). When taxa are lumped, because of either phenoetic or phylogenetic considerations, a taxon name comes to signify a more inclusive grouping than it did previously. Conversely, when a taxon is split into two or more taxa without change in rank, one of the resulting names refers to a less inclusive grouping than it did previously. The terms *sensu lato* and *sensu stricto* are frequently used to clarify the meanings of such names, but confusion can result when a taxon name has been applied to more than two groups with differing circumscriptions.

At the heart of the problem is the manner in which taxon names are defined. In our current system, names below a particular rank (which varies among the codes governing different groups of organisms) are defined as the taxon assigned to rank X that contains type Y (de Queiroz and Gauthier, 1994). For example, Lamiaceae is the taxon of family rank that contains the type of the genus *Lamium*. There is nothing in this definition that refers to evolution. In contrast, de Queiroz and Gauthier (1990) proposed three ways in which taxon names may be defined explicitly in terms of common descent: node-based, stem-based, and apomorphy-based definitions (collectively referred to hereinafter as phylogenetic definitions). In all cases, the resulting name is permanently attached to a clade. The hypothesized membership of the clade may change with new evidence about phylogeny (Bryant, 1996), but a name defined in this manner cannot come to refer to a paraphyletic or polyphyletic group.

Although the definition of taxon names is the most fundamental distinction between our current system of nomenclature (referred to hereinafter as traditional nomenclature) and the proposed phylogenetic system, de Queiroz and Gauthier (1992, 1994) suggested several related conventions for naming supraspecific taxa.

1. Priority would operate within a clade, rather than within a rank. Thus, the earliest name applied to a clade would have priority over all later ones designating the same clade. If a clade originally recognized at one level of the hierarchy is subsequently shifted to a different level, its name does not change in the phylogenetic system because it is still the same clade. In contrast, the traditional system would require a change in the termination (suffix) of the name—and sometimes a change in the whole name because of application of priority within rank.

2. The standard ranks above the species level would be abandoned. A species would be referred to a set of increasingly inclusive clades (thus the system would still be hierarchical), but these would not be called genera, subfamilies, families, etc. The currently mandated, rank-based suffixes could still be used, but they would no longer signify rank (e.g., a plant taxon name ending in -oideae, currently used for subfamilies, would not necessarily be less inclusive than one ending in -aceae, currently used for families). The only reason to retain such endings would be to avoid unnecessary name changes during the conversion to phylogenetic nomenclature when a widely used name unambiguously represents a clade.

3. It would not be necessary to refer a species to a taxon at every level in the hierarchy. A species would be referred to a supraspecific taxon only when there is adequate evidence that it is indeed a member of that clade. For example, it would be acceptable to refer a species to a taxon at the third supraspecific level in the hierarchy but not the less inclusive second one if there is insufficient evidence to determine which second-level clade the species belongs to.

The logical consistency of these proposals is appealing, but their ramifications in practice have received little critical evaluation (Schander and Thollesson, 1995; Bryant, 1996). We used the plant family Lamiaceae (=Labiatae) as a case study. Based on previous parsimony analyses of molec-
ular and nonmolecular data, two phylogenetic classifications of the Lamiaceae were developed, one employing traditional rules and conventions of botanical nomenclature and the other following the phylogenetic system proposed by de Queiroz and Gauthier. The classifications were then compared, with emphasis on nomenclatural stability and efficiency (i.e., lack of redundancy). In addition to being the first botanical comparison of the phylogenetic and traditional systems of nomenclature, this example differs in an important way from those of previous authors. The poor phylogenetic resolution in the Lamiaceae is more representative of the current knowledge of many groups of organisms than are the relatively well-resolved phylogenetic hypotheses used as examples by de Queiroz and Gauthier (1992) and Sunderland and Pleijel (1994), thus it offers a more realistic test of the applicability of phylogenetic nomenclature.

Many of the names used here are new but not validly published according to the ICBN, i.e., they are nominate nuda. This is intentional. We do not favor adopting those names that represent monotypic higher taxa, but provisional names were created to allow comparisons of the ramifications of the nomenclatural systems.

**METHODS**

Currently, the best basis for suprageneric classification in the Lamiaceae is a cladistic analysis of chloroplast DNA (cpDNA) sequences (Wagstaff et al., 1997). That study included separate analyses of ndhF and rbcL sequences and an analysis of the combined data for both genes, totaling over 3,500 bp of sequence. The single most-parsimonious tree from that combined analysis was the primary basis for the classification developed here. A disadvantage of that analysis (as with most molecular studies of large groups) is the very small taxonomic sample. Only 31 genera and 33 species were included in that study, out of approximately 260 genera and 7,000 species in the family (Cantino et al., 1992; Thorne, 1992). This drawback was mitigated by careful selection of exemplars to represent most major subgroups of the Lamiaceae.

A cladistic analysis of nonmolecular (mainly morphological) data (Cantino, 1992) was a secondary basis for our classification. Although that analysis included a larger taxonomic sample (106 taxa, 77 of them genera and the rest sections or species), it was given lower priority here because of three weaknesses. First, there was no systematic effort to search for islands of equally parsimonious trees. The heuristic search used simple addition, whereas random addition with numerous replicates would have been more appropriate for so large a data set. As a result, not all of the most-parsimonious trees were found, and the strict consensus tree in the 1992 study shows a higher degree of resolution than it should have. Second, the analysis was undirected, with subsequent Lundberg rooting (Lundberg, 1972), because data collection had not been completed for the outgroups. There were eight equally parsimonious rooting points in the strict consensus tree. Third, no measure of clade support was provided other than number of character changes; neither bootstrapping nor decay analysis was done. These problems will be rectified in a future analysis of a revised and expanded version of the nonmolecular data set, which will also be analyzed in combination with molecular data once current studies have been completed. However, a provisional classification based mainly on the combined rbcL/ndhF analysis provided an adequate basis to explore the ramifications of different nomenclatural systems applied to the Lamiaceae.

Before a classification can be prepared, one must determine which clades are well enough supported to warrant naming. In doing so, we gave primacy to the molecular analysis, but the nonmolecular analysis was given some consideration. Every clade recognized in our classification was supported by the molecular analysis, but different degrees of support were required depending on whether or not the clade was corroborated by the results of the nonmolecular analysis. Any one of the follow-
ing conditions was considered sufficient to include a clade in the classification that was subsequently used to compare traditional and phylogenetic systems of nomenclature: (1) the clade was supported by the cpDNA sequence data with a bootstrap value of ≥50% and was corroborated by the strict consensus tree based on nonmolecular data (Cantino, 1992); (2) the clade was supported by the cpDNA sequence data with a bootstrap value of ≥70% and was neither supported by nor in conflict with the results of the nonmolecular analysis (i.e., the nonmolecular results were either equivocal because of poor resolution or did not address the monophyly of the group); and (3) the clade conflicted with the consensus tree based on nonmolecular data but was supported by the cpDNA sequence data with a bootstrap value of ≥90%. Although these criteria are somewhat arbitrary, they at least ensure that taxa included in the classification are reasonably well-supported clades.

Two classifications were prepared. Both are phylogenetic in that all taxa are hypothesized clades, but they differ in how names were applied to these clades. For one (classification X), we followed the ICBN, and for the other (classification Y), we followed the phylogenetic system of nomenclature proposed by de Queiroz and Gauthier (1992). For classification X, we also incorporated the principle of exhaustive subsidiary taxa (Simpson, 1961; de Queiroz and Gauthier, 1992), a convention that is nearly universally used in botany although not formally codified in the ICBN. By this convention, if a particular rank is used within a taxon, it must be used for all members of the taxon. For example, if one tribe is recognized within a subfamily, then all genera in that subfamily whose relationships are known must be assigned to some tribe, even if it is monotypic and thus redundant. (However, genera of uncertain relationships may be designated incertae sedis [Wiley, 1979] and left unassigned.) In classification Y, taxon names were defined as clades using phylogenetic definitions (de Queiroz and Gauthier, 1990). The system is hierarchical, but there are no established ranks. The principle of exhaustive subsidiary taxa was not followed, thus no redundant names were included.

RESULTS

Construction of Classifications

Figure 1 shows the ingroup (Lamiaceae) portion of the single most-parsimonious tree obtained in the analysis of cpDNA sequences (Wagstaff et al., 1997). Table 1 lists the clades that have bootstrap values ≥50% (labeled A–V in Fig. 1) and indicates which were supported by the analysis of nonmolecular data (Cantino, 1992). Clades within subfamilies Lamioideae and Nepetoideae sensu Cantino et al. (1992) (clades U and B, respectively) were ignored because representation of these two large groups in the cpDNA study was limited to so few genera that the relationships found within them are not very meaningful.

Eighteen clades (including the family itself) were sufficiently well supported to warrant naming. Genera that emerged within one of these clades in the nonmolecular analysis but were not represented in the cpDNA analysis were assumed to belong to that clade in the absence of any evidence to the contrary (e.g., Spartothamnella in clade M, Renschia in clade S, Anisomeles in clade V).

Two phylogenetic classifications of the Lamiaceae were then prepared (Tables 2, 3), each containing all of the clades that met one of the recognition criteria. Three additional clades were also included in the classifications based on outside evidence: a previously unnamed clade comprising Oxera and Faradaya (Oxerinae in Table 2), a previously unnamed clade comprising these same two genera and Clerodendrum (Clerodendronae in Table 2), and Symphorematoideae. The existence of the first two clades was supported by a cpDNA restriction site analysis (Steane et al., 1997) with bootstrap values of 100% and 99%, respectively; their monophyly was not tested by the analysis in Figure 1, which did not include Faradaya or Oxera. The monophyly of Symphorematoideae has not been tested.
by any formal cladistic analysis, but its unique inflorescence structure with an involucre of winglike bracts provides a clear synapomorphy for this group of three genera.

For classification X (Table 2), we followed traditional nomenclatural rules and conventions, and for classification Y (Table 3), we followed the phylogenetic system proposed by de Queiroz and Gauthier (1992). Some unorthodox ranks were used in classification X to recognize five hierarchical levels between family and genus. The ICBN (Article 4) provides three such ranks (subfamily, tribe, and subtribe) but states that further ranks may be intercalated. We added the ranks supertribe and supersubtribe to accommodate all of the clades in Figure 1 that warrant naming. Because no suffixes are mandated by the
### Table 1. Clades of Lamiaceae with bootstrap values ≥50% in the cpDNA analysis (clades within Nepetoideae and Lamioideae sensu Cantino et al. [1992] are excluded; see Results).

<table>
<thead>
<tr>
<th>Data set</th>
<th>Clade</th>
<th>cpDNA</th>
<th>Nonmolecular</th>
<th>Criterion</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>100</td>
<td>nt</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>100</td>
<td>+</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>100</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>95</td>
<td>0*</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>100</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>90</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>79</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>99</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>95</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>100</td>
<td>eq</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>99</td>
<td>+</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>100</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>72</td>
<td>+</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Q</td>
<td>100</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>100</td>
<td>+</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>S</td>
<td>100</td>
<td>+</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>100</td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>99</td>
<td>+</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>54</td>
<td>+</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

*Letters refer to clades in Figure 1. A = Lamiaceae sensu Junell (1994), including Symphorematoidae; B = Nepetoideae sensu Cantino et al. (1992); C = Petilia and Vitis; D = clades E, P, and Q; E = Teucrionideae sensu Cantino et al. (1992) plus Ajuga; F = clades G and M; G = clades H and L; H = clade J plus Ajuga; J = Carapisera and Trichostema; K = Trichostema and Carapisera sect. Carapisera; L = Clerodendrum and Tetraclea; M = clade N plus Teucrium and Sparrholmella (not included in the molecular data set); N = Teucrium and Oncinocalyx; P = Gmelina and Premna; Q = clades R and T; R = Scutellarioideae sensu Cantino et al. (1992); S = Scutellaria and Timmae plus Renschia (not included in the molecular data set); T = clades U and V; U = Lamiaceae sensu Cantino et al. (1992); V = Pogostemon and Colebrookea plus Anisomeles (not included in the molecular data set).

b Bootstrap percentages.

c + = the clade is supported by the analysis of nonmolecular data (Cantino, 1992); 0 = the clade conflicts with results of the nonmolecular analysis; eq = the nonmolecular analysis is equivocal due to poor resolution; nt = the nonmolecular analysis does not test the monophyly of the grouping.

d Criteria for recognition of clades as named taxa (see Methods). Clades without numbers were not recognized.

*Supported by the nonmolecular analysis if Ajuga is excluded; see text.

ICBN for these ranks, we invented suffixes (-adeae for supertribes and -onae for supersubtribes).

The names of monotypic higher taxa (found only in classification X), which result from employing the principle of exhaustive subsidiary taxa, are shown in boldface in Table 2. It is not evident from Figure 1 why Clerodendrinae (clade L) is monotypic. A molecular study that included more species of Clerodendrum (Steane et al., 1997) demonstrated that Tetraclea is nested within Clerodendrum, thus these genera must be merged in a phylogenetic classification. Hence, Clerodendrinae contains only the genus Clerodendrum.

Because the standard ranks were abandoned in classification Y, the terminations of names in Table 3 have no hierarchical significance. Names in classification Y were selected with clarity and stability in mind. None of the existing names for these taxa have previous phylogenetic definitions. However, the phylogenetic meaning of six of these names can be inferred from the labeling of cladograms (Olmstead et al., 1993 [Labiateae]; Wagstaff et al., 1995 [Lamioidae, Nepetoideae]; Wagstaff et al., 1997 [Pogostemonoideae, Scutellarioideae, Teucrioidae]) or by reference to a previously published cladogram (Cantino et al., 1992 [Teucrioidae]). Such names were used in classification Y to preserve current usage. If a clade had no previous name, a new one was provided in classification Y (Table 3) using a standard ending (-ina).

Kathleen Kron proposed (in a symposium presentation at the 1995 meeting of the American Society of Plant Taxonomists) that this ending be used for all names in a phylogenetic classification, but nomenclatural stability is better served by retaining widely used names whenever possible (Bryant, 1994). The name Labiateae was used in classification Y for the clade that is called Lamiaceae in classification X because the former name was used first to designate this clade (Olmstead et al., 1993); this is one of the few plant families for which two names are sanctioned by the ICBN, thus either could be used in classification X.

In summary, both classifications include 19 suprageneric clades within Lamiaceae. No rank was assigned when phylogenetic nomenclature was employed (Table 3), but the classification using traditional nomenclature (Table 2) recognizes six clades as subfamilies, one as a supertribe, four as tribes, two as supersubtribes, and six as subtribes. In addition, five monotypic su-
Table 2. Phylogenetic classification of Lamiaceae following current nomenclatural rules and conventions (=classification X). Some names are not validly published. Redundant (monotypic) suprageneric taxa are shown in boldface. The unorthodox ranks supertribe and supersubtribe have invented suffixes. Lettering of clades corresponds to that in Table 1 and Figure 1.

<table>
<thead>
<tr>
<th>Clade</th>
<th>Subclade</th>
<th>Classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Subclade A</td>
<td>Lamiaceae (clade A)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subfamily Ajugoideae (clade E)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Supertribe Ajugadeae (clade F)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tribe Ajugae (clade G)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Caryopteridinae (clade H)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Supersubtribe Caryopteridinae (clade K)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>New genus based on Caryopteris divaricata (incertae sedis)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>New genus based on Caryopteris bicolor (incertae sedis)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Supersubtribe Clerodendraceae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Oxerinae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Supersubtribe Ajugoneae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Clerodendrinae (clade L)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Supersubtribe Ajugoneae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tribe Teucrieae (clade M)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Oncinocalycinae (clade N)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Teucrinae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sparthamnella (incertae sedis)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Supersubtribe Cyclonematae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12 genera (incertae sedis)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subfamily Premnoideae (clade P)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subfamily Lamioidae (clade Q)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tribe Scutellariae (clade R)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Scutellariae (clade S)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Holmskioldiinae</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tribe Lamiaceae (clade T)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Lamiinae (clade U)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subtribe Pogostemoninae (clade V)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6 genera (incertae sedis)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subfamily Viticoideae (clade C)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subfamily Nepetoideae (clade B)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subfamily Symphorematoidae (represented by Congea in Fig. 1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>32 genera (incertae sedis)</td>
</tr>
</tbody>
</table>

* The monophyly of Clerodendraceae, Oxerinae, and Symphorematoidae is based on evidence external to this study (see Results).
* It is not evident from Figure 1 why Clerodendraceae is monotypic (see Results).
* Genera of Ajugoideae that cannot be assigned with confidence to a supertribe: Aegiphila, Amasonia, Amethystea, Glossocarya, Hosa, Husleya, Karodia, Monochilus, Peronema, Petranovitex, Rubiaceae, Schnabelia.
* Genera of Lamiaceae that cannot be assigned with confidence to a subtribe: Achyrospernum, Cranioth, Eurysele, Comanthophraceae, Leucocentrum, Rostocinulea. The last three are closely related (Press, 1982; Ryding, 1994) and probably form a clade, but the position of this clade relative to subtribes Lamiinae and Pogostemoninae is unclear.
* Genera of Lamiaceae that cannot be assigned with confidence to a subfamily: Achyro, Adela, Callicarpa, Chileothes, Cornutia, Cryphia, Cyanostegia, Cymaria, Dicrastylis, Gerriella, Hemidra, Hemigenia, Hemiphora, Hololea, Hymenopogonites, Lachnostachys, Mallophora, Microcyclus, Neompinia, Newcastellia, Pararites, Physopsis, Pityrodia, Prostanthera, Pseudocapridium, Tectona, Tsiamannia, Tsoongia, Viticoprema, Wenchengia, Wringaria, Wrixonia. Half of these are generally assigned to Chloanthoideae and Prostantherae, groups that were poorly represented in the cpDNA analysis (see Results).

Definitions of Taxon Names

The Appendix includes phylogenetic definitions (de Queiroz and Gauthier, 1990) for the names of all taxa in classification Y except those treated as genera in classification X. One might argue that such definitions should also be provided for the names of taxa traditionally classified as genera because the phylogenetic system of de Queiroz and Gauthier abandons all ranks above the species level. However, this is not possible here because (with very few exceptions) the monophyly of genera was not tested by the cladistic analyses upon which the classification was based.

The definitions are node based in most cases, but stem-based definitions are provided for Achyrosperma and Lamioideae to avoid having to cite in the defini-
TABLE 3. Phylogenetic classification of Lamiaceae following nomenclatural conventions of de Queiroz and Gauthier (1992) (=classification Y). Terminations of names do not imply rank. Six names have been defined unambiguously in the past by reference to cladograms (see Results). All other clades, except those traditionally classified as genera, are assigned names with a standard ending (-ina) (see Appendix for definitions). No redundant taxa are recognized. Lettering of clades corresponds to that in Table 1 and Figure 1.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Clade</th>
</tr>
</thead>
<tbody>
<tr>
<td>Labiatae (clade A)</td>
<td></td>
</tr>
<tr>
<td>Teucrioideae (clade E)</td>
<td></td>
</tr>
<tr>
<td>Clerodendrina (clade F)</td>
<td></td>
</tr>
<tr>
<td>Ajugina (clade G)</td>
<td></td>
</tr>
<tr>
<td>Caryopteridina (clade J)</td>
<td></td>
</tr>
<tr>
<td>Trichostematina (clade K)</td>
<td></td>
</tr>
<tr>
<td>Caryopteris divaricata</td>
<td></td>
</tr>
<tr>
<td>Caryopteris bicolor</td>
<td></td>
</tr>
<tr>
<td>Faradaya</td>
<td></td>
</tr>
<tr>
<td>Oxerina</td>
<td></td>
</tr>
<tr>
<td>Clerodendrum (clade L)</td>
<td></td>
</tr>
<tr>
<td>Ajuga</td>
<td></td>
</tr>
<tr>
<td>Teucrina (clade M)</td>
<td></td>
</tr>
<tr>
<td>Oncinocalycina (clade N)</td>
<td></td>
</tr>
<tr>
<td>Teucrium</td>
<td></td>
</tr>
<tr>
<td>Spartothenella</td>
<td></td>
</tr>
<tr>
<td>Cyclomina</td>
<td></td>
</tr>
<tr>
<td>Aegiphila, Amasonia, Anethystea, etc.</td>
<td></td>
</tr>
<tr>
<td>Premnina (clade P)</td>
<td></td>
</tr>
<tr>
<td>Lamina (clade Q)</td>
<td></td>
</tr>
<tr>
<td>Scutellariae (clade R)</td>
<td></td>
</tr>
<tr>
<td>Scutellarina (clade S)</td>
<td></td>
</tr>
<tr>
<td>Holmskioldia</td>
<td></td>
</tr>
<tr>
<td>Achyrospermina (clade T)</td>
<td></td>
</tr>
<tr>
<td>Lamioideae (clade U)</td>
<td></td>
</tr>
<tr>
<td>Pogostemonoideae (clade V)</td>
<td></td>
</tr>
<tr>
<td>Achyrospermum, Cranitome, etc.</td>
<td></td>
</tr>
<tr>
<td>Vittica (clade C)</td>
<td></td>
</tr>
<tr>
<td>Nepetoideae (clade B)</td>
<td></td>
</tr>
<tr>
<td>Symphoromatina</td>
<td></td>
</tr>
<tr>
<td>Acrymia, Adelosa, Callicarpa, etc.</td>
<td></td>
</tr>
</tbody>
</table>

* These three clades are recognized on the basis of external evidence and thus are not shown in Figure 1 (see Results).

* Tetracle is included within Clerodendrum based on outside evidence (see Results).

* 12 genera whose phylogenetic relationships within Teucrioideae are uncertain: Aegiphila, Amasonia, Anethystea, Glossocarya, Hosea, Huzleya, Karomia, Monochilus, Prunema, Petrocosutex, Ruhticeuris, Schnabelia.

* 6 genera whose phylogenetic relationships within Achyrospermina are uncertain: Achyrospermum, Cranitome, Eurysolex, Canthanthosphae, Leucosceptrum, Rostrinula.


tion a large number of probable members that have not been included in any cladistic analysis but that might occupy a basal position in the clade. The wording of both kinds of definitions is similar to that of Schander and Thollesson (1995). Thus, in a node-based definition, a taxon name is defined as the least inclusive clade that contains taxa A and B. In a stem-based definition, a taxon name is defined as the most inclusive clade that contains taxon A but not taxon C. This format is less cumbersome than the more widely used wording proposed by de Queiroz and Gauthier (1990) to denote the same clade.

An apomorphy-based definition was used for Symphoromatina. Apomorphy-based definitions are problematic and should generally be avoided because subsequent discovery of homoplasy in the delimiting character can lead to major changes in clade membership (Bryant, 1994; Schander and Thollesson, 1995). However, this problem is unlikely in the present case because of the complex nature of the synapomorphy. Alternatively, one could provide a node-based definition citing all three genera of Symphoromatina, but there would be no reference phylogeny (as recommended by Bryant, 1996) because the monophyly of the group has never been tested in a cladistic analysis. A stem-based definition is not advisable because the sister-group hypothesis for Symphoromatina (represented in Fig. 1 by Congea tomentosa) is poorly supported.

Bryant (1996) pointed out various sources of ambiguity in phylogenetic definitions and recommended ways to avoid them. One concern is that the taxon names cited in definitions be unambiguous because the meaning of the defined name depends on the meanings of the names included in the definition. If a taxon name cited in the definition of a more inclusive group is not itself clearly defined, the name of the more inclusive group will be ambiguous as well. For this reason, only species are cited in the definitions of higher taxa in the Appendix (one of two options suggested by Bryant). It was necessary to cite two species of Karomia in the
definition of Teucrioideae because this genus may be polyphyletic. Bryant (1996) also recommended that a reference phylogeny be specified. The primary reference phylogeny for the names defined in the Appendix is shown in Figure 1, but some of the species cited in the definitions are included on the basis of other cladograms (Cantino, 1992 [Labiatae, Teucrioideae, Teucrina, Scutellarina]; Wagstaff et al., 1995 [Nepetoideae]). The reference phylogeny for Faradayina and Oxerina is figure 1 of Steane et al. (1997).

The species cited in the node-based definitions were chosen to minimize the likelihood that taxon membership will change in the future; i.e., an effort was made to cite representatives of all genera that lie at or near the base of the clade in this or other studies unless there was a reasonable doubt that the genus belongs in the clade at all. Whenever possible, we cited species that were used in the cpDNA analysis, which was the primary basis for this classification (Fig. 1). When it was necessary to cite representatives of genera that were not included in that study, priority was given to species that were included in other cladistic analyses or that were represented by DNA samples likely to be included in future analyses.

Genera Omitted from the Analyses

Classification of the many genera of Lamiaceae that have not been included in cladistic analyses presented a challenge because of the absence of a reference phylogeny (Bryant, 1996). Of the approximately 260 genera in the family (Cantino et al., 1992), only 31 were included in the cpDNA data set and 77 were included in the non-nucleotide data set. Fortunately, most of the omitted genera are provisionally referable to infrafamilial clades based on morphological and phytochemical synapomorphies. For example, only 5 of the approximately 130 genera of subfamily Nepetoideae (clade B) were included in the cpDNA study; but membership in this clade is easily diagnosed by the presence of hexacolpate three-celled pollen, an investing embryo, myxocarp, and rosmarinic acid (Cantino and Sanders, 1986; Cantino, 1992; Ryding, 1992). Similarly, membership in clade E, which corresponds closely to clade B of Cantino (1992), is diagnosed by a distinctive pollen exine structure with branched to granular cololete (Abu-Asab and Cantino, 1992, 1993; Cantino, 1992).

Although it might be argued that this apomorphy-based approach is inconsistent with our use of node-based definitions for the names of these two clades, we used synapomorphies here not to define taxon names but, rather, to permit provisional placement of genera that have not been included in a phylogenetic analysis. That is, characters were used to diagnose taxa, not to define them (de Queiroz and Gauthier, 1990). Because a taxon with a node-based name is less inclusive than its apomorphy-based counterpart (de Queiroz and Gauthier, 1990), there is a risk that some genera referred to a clade on the basis of synapomorphies may actually fall outside the node-based taxon. However, the likelihood of this occurring is reduced by our having cited representatives of many genera in our node-based definitions of these two taxon names (Nepetoideae and Teucrioideae; Appendix), including all genera that we believe lie near the base of the clade.

The approximately 50 genera of clade U (Lamiioideae sensu Cantino et al., 1992) are more problematic because the synapomorphies are cryptic characters that have been examined in relatively few genera (embryosac shape and laballenic acid in the seed oils; Hagemann et al., 1967; Wunderlich, 1967; Abu-Asab and Cantino, 1987; Rudall and Clark, 1992). The provisional referral of all of Bentham's (1876) Prasiaceae and most of Bentham's Lamieae to this clade by Cantino et al. (1992) and here was based on the assumption that Bentham's understanding of relationships in the group was correct, i.e., that the genera of Lamieae and Prasiaceae that have not yet been examined with respect to these characters are indeed closely related to those that have been examined. Because there is a distinct possibility that some genera have been incorrectly referred to clade U in this way, whereas its broader relationships can
be inferred with confidence from Figure 1, we applied a stem-based definition to its name (Lamioideae; Appendix). This definition refers only to taxa that belong to clade U or its sister group in the reference phylogeny (Fig. 1), and the name is therefore likely to be more stable than one with a node-based definition that includes taxa provisionally referred to the clade based on weak evidence. The use of a stem-based definition for Lamioideae runs contrary to the recommendation (de Queiroz and Gauthier, 1992; Bryant, 1996) that widely used names be restricted to crown clades, but this convention would reduce stability in the present case.

Orphan Genera

After referring genera to clades B, E, and U, 32 genera remained (orphan genera) that could not be placed with confidence in any clade less inclusive than Lamiaceae. Figure 1 shows possible phylogenetic positions for three of them (Callicarpa, Prostanthera, and Tectona), but the bootstrap support was too low to refer them to a clade on this basis. The other 29 orphan genera were not included in this cpDNA analysis nor in any other study in which clade support was assessed through bootstrapping or decay analysis. Half of the orphan genera are Australian, and Cantino’s (1992) analysis of nonmolecular data suggested that they fall into two clades (widely called Prostanthraceae and Chloanthoideae), which may be sister groups; these two taxa were provisionally merged under the name Chloanthoideae (s.l.) by Cantino et al. (1992). However, the support for these clades was not sufficient to recognize them here for two reasons: (1) the nonmolecular analysis included no measure of clade support other than number of character changes, and (2) three of the eight equally most-parsimonious rooting points for the unrooted consensus tree (Lundberg rooting) fall within or at the base of Chloanthoideae (s.l.). Molecular studies currently in progress should clarify the relationships of these Australian genera.

If one were to adhere strictly to the principle of exhaustive subsidiary taxa, each of the 32 orphan genera would have to be assigned to a monotypic subfamily in classification X. However, a very large number of redundant names would result. Alternatively, supraspecific taxa may be designated incertae sedis under the traditional system (Wiley, 1979), which is the approach we adopted in classification X. No such convention was needed in classification Y. The orphan genera were not referred to any clade less inclusive than Labiatae, which is permissible in the phylogenetic system.

Similarly, 21 orphan genera were designated incertae sedis in classification X because they could not be referred with confidence to a supertribe or subtribe. Two of them are undescribed genera based on species of Caryopteris that are left without a genus because the type species of the paraphyletic Caryopteris belongs to a clade (K; Fig. 1) that excludes these two species. New genera will have to be described to accommodate these species, because the binominal system does not permit one to designate a species incertae sedis with regard to genus. In classification Y, these 19 genera and two species were not referred to any taxon at a hierarchical level for which phylogenetic evidence was insufficient to do so. For example, Spartothammella (incertae sedis at the subtribe rank in classification X) was included within Teucrinae in classification Y but was not referred to any less inclusive clade. Similarly, Caryopteris disticarica and C. bicolor were included within Caryopteridina but not in any less inclusive supraspecific taxon. In contrast, C. incana was included within a less inclusive taxon (Trichostematina) because Figure 1 provides the evidence to do so.

Discussion

The proposed alternative to our traditional system has been called a phylogenetic system of nomenclature (de Queiroz and Gauthier, 1994), although it is part of a more general phylogenetic approach to taxonomy (Hennig, 1966; de Queiroz and Gauthier, 1992), a distinction discussed by de Queiroz (1997). Although some of the issues discussed below extend beyond no-
menclature (e.g., efficiency of classifications), the term phylogenetic nomenclature is used throughout for simplicity.

Redundant Names

As noted by de Queiroz and Gauthier (1992), classifications employing traditional nomenclature often include monotypic taxa, i.e., taxa that are identical in content to the single included taxon at the next lower rank, thus their names are redundant. Such names add no information to a classification. The inclusion of many monotypic taxa creates a cumbersome and inefficient classification. How do the two classifications of Lamiaceae compare in this regard?

Under the phylogenetic system (Table 3), a single name is applied to each clade, thus there is no redundancy. When traditional nomenclature is used, 5 of the 25 suprageneric taxon names (20%) are redundant (boldface, Table 2). These five monotypic taxa must be included when following the principle of exhaustive subsidiary taxa to accommodate genera that are left over when, for example, the rest of their tribe is referred to a subtribe. The frequency of this situation depends on the topology of the cladogram upon which the classification is based. The more asymmetrical (comblike) the topology, the more monotypic taxa are required if all clades are named; as the number of taxa in a maximally asymmetrical cladogram becomes larger, the proportion of monotypic taxa approaches 50% (there may be fewer monotypic taxa if some clades are not named). In contrast, a perfectly symmetrical topology in which every clade contains two subsidiary clades would yield a classification with no monotypic taxa.

Monotypic taxa might be included in the traditional system for another reason, to accommodate taxa of uncertain relationships. If one were to apply the principle of exhaustive subsidiary taxa but reject the incertae sedis convention, an additional 53 monotypic taxa would be needed to accommodate the orphan genera in Table 2, producing a cumbersome classification with 74% of the suprageneric taxa (58 of 78) redundant.

In the phylogenetic system of nomenclature (de Queiroz and Gauthier, 1992), the principle of exhaustive subsidiary taxa is not employed, and there are no mandatory ranks above species. A taxon whose affinities are unclear at a given level in the hierarchy does not have to be referred to any clade at that level. Neither a monotypic taxon nor the incertae sedis convention is needed. For example, in Table 3 Callicarpa is a member of Labiatae but is not referred to any less inclusive clade because there is insufficient evidence to do so. The same approach is used at other levels in the hierarchy. Aegiphila is a member of Teucrioideae but is not referred to any less inclusive clade. Holmskioldia is not referred to any less inclusive taxon within Scutellarioideae for a different reason; it is the only genus of Scutellarioideae outside of the clade Scutellariina. There is no redundancy in this classification because every taxon name represents a different clade.

Proliferation of Ranks

As knowledge of phylogenetic relationships improves, there is a corresponding increase in the number of hierarchical levels needed to reflect phylogeny (Wiley, 1979; de Queiroz and Gauthier, 1992). Thus, four ranks are needed between subfamily and genus within Ajugoideae (Table 2), where the phylogeny is relatively well resolved, versus only two ranks within the much larger subfamily Lamioideae, where the phylogeny is poorly known. Although the ICBN does not limit the number of ranks, the fact that the categories themselves (not just the taxa) must have names creates a problem. Intercalation of the many invented ranks required to reflect the well-resolved phylogeny of a large group would lead to a humorously cumbersome classification. (The supersubtribes in Figure 2 are bad enough. Do we really want supersupersubtribes?) This problem does not exist in phylogenetic nomenclature because the hierarchical levels do not require names.

The phyletic sequencing convention
(Nelson, 1972; Wiley, 1979) is one way to circumvent this problem within the traditional system when dealing with an asymmetrical cladogram. However, when this convention is employed, many clades are left unnamed. For example, one could reduce the number of ranks within clade E (Fig. 1; Table 2) via the sequencing convention by treating the following as a sequence of tribes: Cyclonema (as a monotypic tribe), clade M, clade L, Ajuga (as a monotypic tribe), and clade J. However, clades E, G, and H would lack names in this system. Although this is not a serious problem in this example, it would be undesirable if an unnamed clade happened to be distinctive or economically important and thus needed a name to facilitate communication.

Nomenclatural Clarity

De Queiroz and Gauthier (1994) pointed out that biological nomenclature should be explicit, universal, and stable if it is to serve its function of communication, and they argued that our traditional nomenclatural system "promotes neither explicitness, universality nor stability with regard to the phylogenetic meanings of taxon names" (1994:28). A comparison of the two systems as applied to the Lamiaceae reveals a number of examples that support this contention.

Taxon names in the phylogenetic system (Table 3) are explicitly tied to clades through their definitions (Appendix). (This approach has rarely been taken in botanical papers, but Judd et al. [1993, 1994] provided such definitions for several plant family names; Doyle and Donoghue [1993] explicitly tied the name "angiosperms" to a crown group but without a formal node-based definition.) When traditional nomenclature is applied to the same set of clades (Table 2), the type method is used to select the correct name at the rank at which the clade happens to be recognized. This approach leads to both instability and nonuniversality.

Instability and nonuniversality of names can have a number of causes, including change of rank, new evidence aboutphylogeny, and discovery of an older name. A change in rank is a problem only under the traditional system, but the other two causes can create nomenclatural instability under either system. Discovery of older names is a potential source of instability in any system that involves priority. Under the traditional nomenclatural system, application of priority within rank may lead to a name change if an earlier legitimate name is discovered in the literature, although recent modifications of the ICBN (the 1994 Tokyo Code) encourage conservation of names as an alternative. In the proposed phylogenetic system of nomenclature, where priority operates within a clade instead of within a rank, a comparable problem might arise through the discovery of an older name explicitly tied to a clade. However, because the system is new, rules could be instituted to avoid this problem, e.g., by requiring that all names in the phylogenetic system be registered.

Nomenclatural instability due to change in rank is a problem unique to the traditional system, where the transfer of a clade to a different rank necessitates a name change. A rank may change because one wishes to recognize a more inclusive clade for the first time. For example, the clade to which Cantino et al. (1992) applied the name Scutellarioideae (clade R) must be renamed Scutellarieae in Table 2 because a newly recognized, more inclusive clade (Q) has been added to the classification at the subfamily level. Both instability and nonuniversality result. This problem does not occur in the phylogenetic system because names are not tied to a rank. Once a clade is named, it retains that name regardless of its position in the hierarchy.

The most frequent cause of nomenclatural instability in phylogenetic systematics is new evidence about phylogeny. If classification is to remain current, it must change as knowledge of phylogeny improves. However, under the traditional system a classificatory change frequently alters the nomenclature as well. For example, the name Viticoideae in Table 2 refers to a different group than does Viticoideae sensu Briquet (1895). In both classifications, this name is applied to a
taxon of subfamilial rank that includes *Vi
tex*, in accordance with the ICBN (there is no older subfamilial name based on an in-
cluded genus), but Viticeoidae sensu Bri-
quet is paraphyletic and far more inclusive
than the clade called Viticeoidae here. Vi-
ticeoidae sensu Cantino et al. (1992) is yet
another grouping, intermediate in inclusi-
siveness between the other two with the
same name, which may or may not be monophyletic. (Figure 2 suggests that this
group is paraphyletic, but the bootstrap
support for this hypothesis is low.)

The inherent instability of the traditional
system of nomenclature is particularly ev-
dent in situations in which new evidence
about the relationships of a single genus
can change the name of a higher taxon. A
good example concerns *Ajuga*. Cantino et
al. (1992) applied the name Teurcioideae to
a hypothesized clade that comprised 23
genera and excluded *Ajuga*. *Ajuga* and a
few other genera were grouped together as
Ajugoideae in that classification. The cpDNA study (Fig. 1) supports the mono-
phyly of Teurcioideae sensu Cantino et al.
(1992) but indicates that *Ajuga* belongs
within the group. Under the traditional
rules, the transfer of this single genus re-
quires that the subfamily be renamed Aju-
goideae, an older name than Teurcioideae.
Both nomenclatural instability and non-
universality result. The name Ajugoideae
has been applied to at least three different
groupings in the past (Briquet, 1895–1897;
Wunderlich, 1967; Cantino et al., 1992).
Under the traditional system, this phenom-
eron will create instability whenever an
old name is based on a nomenclatural type
of uncertain phylogenetic position. Under
the phylogenetic system of nomenclature,
the problem disappears. The clade that
was called Teurcioideae by Cantino et al.
(1992) is still the same clade regardless of
whether a single genus of uncertain affini-
ties is included or excluded. It therefore
retains the name Teurcioideae in Table 3.

Infrafamilial taxon names based on the
type of the family are particularly unstable
because of their automatic priority. Ac-
cording to the 1994 ICBN (Article 19.4), the
name of any subdivision of a family that
includes the type of the family name must
be based on the generic name of the type.
Thus, every infrafamilial grouping at a
particular rank that happens to include the
type of the family must have the same
name. Over the course of many years and
changing understanding of relationships,
it is inevitable that such names will be ap-
plied to many different groupings, leading
to nomenclatural instability and nonuni-
versality. In the present case, every sub-
family-level taxon that contains *Lamium*
must be called Lamioideae. Not surpris-
ingly, this name has been applied to many
groupings. Indeed, this rule has forced one
of us (PDC) to apply the name Lamioi-
deae three different ways in the course of
a decade (Cantino and Sanders, 1986; Can-
tino et al., 1992; the present study, Table
2)! Under the phylogenetic system, this
problem does not exist. In Table 3, the
name Lamioideae is applied to the only
clade that has been explicitly associated
with this name in the past (by annotation of a cladogram; Wagstaff et al., 1995).

Although we have emphasized the prob-
lems of the traditional system of nomen-
clature, the phylogenetic system also can
lead to confusion if names are not defined
with care. A name that has been given a
phylogenetic definition is permanently tied
to a clade, but the hypothesized member-
ship of the clade may change greatly with
new evidence about relationships (de Queiroz and Gauthier, 1990; Schander and
Thollesson, 1995; Bryant, 1996). This lack
of stability is problematic for many users
of classifications, for whom the meaning of
a taxon name is associated at least in part
with its membership and not solely with
its phylogenetic definition.

The extent to which this instability may
cause confusion depends on the degree to
which the membership changes. Minor
changes, such as the inclusion or exclusion
of *Ajuga* from Teurcioideae, are not a
problem because the overall membership of
the clade is little altered. However, a node-
based definition that includes genera of
uncertain affinity may lead subsequently
to very large changes in the membership
of the clade as understanding of relation-
ships changes. For example, the genus *Tetrachondra* has been placed in the Lamiaceae by some authors (Cronquist, 1981; Takhtajan, 1986) based on its gynoecial morphology, but an analysis of sequence data from the rbcL gene (Wagstaff and Olmstead, 1997) suggested that it is the basal genus of Lamiales sensu Olmstead et al. (1993). If, in ignorance of the molecular data, one were to include *Tetrachondra* in a node-based definition of the Lamiaceae (e.g., the most recent common ancestor of *Lamiium* and *Tetrachondra* and all of its descendants), Lamiales would come to include the entire order Lamiales if the position of *Tetrachondra* based on rbcL sequences were subsequently accepted. One may argue that there is no instability here because the name Lamiaceae applies to the same clade regardless of changing ideas about membership, but the meaning of the name Lamiaceae would change greatly for many users, and in that sense the name would be unstable.

The frequency and magnitude of changes in the membership of a clade can be minimized through careful choice of taxa employed in node-based definitions. We make or endorse the following recommendations in this regard.

1. A group should be formally named, and the name given a phylogenetic definition, only if there is substantial evidence that it is a clade. This recommendation goes beyond that of Bryant (1996), that all named clades be identified through phylogenetic analysis, because many nodes on a cladogram may be too poorly supported to warrant naming. Standard measures of support (e.g., bootstrap or decay values) can be used to assess which groups should be named. Reasonable people may disagree about what constitutes substantial evidence, but as a minimal guideline, we suggest that the appearance of a grouping on a single cladogram with a bootstrap value <50% is not sufficient basis to name it; 70% may be a more reasonable cutoff if only a single cladogram is available. The criteria used here provide an example of the thought process that should go into decisions of this sort. Irresponsible naming of poorly supported groups will create confusion through proliferation of phylogenetic synonyms (i.e., different names referring to the same clade; de Queiroz and Gauthier, 1992), which can occur in spite of explicit phylogenetic definitions of taxon names because different definitions may refer to the same clade (de Queiroz and Gauthier, 1990).

2. When selecting taxa to cite in a node-based definition, one should avoid taxa whose membership in the clade is questionable (Schander and Thollesson, 1995). The example involving *Tetrachondra* illustrates how poor judgment in preparing a node-based definition may lead to subsequent large changes in our understanding of clade membership.

3. In a node-based definition, one should cite all taxa that are likely to be basal (or species representing them) to avoid defining a less inclusive clade than intended (hence the lengthy definitions of some of the taxon names in the Appendix). When there are relatively few subsidiary taxa, it is worth representing all of them in the definition, provided that doing so does not violate recommendation 2. This recommendation is trivial if the phylogeny is fully resolved, and one elects to name every clade, because each taxon will contain only two subsidiary taxa, but a taxon may have more subsidiary taxa because of poor resolution or because one chooses not to name every clade.

Recommendations 2 and 3 may conflict, i.e., a taxon may be thought to be either the basal member of a clade or to lie far outside it, based on different evidence. This situation creates a dilemma. If the taxon is omitted from the node-based definition, one runs the risk of assigning a name to a less inclusive clade than intended. However, inclusion of the taxon in the definition may result in naming a larger clade than intended, perhaps much larger if it turns out that the taxon is only distantly
related to the clade being named. Incorrect inclusion would be undesirable because the membership of the clade (and thus the meaning of the taxon name to many users) would change greatly.

One possible solution to this dilemma is to include a contingency clause in the definition of the name, as suggested by K. de Queiroz and M. Donoghue (pers. comm.). As an example, Donoghue defined the name Paradoxa as the most recent common ancestor of Adoxa, Tetradoxa, and Sinodoxa, and all of its descendants if Sinodoxa is more closely related to Adoxa and/or Tetradoxa than it is to anything else. It is not clear, however, what the status of such a name should be if the contingency turns out to be untrue. If, for example, the sister group of Sinodoxa turns out to be something other than Adoxa or Tetradoxa, should the name be invalidated or should its definition automatically change to exclude Sinodoxa? An adaptive definition (Schander and Thollesson, 1995) solves this problem by specifying how the definition is to be emended if a contingency proves untrue. Thus, Paradoxa could be defined as either the most recent common ancestor of Adoxa, Tetradoxa, and Sinodoxa and all of its descendants, if Sinodoxa is more closely related to Adoxa and/or Tetradoxa than it is to anything else, or, if the sister group of Sinodoxa is not Adoxa and/or Tetradoxa, the most recent common ancestor of Adoxa and Tetradoxa and all of its descendants. Although cumbersome, such a definition is explicit and restricts clade membership to the taxa the author intended to include.

Alternatively, the dilemma posed by a conflict between recommendations 2 and 3 could be avoided by providing taxon names with recommended usages (Bryant, 1996). For example, the name Paradoxa could be restricted to a phylogenetic hypothesis in which Adoxa, Tetradoxa, and Sinodoxa form a clade exclusive of all other species. The two approaches differ in outcome if the contingency proves false. If Sinodoxa turned out not to be closely related, the adaptive definition would retain the name Paradoxa for the rest of the clade envisioned by the author, whereas a name tied to a recommended usage would be abandoned if the phylogenetic hypothesis upon which it was based proved false.

A third alternative is to use a stem-based definition in this situation, as was done with Lamioidae. If the sister group of a clade can be hypothesized with greater confidence than its basal members, a stem-based name is likely to be more stable than a node-based one. In this situation, it may be preferable not to follow the recommendation (de Queiroz and Gauthier, 1992; Bryant, 1996) that widely known names be given node-based definitions. However, one may prefer to reserve the stem-based name to accommodate extinct outgroups of the extant clade. This is not a serious concern in the present case because the fossil record of Lamiaceae is very poor.

**Referral of Newly Studied Species to Previously Named Clades**

One aspect of the phylogenetic system that has not been addressed is the classification of newly studied species. A stem-based or node-based definition specifies the relationships that a species must have to be considered a member of the named taxon, but the only direct way to determine whether a species has these relationships is to include it in a cladistic analysis. It is not realistic to expect that this be done with every newly studied species before it can be classified.

In the phylogenetic system, as in traditional taxonomy, new species are referred to previously named taxa by means of characters. Characters do not define taxa in the phylogenetic system but they may be used to diagnose them (de Queiroz and Gauthier, 1990). Although node-based and stem-based definitions do not refer to characters, species may be referred provisionally to a named taxon on the basis of synapomorphies. Some errors may occur because of homoplasy or because a synapomorphy possessed by a newly studied species arose below the base of a taxon with a node-based name. However, the un-acceptable alternative is to refrain from classifying the vast number of species that
have never been included in any cladistic analysis.

So that newly studied species can be referable to previously named taxa in the phylogenetic system, we recommend that definitions of names be accompanied by a list of synapomorphies and a statement of clade membership (see the Appendix for examples). This supplementary information is not part of the definition but is essential to users (e.g., the authors of floras and faunas) who must classify species that were not included in the reference phylogeny.

Prospects for the Future

This case study provides examples of the confusion that can result when the traditional system of nomenclature is employed in a phylogenetic context. If one accepts the premise that supraspecific taxa should be clades, the phylogenetic system of nomenclature proposed by de Queiroz and Gauthier (1990, 1992, 1994) appears to provide more stable names and more efficient classifications than does the traditional system.

Although we find the advantages of phylogenetic nomenclature compelling, we must continue to operate within the traditional rules until they are modified or until a comprehensive alternative code is developed. However, there are elements of the phylogenetic system that can be adopted within the confines of the existing codes. One such step is abandonment of the principle of exhaustive subsidiary taxa because it involves a convention that is not a formal rule in any of the current codes of nomenclature (de Queiroz and Gauthier, 1992). Monotypic taxa add no information to a classification, and we agree with de Queiroz and Gauthier that they should be avoided where possible. There is no good reason why, for example, the recognition of some subfamilies within a family should necessitate referring every genus to a subfamily. Without violating the ICBN, genera may be left “loose” in the family if their relationships are uncertain or if they are left over as a single-genus clade when all other genera have been grouped into subfamilies.

More generally, we recommend referring a taxon to a higher level taxon only when there is adequate evidence that it belongs to that clade. In botany, this is possible above the genus level but not at or below it. In the binomial system of nomenclature, the genus is a mandatory category. Furthermore, although the principle of exhaustive subsidiary taxa is not formalized in the ICBN, it is indirectly mandated below the genus level by Article 22.3. When one publishes the name of a subdivision of a genus that does not contain the type of the genus, a name at the same rank based on the type (i.e., an autonym) is automatically established. This rule is particularly incongruent with the goals of phylogenetic systematics because it may automatically establish paraphyletic groupings. Fortunately, an equivalent rule in previous editions of the ICBN, which established autonyms within families, was eliminated in the 1994 Tokyo Code.

There is a precedent in the traditional system for declining to refer a taxon to a higher level taxon because of inadequate evidence. The ICBN (Article 3.3) states that genera of fossil plants may not be assignable to a family because of the fragmentary nature of the specimens, although they may be referable to a taxon of higher rank. This situation is analogous to the inability to refer a taxon to a more inclusive one because of inadequate phylogenetic evidence.

We recommend that explicit phylogenetic definitions (e.g., see the Appendix) be provided for supraspecific taxon names whenever phylogenetic hypotheses are translated into classifications. These definitions have no status under our current rules, but they help to clarify the phylogenetic meaning of taxon names. Moreover, if a phylogenetic system of nomenclature is adopted in the future, priority may be extended back to include explicitly defined names already published.

We hope that the systematics community will not be daunted by the prospect of major changes in our rules of nomenclature.
ture. We are not urging blind acceptance of the system that de Queiroz and Gau-
thier have proposed. On the contrary, we should evaluate its applicability to a wide
variety of groups. But if, after doing so, it is clear that the phylogenetic system is not
only logically appealing but also improves the clarity and stability of our classifica-
tions (as it seems to in the Lamiaceae), then we must be willing to make the rad-
cial changes that are called for. The scient-
ific community depends on systematists
to produce classifications that are informa-
tive and stable. A realistic goal for the
current generation of systematists is a sin-
gle code for all organisms that will enable
the application of phylogenetic principles
to produce unambiguous, informative
classifications.

ACKNOWLEDGMENTS

We are grateful to K. de Queiroz, W. Judd, and two
anonymous reviewers for their constructive comments
on earlier drafts of the manuscript. Discussions with
O. Ryding were very helpful in clarifying our under-
standing of relationships within Lamioideae. The data
sets used in this paper were generated with the sup-
port of NSF grants to P.D.C. (BSR-9006209) and R.G.O.
(BSR-9107827) and an Ohio University Baker Fund Award (88-10) to P.D.C.

REFERENCES

ABU-ASAB, M., AND P. D. CANTINO. 1987. Phylo-
genetic implications of leaf anatomy in subtribe Melit-
tidinae (Labiatae) and related taxa. J. Arnold Arbor.
Harv. Univ. 68:1–34.
ABU-ASAB, M., AND P. D. CANTINO. 1992. Pollen mor-
phology in subfamily Lamioideae (Labiatae) and its
phylogenetic implications. Pages 97–112 in Advar-
ce in labiate science (R. M. Harley and T. Reynolds,
ABU-ASAB, M., AND P. D. CANTINO. 1993. Phylo-
genetic implications of pollen morphology in tribe
BENTHAM, G. 1876. Labiatae. Pages 1160–1223 in Gen-
era plantarum, Volume 2 (G. Bentham and J. D.
BRIQUET, J. 1895. Verbenaceae. Pages 132–182 in Die
natürlichen Pflanzenfamilien, Teil 4, Abt. 3a (A. En-
BRIQUET, J. 1895–1897. Labiatae. Pages 383–375 in Die
natürlichen Pflanzenfamilien, Teil 4, Abt. 3a (A. En-
BRYANT, H. N. 1994. Comments on the phylogenetic
definition of taxon names and conventions regard-
ing the naming of crown clades. Syst. Biol. 43:124–
130.
BRYANT, H. N. 1996. Explicitness, stability, and uni-
versality in the phylogenetic definition and usage
of taxon names: A case study of the phylogenetic
CANTINO, P. D. 1992. Evidence for a polyphyletic or-
379.
CANTINO, P. D., R. M. HARLEY, AND S. J. WAGSTAFF.
Pages 511–522 in Advances in labiate science (R. M.
Harley and T. Reynolds, eds.). Royal Botanic Gar-
dens, Kew, England.
CRONQUIST, A. 1981. An integrated system of classifi-
cation of flowering plants. Columbia Univ. Press,
New York.
DE QUEIROZ, K. 1997. The Linnaean hierarchy and the
evolutionization of taxonomy, with emphasis on the
problem of nomenclature. Also 15 (in press).
DE QUEIROZ, K., AND J. GAUTHIER. 1990. Phylogeny
as a central principle in taxonomy: Phylogenetic de-
DE QUEIROZ, K., AND J. GAUTHIER. 1994. Toward a
phylogenetic system of biological nomenclature.
and angiosperm diversification. Paleobiology 19:
141–167.
237–250.
GREUTER, W., F. R. BARRIE, H. M. BURDET, W. G. CHAL-
oner, V. DEMOULIN, D. L. HAWKSWORTH, P. M. JØR-
gensen, D. H. NICOLSON, P. C. SILVA, P. TRELHANE,
AND J. MCNEILL. 1994. International code of botan-
cal nomenclature (Tokyo Code). Koeltz, Königstein,
Germany.
Search for new industrial oils. XIV. Seed oils of La-
HENNING, W. 1966. Phylogenetic systematics. Univ. Il-
ninois Press, Urbana.
JUDD, W. S., R. W. SANDERS, AND M. J. DONOHOUE.
1994. Angiosperm family pairs: Preliminary phy-
Phylogenetic position of Apostasia and Newwiedia
JUNELL, S. 1934. Zur Gynäecemorphologie und
Systematik der Verbenaceen und Labien. Symb.
LUNDBERG, J. G. 1972. Wagner networks and ances-
NELSON, G. J. 1972. Phylogenetic relationship and clas-
OLMSTEAD, R. G., B. BREMER, K. M. SCOTT, AND J. D.
PALMER. 1993. A parsimony analysis of the Aster-


Received 24 April 1996; accepted 15 January 1997

Associate Editor: John Wiens

APPENDIX

DEFINITIONS OF TAXON NAMES

The following definitions are node based in most cases. Stem-based definitions are provided for Achyrospermin and Lamioideae, and an apomorphy-based definition is used for Sympomoretina. The wording of node-based and stem-based definitions is adopted from Schander and Thollesson (1995). The primary reference phylogeny (Bryant, 1996) is shown in Figure 1, but some of the taxa cited in the definitions are included on the basis of other cladograms.

The supplementary information on membership and synapomorphies is not part of the definition. Names are arranged as in Table 3. Lettered clades are identified in Figure 1.


Clerodendrina (clade F).—The least inclusive clade that contains Caryopteris incana, Clerodendron chinense, and Teucrium fruticans. Membership: Ajuga, Caryopteris, Clerodendron (including Tetracea), Faradaga, Oncocalyx, Oxera, Spartothammella, Teuridium, Teucrium, and Trichostema.

Ajugina (clade G).—The least inclusive clade that contains Caryopteris incana, Clerodendron chinense, and Ajuga reptans. Membership: Ajuga, Caryopteris, Clerodendron (including Tetracea), Faradaga, Oxera, and Tri chostema.

Caryopteridina (clade J).—The least inclusive clade that contains Trichostema dichotomum, Caryopteris incana, Caryopteris dactylicata, and Caryopteris bicolor. Membership: Caryopteris and Trichostema.


Faradagynina.—The least inclusive clade that contains Faradaga splendida and Clerodendron chinense. Membership: Clerodendrum (including Tetracea), Faradaga, and Oxera.

Oxerina.—The least inclusive clade that contains Oxera macrocalyx and Faradaga splendida. Membership: Faradaga and Oxera.


Oncocalycina (clade N).—The least inclusive clade that contains Oncocalyx betchei and Teuridium parvifolium. Membership: Oncocalyx and Teuridium.

Premminis (clade P).—The least inclusive clade that contains Premna microphylla and Gmelina philippensis. Membership: Gmelina and Premna.

Lamini (clade Q).—The least inclusive clade that

**Scutellarioideae (clade R).**—The least inclusive clade that contains *Scutellaria bolanderi* and *Holmskioldia sanguinea*. Synapomorphies: surface of fruit with tuberculate or elongate hairlike outgrowths; calyx lobes rounded. Membership: *Holmskioldia*, *Renschia*, *Scutellaria*, and *Tinnea*.

**Scutellariina (clade S).**—The least inclusive clade that contains *Scutellaria bolanderi*, *Renschia heterotypica*, and *Tinnea zambesiaca*. Synapomorphies: calyx two lipped, the lips entire, their margins becoming appressed after fertilization to enclose the nutlets; anther suture ciliate. Membership: *Renschia*, *Scutellaria*, and *Tinnea*.

**Achyrorperminia (clade T).**—The most inclusive clade that contains *Lamium purpureum* and *Pogostemon cablin* but not *Scutellaria bolanderi*. Synapomorphy: gynobasic style. Membership: genera referred to Lamioideae and Pogostemonoideae plus *Achyrorperminia*, *Comanchephace*, *Craniotome*, *Euryrobin*, *Leucocephala*, and *Rosinucula*.

**Lamiioideae (clade U).**—The most inclusive clade that contains *Lamium purpureum*, *Prasium major*, and *Physostegia virginiana* but not *Pogostemon cablin*. Synapomorphies: seed oil contains an allenic component (probably laballenic acid; Hagemann et al., 1967); embryo sac with micropylar lobe both longer and broader than the chalazal lobe (Wunderlich, 1967; Rudall and Clark, 1992). Membership: *Ballota*, *Brazoria*, *Cheilanthopsis*, *Colquhounia*, *Eremostachys*, *Galeopsis*, *Lamium*, *Leonotis*, *Leonurus*, *Leucas*, *Marrubium*, *Melittis*, *Molucella*, *Otostegia*, *Phlomis*, *Physostegia*, *Prasium*, *Sideritis*, *Stachys*, and *Wiedemannia*. Less certain members are all other genera assigned to Lamioideae by Cantino et al. (1992) except *Achyrorperminia*, *Craniotome*, and *Euryrobin*.

**Pogostemonoideae (clade V).**—The least inclusive clade that contains *Pogostemon cablin* and *Colebrookea oppositifolia*. Membership: *Anisomeles*, *Colebrookea*, and *Pogostemon*.

**Viticina (clade C).**—The least inclusive clade that contains *Vitis aegus-castus* and *Petitia domingensis*. Membership: *Petitia* and *Vitex*.

**Nepetoideae (clade B).**—The least inclusive clade that contains *Collinsonia canadensis*, *Lavandula multifida*, *Melissa officinalis*, *Mentha rotundifolia*, *Nepeta cataria*, *Plectranthus barbatus*, *Prunella vulgaris*, *Salvia officinalis*, and *Tetradenia riparia*. Synapomorphies: hexacolpate tricellular pollen; investing embryo; rosmarinic acid; myxocarp; gynobasic style; fruit a schizocarp (Cantino and Sanders, 1986; Cantino, 1992; Ryding, 1992). Membership: genera assigned to Nepetoideae by Cantino et al. (1992).

**Symphorematinina.**—the first member of Labiatae with a paniculiform inflorescence composed of cymes that are surrounded by an involucre of large and winglike bracts, and all of its descendants. Membership: *Consea*, *Sphenodesme*, and *Symphoremata*. 