

Caryopteris (Lamiaceae) and the Conflict Between Phylogenetic and Pragmatic Considerations in Botanical Nomenclature

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ABSTRACT. The delimitation of *Caryopteris* (Lamiaceae) exemplifies the conflict between the representation of monophyletic groups and pragmatic concerns in Linnaean classification. Cladistic analyses of nonmolecular (mainly morphological) data and chloroplast DNA (*rbcl* and *ndhF*) sequences were performed to test the monophyly of the eastern Asian genus *Caryopteris*. The results corroborate earlier studies indicating that *Caryopteris* is either para- or polyphyletic. If paraphyletic, other genera whose sister groups lie within the currently accepted limits of *Caryopteris* include *Trichostema*, *Rubiteucris*, and probably *Ajuga*, *Schnabelia*, and *Amethystea*. Because phylogenetic resolution is too poor to refer all of the species of *Caryopteris* to well supported clades, a choice must be made between recognizing a paraphyletic genus or several monotypic ones, three of which would comprise morphologically quite similar species. A compromise solution is adopted in which three new genera are described (*Pseudocaryopteris*, *Discretitheca*, and *Tripora*), the latter two monotypic, and four species of *Caryopteris* are transferred to other genera, one of which may not be monophyletic. Nine new combinations are provided: *Discretitheca nepalensis*, *Pseudocaryopteris bicolor*, *Pseudocaryopteris foetida*, *Pseudocaryopteris paniculata*, *Rubiteucris siccanea*, *Schnabelia aureoglandulosa*, *Schnabelia nepetifolia*, *Schnabelia terniflora*, and *Tripora divaricata*. For comparative purposes, an alternative classification is provided that employs de Queiroz and Gauthier's phylogenetic system of nomenclature. Using this system, no new names are required, and all supraspecific taxa are both monophyletic and easily recognizable.

For more than a decade, plant taxonomy has experienced a controversy over whether to accept paraphyletic groups in classification (e.g., Cronquist 1987; Donoghue and Cantino 1988; Brummitt 1997; Sosef 1997; Brummitt and Sosef 1998; Freudenstein 1998, Schander 1998; Welzen 1998). The opposing viewpoints, which are argued with heartfelt conviction by systematists on both sides, reflect a fundamental conflict between two imperatives of modern systematics, which we will call the phylogenetic and pragmatic imperatives.

The phylogenetic imperative dictates that all supraspecific taxa should be monophyletic (i.e., each should comprise a common ancestor and all of its descendants). This principle is central to the professional world view of many phylogenetic systematists. It stems (for us and, we suspect, for many others) from a deep conviction that formally named taxa, the most concrete products of the science of systematics, should be objective natural entities that are discovered rather than created. Monophyletic taxa qualify, as do species if they are con-

ceived of as segments of population level evolutionary lineages (de Queiroz, 1998), but paraphyletic and polyphyletic supraspecific taxa are subjective human constructs.

The pragmatic imperative, which is also a central maxim of many taxonomists (including many phylogenetic systematists), requires that named taxa be recognizable; that is, there should be a large enough phenetic gap between taxa so that they can be identified "by ordinary means" (Cronquist 1978). What constitutes "ordinary means" will vary for different groups of organisms, but we suspect that most people would agree that a taxon distinguished only on the basis of gene sequence variations is not a practical unit in a general-purpose classification. There also is an expectation that genera will be more easily distinguished (i.e., more divergent morphologically) than are species within the same family.

The arguments for and against the acceptance of paraphyletic taxa have emphasized theoretical issues, but the intensity of feeling generated by the controversy may stem largely from disagreement

whether phylogenetic or pragmatic concerns should have primacy. Phylogenetic systematists ("cladists") give primacy to monophyly, while "evolutionary taxonomists" sometimes give more weight to phenetic gaps, but we suspect that most members of both schools consider both recognizability of taxa and congruence with phylogeny to be desirable attributes for a classification to have. In comparisons of the two schools, it is sometimes stated that evolutionary taxonomists take phenetic gaps into consideration in constructing classifications, whereas cladists do not. This is an oversimplification. For cladists, recognizability (gap size) is a useful criterion when deciding which monophyletic groups warrant naming. However, a cladist would not give formal recognition to a clearly paraphyletic group even if it were separated from other taxa by a large gap, whereas an evolutionary taxonomist might well do so.

Until recently, the discussion about paraphyletic taxa has been carried out solely in the framework of our traditional ("Linnaean") system of nomenclature, as embodied in the ICBN and the equivalent zoological and bacteriological codes. Treating this system as a constant rather than a variable has forced systematists whose taxonomic decisions are guided by both the pragmatic and phylogenetic imperatives to choose between them when they are in conflict, without recognizing that the system itself could in part be responsible for their dilemma. The introduction of a new and fundamentally different phylogenetic system of nomenclature (de Queiroz and Gauthier 1992, 1994; de Queiroz 1996, 1997), which eliminates the conflict between the two imperatives in at least some situations (as demonstrated in this paper), may provide an alternative to choosing between them. Rejection of Linnaean nomenclature is a radical choice to be sure, but it should be acknowledged as a possibility.

Phylogenetic and pragmatic imperatives are not always in conflict, even under the current system. In some groups, there is a good correspondence between clades and easily recognizable taxa. But in other groups, species cannot be classified without accepting either paraphyletic taxa (counter to the phylogenetic imperative) or a set of marginally different monotypic genera (counter to the pragmatic imperative). In this paper, we will document an example of this kind of situation in the genus *Caryopteris* Bunge (Lamiaceae).

Caryopteris, as currently delimited, comprises 16 species of perennial herbs and shrubs of temperate and subtropical eastern Asia, most of them endemic to China. A horticultural hybrid, *C. x clandonensis*

A. Simmonds, is a widely grown ornamental, and several species are used medicinally in China (Chen and Gilbert 1994). The familial assignment of *Caryopteris* (Verbenaceae vs. Lamiaceae) and the history of its infrageneric classification are discussed by Abu-Asab et al. (1993). The most recent classification (Pei and Chen 1982) recognizes two sections: *Pseudocaryopteris* and *Caryopteris*.

Caryopteris exhibits an exceptional amount of variation in floral, fruit, and pollen morphology (Abu-Asab et al. 1993), including some characters that rarely vary within genera in the Lamiaceae (e.g., anther thecae confluent vs. separate at dehiscence; pollen apertures porate vs. colpate and three vs. six). The range of pollen surface sculpturing—psilate to suprareticulate, verrucate, spinulose, and spinose—is greater than that recorded in any other genus in the family. Furthermore, some species share unusual features with other genera, suggesting that *Caryopteris* may not be monophyletic. The genera that appeared at the outset of this study to be closely related to *Caryopteris* are *Amethystea* L., *Rubiteucris* Kudo, *Schnabelia* Hand.-Mazz., and *Trichostema* L. The former three are Asian, but *Trichostema* is North American. Although all five genera are included in the Lamiaceae here (following Cantino et al. 1992), the complex straddles the traditional boundary between Lamiaceae and Verbenaceae (e.g., Cronquist 1981); two of the genera, *Caryopteris* and *Schnabelia*, have frequently been placed in the Verbenaceae.

In a cladistic analysis of nonmolecular data (morphology and anatomy plus one phytochemical character), Cantino (1992) found *Caryopteris* to be polyphyletic. Although that study focused on the Lamiaceae as a whole and their relationship to Verbenaceae, and thus most unit taxa were genera, *Caryopteris* was represented by nine taxa because it was suspected to be non-monophyletic. In another cladistic analysis of Lamiaceae and Verbenaceae, which utilized a combination of morphological and phytochemical (iridoid) data, Rimpler et al. (1992) also found *Caryopteris* to be polyphyletic. Five species of *Caryopteris* were included in that study.

There have been two previous analyses of chloroplast DNA sequence data that included *Caryopteris*. An analysis of *rbcl* data in Lamiaceae and related families (Wagstaff and Olmstead 1997) included only one species of *Caryopteris*, which paired with the sole representative of *Trichostema*. In a second study using both *rbcl* and *ndhF* sequence data, Wagstaff et al. (1998) included three species of *Caryopteris*. This analysis yielded a single most parsimo-

nious tree, in which *Caryopteris* was paraphyletic. *Caryopteris* and *Trichostema* (represented by *T. dichotomum* L.) formed a clade, with *Trichostema* the sister group of *C. incana* (Thunb. ex Houtt.) Miq. (representing *C. sect. Caryopteris*). The sister group of this pair of taxa was a clade comprising *Caryopteris divaricata* Maxim. and *C. bicolor* (Hardw.) Mabb. (both representing *C. sect. Pseudocaryopteris*). The bootstrap support was very strong for both the *Caryopteris-Trichostema* clade (99%) and the clade comprising *Trichostema* and *C. incana* (95%), thus the hypothesis that *Caryopteris* is not monophyletic was strongly supported. However, it remains unclear whether the genus is para- or polyphyletic, because many species of *Caryopteris* that were included in Cantino's (1992) analysis of nonmolecular data, in which *Caryopteris* came out polyphyletic, were not included in the molecular data set.

MATERIALS AND METHODS

Three primary analyses were conducted: (1) the *rbcL* and *ndhF* sequence data of Wagstaff et al. (1998) were combined with nonmolecular (mainly morphological) data for the 28 taxa of Lamiaceae for which both data sets were available; (2) the data set in analysis 1 was expanded to include 10 additional taxa for which molecular data were not available (i.e., seven species of *Caryopteris* and the apparently related genera *Amethystea*, *Schnabelia*, and *Rubiteucris*); these 10 taxa were represented by nonmolecular data only, with a "missing data" symbol entered for the molecular characters, but the other 28 taxa were scored for both sets of characters; and (3) the 38 taxa in analysis 2 were analyzed using only the nonmolecular characters. The percentage of matrix cells scored as missing data in analyses 1, 2, and 3 were 3.0%, 28.2%, and 6.9%, respectively. Because these data sets included no taxa outside the Lamiaceae, the resulting trees were rooted with Symphorematoideae, which emerged as the basal clade of Lamiaceae in the broader analysis of Wagstaff et al. (1998).

In addition to the three primary analyses, 24 constrained analyses were performed to test the relative parsimony of various phylogenetic hypotheses. Particular groupings were constrained to monophyly in order to determine the number of additional steps required by these tree topologies when compared to the set of most parsimonious trees.

A total of 3,621 characters were used in these analyses, 64 nonmolecular (50 informative) and 3,557 molecular (509 informative). The nonmolecular data

set was derived from that of Cantino (1992) but with the addition of some data, restructuring of a few characters, and removal of characters that are uniform within the smaller set of taxa used here. See Appendix 2 for a list of nonmolecular characters used in this study. The nonmolecular data matrix is available from the first author. See Wagstaff et al. (1998) for a description of the methods used to obtain the molecular data and a list of GenBank accession numbers. The complete data sets for all three primary analyses reported here have been submitted to Tree BASE (<http://herbaria.harvard.edu/treebase>). Subfamily Symphorematoideae is represented by *Congea* Roxb. in the molecular data set but was broadened to include the full subfamily in the combined analyses because the nonmolecular data for this taxon were based on a study of all three genera of Symphorematoideae.

All analyses were performed with PAUP 3.1 (Swoford 1991), using the heuristic search option with MULPARS. In order to search for islands of equally most parsimonious trees (Maddison 1991), the strategy of Maddison et al. (1992) was adopted: Random addition was used with 1,000 replicates, TBR branch-swapping, and MULPARS, but saving no more than two trees per replicate. The resulting pairs of trees were then subjected to additional TBR swapping with no predetermined limit on the number of trees saved.

In analysis 3, the number of equally most parsimonious trees was extremely large. The tree storage capacity was exceeded at 32,700 trees, all of which underwent TBR branch-swapping before the analysis was terminated. Following a procedure used by Catalán et al. (1997) and Rice et al. (1997), the strict consensus tree from this initial analysis was then used as a reverse constraint, and the process was repeated, saving only those equally most parsimonious trees that did not match the constraint. This facilitated the search for equal-length or shorter trees that are incongruent with the strict consensus of those found already, in spite of the overflow of the tree buffer.

Clade support was assessed by bootstrapping (Felsenstein 1985), with 1,000 bootstrap replicates, one random taxon entry sequence per replicate, TBR branch swapping, and MULPARS, with 10 trees saved per replicate (parameters adopted from Davis 1995).

RESULTS

Analysis 1 (28 taxa, both data sets) yielded a single most parsimonious tree (1,755 steps; CI = 0.462; RI = 0.517) (Fig. 1). The portion of its topology that corresponds to subfamily Ajugoideae

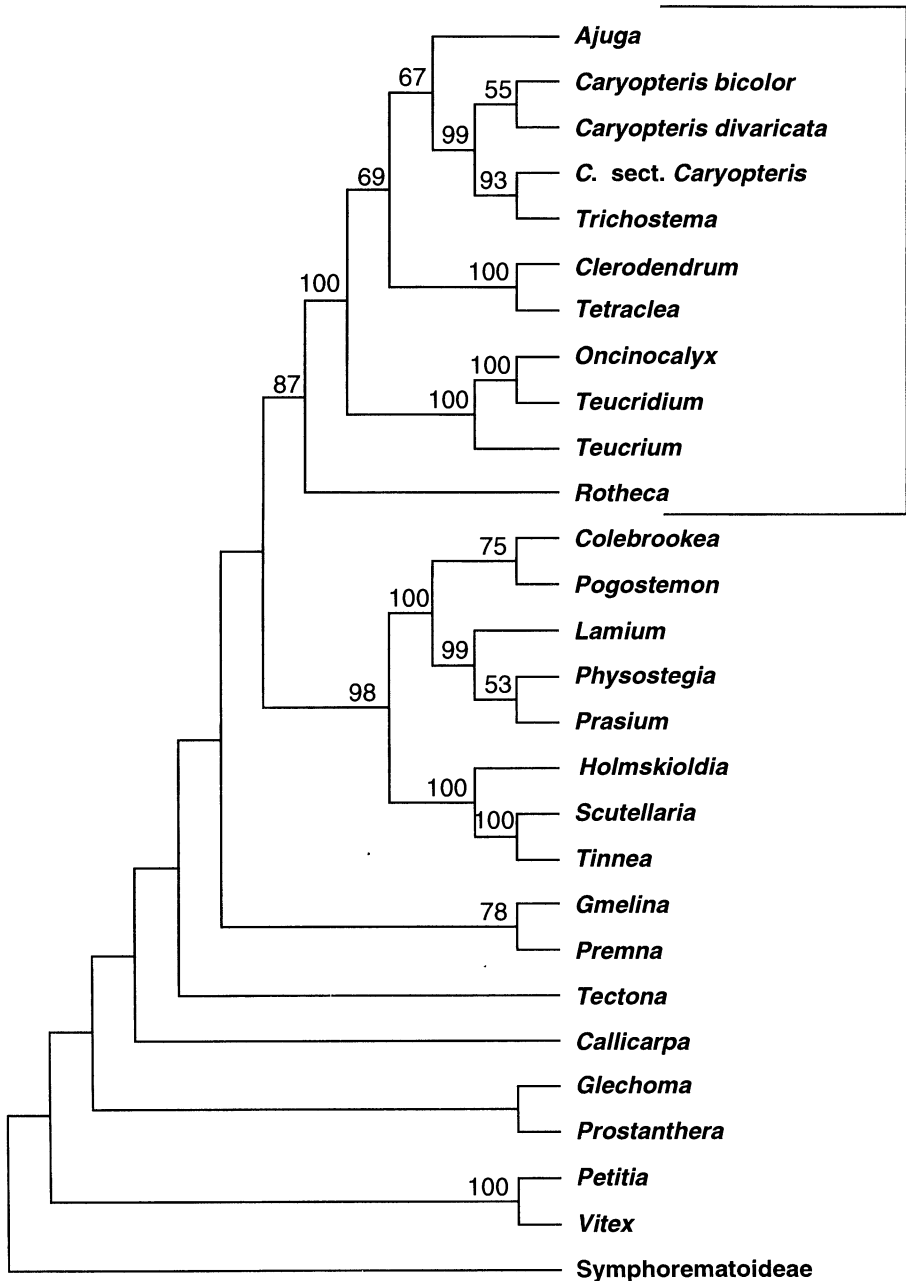


FIG. 1. Single most parsimonious tree resulting from analysis 1 (molecular and nonmolecular data included for all taxa). Bootstrap percentages greater than 50% are shown. Subfamily Ajugoideae is bracketed.

(bracketed in Fig. 1) is identical to that of Wagstaff et al. (1998), which was based on the molecular data alone. The hypothesis that *Caryopteris* is paraphyletic, with sect. *Caryopteris* more closely related to *Trichostema* than to the rest of *Cary-*

opteris, received strong bootstrap support (93%) in this analysis. However, only three species of *Caryopteris* were included, and the morphologically similar genera *Amethystea*, *Schnabelia*, and *Rubiteu-*

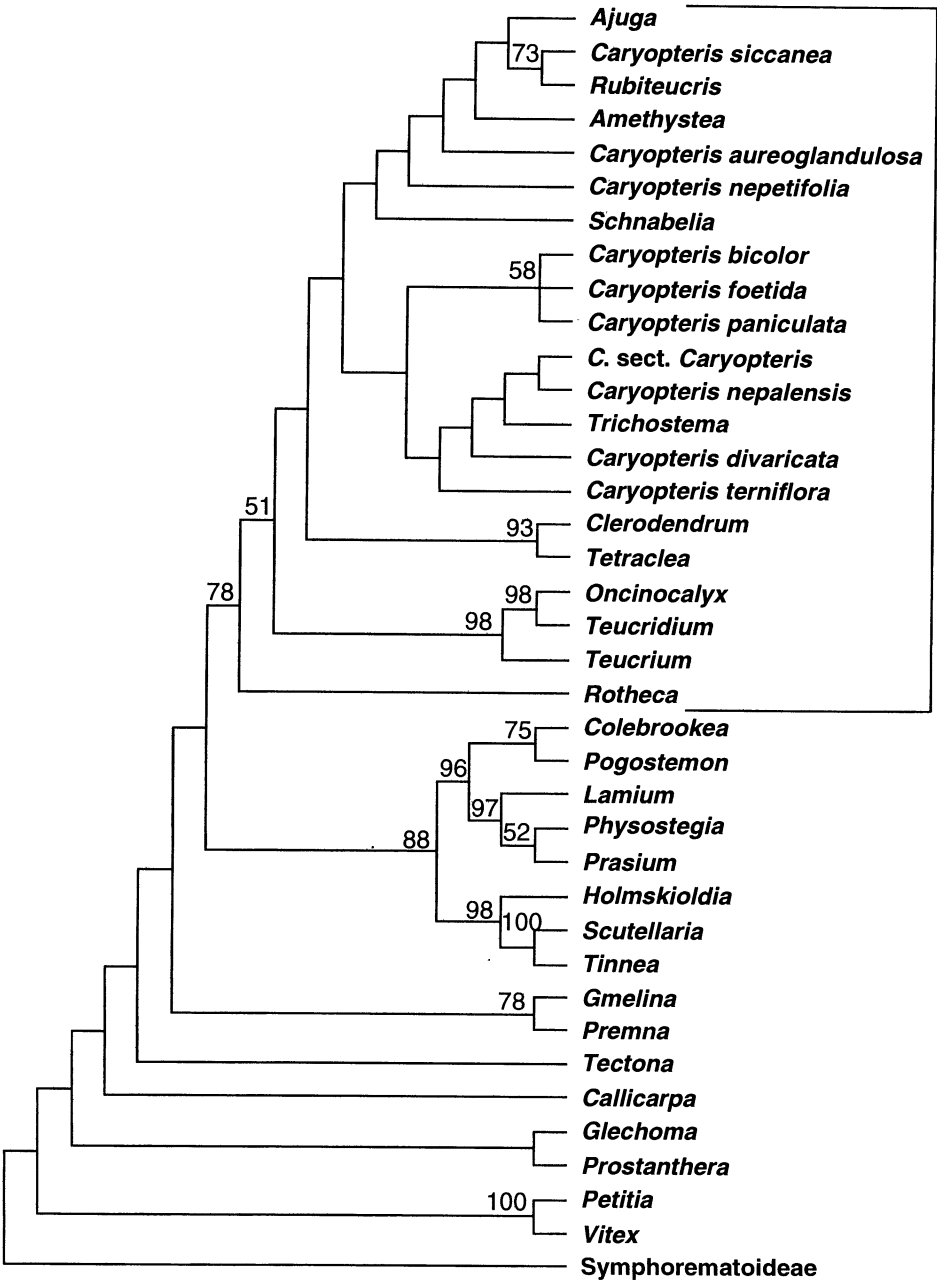


FIG. 2. Strict consensus of the three equally most parsimonious trees resulting from analysis 2 (non-molecular data included for all taxa; molecular data included where available). Bootstrap percentages greater than 50% are shown. Subfamily Ajugoideae is bracketed.

Analysis 2 (38 taxa, both data sets) yielded three equally most parsimonious trees (1,778 steps; CI = 0.457; RI = 0.526). In the strict consensus (Fig. 2), *Caryopteris* is paraphyletic, with five other genera nested within it. There is low bootstrap support for

most relationships within the clade comprising *Caryopteris* and the five related genera, but moderate support (73%) for a sister-group relationship between *Rubiteucris* and *Caryopteris siccanea* W. W. Sm.

Analysis 3 (38 taxa, nonmolecular data only) yielded an undetermined number ($>32,700$) of equally most parsimonious trees (157 steps; CI = 0.490; RI = 0.683). Additional searches using the reverse constraint procedure described above found no additional trees of 157 or fewer steps that were not congruent with the strict consensus of the 32,700 trees saved, thus this tree (Fig. 3) is likely to be the strict consensus of all equally most parsimonious trees, even though not all were found (Catalán et al. 1997). This analysis, like previous ones based on nonmolecular data (Cantino 1992; Rimpler et al. 1992), suggests that *Caryopteris* is polyphyletic. The bootstrap support for most parts of this topology is very poor, but a sister-group relationship between *Rubiteucris* and *Caryopteris siccanea* has a bootstrap value of 73%.

Constrained analyses were performed to test various phylogenetic hypotheses concerning *Caryopteris* and related genera (Table 1). The hypothesis that *Caryopteris* is monophyletic (constraint 1) is very unparsimonious; the shortest trees found with *Caryopteris* constrained to monophyly were six, eleven, and eight steps longer in analyses 1, 2, and 3, respectively. The hypothesis that *Caryopteris* plus *Trichostema* form a clade (constraint 2), seemingly supported by analysis 1 (which excluded the closely related genera *Amethystea*, *Rubiteucris*, and *Schnabelia*), is very unparsimonious in analyses 2 and 3, where one or more of these related genera are also nested within *Caryopteris*. The results of the other constrained analyses are discussed below.

DISCUSSION

Classification. All cladistic analyses, three previous ones and three presented here, agree that *Caryopteris* is not a clade. This is true regardless of whether molecular, nonmolecular or combined data are used. It is unclear whether *Caryopteris* is paraphyletic or polyphyletic as currently delimited, but the hypothesis that it is monophyletic is very unparsimonious (constraint 1, Table 1). From the perspective of phylogenetic systematics, the current delimitation of *Caryopteris* is untenable. Even those who argue against the abandonment of paraphyletic groups (Cronquist 1987; Brummitt 1997; Sosef 1997) should be concerned that *Caryopteris* emerges as polyphyletic in all analyses based on nonmolecular data alone (Cantino 1992; Rimpler et al. 1992; analysis 3 in this paper).

The possible recircumscriptions of *Caryopteris* fall into two general categories, which involve "lumping" and "splitting." Adopting the lumping

approach, one could merge *Caryopteris* and its relatives into a single monophyletic genus. Alternatively, one could split *Caryopteris* into smaller, monophyletic genera. The former approach has both theoretical and practical problems. First, lumping is unsatisfactory because it simply shifts the problem to a different taxonomic level (if one wishes to delimit infrageneric taxa within the expanded genus). Second, it is not at all clear where one must stop lumping in order to delimit a monophyletic genus. At the very least, the expanded genus must include *Caryopteris* and *Trichostema*, but analysis 2 suggests that *Amethystea*, *Rubiteucris*, *Schnabelia*, and *Ajuga* L. should also be included (Fig. 2), and other analyses (Fig. 3; Cantino 1992; Rimpler et al. 1992) find *Caryopteris* to be polyphyletic. The hypothesis that *Caryopteris*, *Trichostema*, *Amethystea*, *Rubiteucris*, *Schnabelia*, and *Ajuga* form a clade, which is weakly supported by analysis 2 (Fig. 2), is four steps longer than the most parsimonious trees in analysis 3 (constraint 3). Finally, even if one accepts the minimal paraphyly hypothesis, in which *Caryopteris* would be monophyletic if *Trichostema* were not segregated, merging these two genera would require that 16 species receive new combinations under *Trichostema* (which has priority). In contrast, splitting *Caryopteris* into smaller, monophyletic genera necessitates new names for only nine species (see below) and is therefore preferable from the standpoint of nomenclatural stability. For all of these reasons, the splitting approach is adopted here.

The next step is to identify monophyletic groups within *Caryopteris* that could be recognized as genera. One of these is *C. sect. Caryopteris*, a tightly knit group of seven species. Although its monophyly was not tested here, there is no question that it is a clade. It has several highly distinctive features that are rare to unique in the larger clade to which *Caryopteris* belongs (Teucroideae sensu Cantino et al. 1992, which must be called Ajugoideae according to the ICBN now that *Ajuga* is known to be a member). These presumed synapomorphies include the absence of bracts and bracteoles in the inflorescence, an annulate corolla tube, a dentate to lacinate lower corolla lobe, and winged nutlets. Because the monophyly of this group was never in question, it was treated as a single terminal taxon in our analyses; it was represented by *C. incana* in the molecular data set. This group includes the type of the genus (*C. mongholica* Bunge) and will retain the name *Caryopteris*. Henceforth, we will refer to this group as *Caryopteris* s. str. and the traditional circumscription as *Caryopteris* s.l.

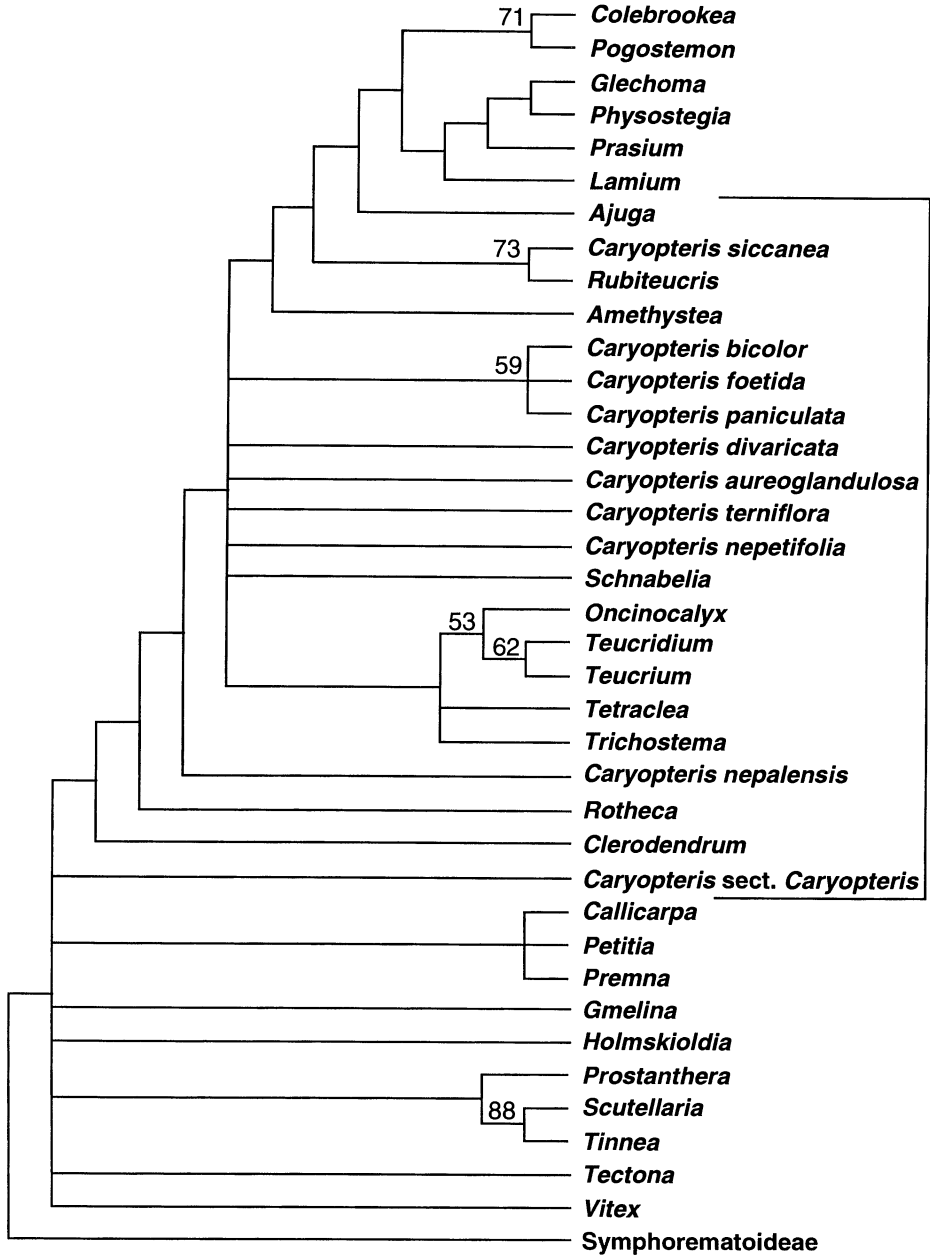


FIG. 3. Strict consensus of the 32,700 trees saved in analysis 3 (nonmolecular data only). The actual number of most-parsimonious trees is unknown, but all are congruent with this consensus tree (see text). Bootstrap percentages greater than 50% are shown. Subfamily Ajugoideae (paraphyletic in this analysis) is bracketed.

The taxonomic treatment of the other nine species of *Caryopteris* s.l. (i.e., sect. *Pseudocaryopteris* sensu Pei and Chen 1982) is more difficult. Analysis 1 provides little guidance because it includes only two of these species, but analyses 2 and 3 include all nine. The simplest solution would be to erect a

new genus to accommodate them, but the hypothesis that they form a clade is very unparsimonious (constraint 4, Table 1). There are two clades involving species of *Caryopteris* s.l. that appear in the strict consensus trees of both analyses 2 and 3 (Figs. 2, 3). The most strongly

TABLE 1. Number of additional steps required in the constrained analyses. Data sets 1, 2, and 3 correspond to Analyses 1, 2, and 3 in text. N/A=Not applicable; data set 1 does not include the necessary taxa to perform these constrained analyses. ¹Description of constraints: 1: *Caryopteris* must form a clade. 2: *Caryopteris* and *Trichostema* must form a clade. 3: *Caryopteris*, *Ajuga*, *Amethystea*, *Rubiteucris*, *Schnabelia*, and *Trichostema* must form a clade. 4: *Caryopteris* sect. *Pseudocaryopteris* sensu Pei and Chen must be a clade. 5: *Caryopteris aureoglandulosa*, *C. divaricata*, *C. nepalensis*, *C. nepetifolia*, and *C. terniflora* must form a clade. 6: *Caryopteris aureoglandulosa*, *C. nepetifolia*, and *C. terniflora* must form a clade. 7: *Caryopteris aureoglandulosa*, *C. nepetifolia*, *C. terniflora* and *Schnabelia* must form a clade. 8: *Caryopteris nepalensis* and *C. divaricata* must form a clade. 9: *Caryopteris nepalensis* and *Rothea* must form a clade. 10: *Caryopteris* except *C. siccanea*, *C. divaricata*, *C. bicolor*, *C. foetida*, and *C. paniculata* must form a clade. 11: Three separate constraints: *Schnabelia*, *Rubiteucris*, and *Pseudocaryopteris* as circumscribed here must each form a clade.

Constraint ¹	Data Set 1	Data Set 2	Data Set 3
1	6	11	8
2	0	4	9
3	N/A	0	4
4	N/A	6	6
5	N/A	3	3
6	N/A	2	1
7	N/A	2	1
8	N/A	2	3
9	N/A	1	1
10	N/A	3	7
11	N/A	2	1

supported one comprises *Caryopteris siccanea* and *Rubiteucris* and has a bootstrap value of 73% in both analyses. Based on this evidence, we hereby expand the monotypic *Rubiteucris* to encompass this clade. Its synapomorphies are a strongly bilabiate calyx and subglobose nutlets. *Rubiteucris* also differs from most of the *Caryopteris* complex in being unbranched perennial herbs with slender horizontal rhizomes. *Caryopteris siccanea* was originally described as a monotypic genus *Cardioteucris* C. Y. Wu (Wu and Chow 1962), but *Rubiteucris* was cited in the protologue as the closest relative. Although the two species differ in three conspicuous characters (length of nutlet attachment scar; corolla unilabiate vs. bilabiate; leaves simple vs. mostly deeply lobed to trifoliate), we prefer not to treat them as separate monotypic genera. Similar variation in corolla and leaf shape can be found within the related genus *Teucrium* L., and the occasional unlobed lower leaves of *Rubiteucris* s. str. resemble those of *C. siccanea*. Another difference cited by Wu and Chow is inaccurate; eight principal calyx nerves, supposedly a distinction of *Rubiteucris* s. str., can also be found in

some specimens of *C. siccanea*. More generally, monotypic genera are phylogenetically redundant (de Queiroz and Gauthier 1992; Cantino et al. 1997), and there is little to be gained from recognizing them if it is possible to group the species into genera that represent well supported clades.

Another clade that appears in both analyses 2 and 3 comprises *Caryopteris bicolor*, *C. foetida* (D. Don) Thell., and *C. paniculata* C. B. Clarke. The bootstrap support for this clade (58–59%) is weak, but given that every species must be assigned to a genus under the Linnaean system, we prefer to delimit a genus that is arguably monophyletic rather than treat each species as a monotypic genus. The latter approach would be undesirable from a pragmatic perspective because two of the species (*C. foetida* and *C. paniculata*) are so similar morphologically that they are frequently confused. This clade will be given the name *Pseudocaryopteris* because it corresponds to Briquet's (1895) circumscription of *Caryopteris* sect. *Pseudocaryopteris*. The one synapomorphy that distinguishes *Pseudocaryopteris* from the rest of the *Caryopteris* complex is the verrucate sculpturing of the pollen. In addition, three apomorphic fruit characters (unsculptured, concave nutlets or mericarps with an attachment scar as long as the fruit) distinguish *Pseudocaryopteris* from most of its sister group in the strict consensus tree (Fig. 2), but not from *Caryopteris* s. str. (a derived member of the sister group), in which these features evolved in parallel.

The classification of the remaining five species of *Caryopteris* s.l. [i.e., *C. aureoglandulosa* (Vaniot) C. Y. Wu, *C. divaricata*, *C. nepalensis* Moldenke, *C. nepetifolia* (Benth.) Maxim., and *C. terniflora* Maxim.] is problematical. Their relationships are unresolved in Fig. 3 and poorly supported in Fig. 2. A group comprising just these five species would be polyphyletic according to analysis 2 (Fig. 2), and the hypothesis that it is a clade (constraint 5, Table 1) is three steps longer than the most parsimonious tree topologies in both analyses. We would like to designate these species "incertae sedis" with regard to genus (i.e., refer them to a more inclusive taxon but not to a genus). This would provide an honest reflection of our current ignorance of their relationships, and if we were dealing with (for example) genera of uncertain subfamily relationship, that is the approach we would take. However, the binomial system does not permit a species to be "incertae sedis" with regard to genus. This is one of several disadvantages of Linnaean binomial nomenclature (Cain 1959; Michener 1964; de Queiroz and Gauthier 1992; Cantino, 1998), the most serious one being nomenclatural instability.

Every time generic limits are changed due to new knowledge of relationships, species names must be altered as well. For example, nine new combinations are made below, owing solely to an improved understanding of generic limits.

Given the poor phylogenetic resolution of these five remaining species of *Caryopteris* s.l., the probable non-monophyly of a group comprising all five, and the requirement that every species be placed in a genus, there is no satisfactory way to classify them. They could be treated as five monotypic genera, but three of them (*C. aureoglandulosa*, *C. nepetifolia*, and *C. terniflora*) are so similar that they are frequently confused; classifying them as different genera would be difficult to justify from a pragmatic perspective.

The best we can do within the confines of the binomial system is to treat the two relatively distinctive species (*Caryopteris divaricata* and *C. nepalensis*) as monotypic genera and combine the three similar ones (*C. aureoglandulosa*, *C. nepetifolia*, and *C. terniflora*) in a single genus, so long as the hypothesis that the latter as a clade is not very unparsimonious (which is, fortunately, the case). Trees in which these three species form a clade are only one step longer than the most parsimonious topologies in analysis 3 and two steps longer in analysis 2 (constraint 6, Table 1). However, an equally parsimonious hypothesis (constraint 7) groups these three species with *Schnabelia*. Thus treating the three species as a new genus and transferring them to *Schnabelia* are equally valid from a phylogenetic perspective (but neither approach is fully consistent with the best estimate of their phylogenetic relationships). We prefer to transfer these species to *Schnabelia* because we suspect that the sister group of *Schnabelia* is *Caryopteris nepetifolia*, in which case a genus that included *C. nepetifolia* but excluded *Schnabelia* would be paraphyletic. Although *Schnabelia* s. str. differs from the three species we propose to transfer to it in two conspicuous autapomorphies (winged stems and caducous leaves), it is otherwise rather similar to *C. nepetifolia* (e.g., both are low perennial herbs with ovate leaves, solitary flowers, and unilabiate corolla; at least the latter two features appear to be synapomorphic). The reported occurrence of cleistogamy in *Schnabelia* and *C. nepetifolia* (Su 1985) is particularly noteworthy in view of its rarity in the family as a whole (Owens and Uberta-Jiménez 1992).

The positions of the remaining two species of *Caryopteris* s.l., *C. nepalensis* and *C. divaricata*, have poor bootstrap support (Figs. 2, 3). They resemble

each other in leaf shape, corolla shape, and inflorescence structure, but they differ in many ways. *Caryopteris divaricata* is a tall herb with divaricate anther thecae that are confluent at dehiscence, triporate pollen, and a shallowly lobed ovary; the fruit breaks up readily into nutlets, and the attachment scar is 0.5–0.7 times the length of the nutlet. *Caryopteris nepalensis* is a shrub with parallel anther thecae that remain separate at dehiscence, hexapantocolpate pollen, and an unlobed ovary; the fruit breaks into nutlets only with pressure, and the attachment scar is fully as long as the nutlet. The pollen distinctions are particularly significant. *Caryopteris divaricata* is the only species of Lamiaceae known to have porate pollen, and the hexapantocolpate condition found in *C. nepalensis* is rare in the family (Abu-Asab et al. 1993). It is very unlikely that these species are closely related, in spite of their superficial similarity. The hypothesis that they form a clade (constraint 8, Table 1) is relatively unparsimonious. A more likely position for *C. nepalensis* is as sister group of *Caryopteris* s. str. (Fig. 2) or of *Rotheca* Raf. (constraint 9). Although we object to monotypic genera for reasons discussed above, we have little choice but to treat *C. nepalensis* and *C. divaricata* as monotypic genera, which we have named *Discretitheca* P. D. Cantino and *Tripura* P. D. Cantino, respectively.

A reviewer of this paper favored an alternative treatment in which *C. nepalensis*, *C. aureoglandulosa*, *C. nepetifolia*, and *C. terniflora* are retained within *Caryopteris*, based on the reasoning that a minimum threshold of confidence in a hypothesized phylogeny must be met before nomenclatural changes are made. However, this viewpoint assumes that declining to change nomenclature implies neutrality about relationships, whereas our view is that in the Linnaean binomial system, a species name always implies relationship. If *Pseudocaryopteris* is recognized as a distinct genus and *Caryopteris siccanica* is transferred to *Rubiteucris* (both of which are supported by analyses 2 and 3), and *C. divaricata* is segregated as a monotypic genus in order to avoid the paraphyly that would result from its retention in *Caryopteris* (strongly indicated by analysis 1), retention of the rest of *Caryopteris* as a genus, as proposed by the reviewer, implies that there is a reasonable likelihood that it is monophyletic. This is not the case. The hypothesis that this grouping is a clade (constraint 10, Table 1) is three and seven steps longer than the shortest trees in analyses 2 and 3, respectively. In contrast, the treatment adopted here (constraint 11, Table 1) is only one to two steps

longer than the shortest trees in these analyses. Our treatment is a compromise between phylogenetic and pragmatic concerns. Strict adherence to the phylogeny, even where poorly supported, would require naming three very similar species as new monotypic genera. On the other hand, segregation of only those genera that are well supported clades would leave a residual genus that is almost certainly not monophyletic. In our opinion, the compromise solution we have adopted is the least objectionable of the various unsatisfactory options available within the confines of the binomial system (see further discussion of this point below).

Traditional and Phylogenetic Nomenclature. Based on the considerations discussed above, we have devised a classification (Table 2) that is a compromise between phylogenetic and pragmatic concerns. It entails naming three new genera and making new combinations for nine species. Its strengths are that *Caryopteris* is no longer para- or polyphyletic, and all of the genera are easily recognizable units (see key in Appendix 1). Its weaknesses are the possible non-monophyly of *Schnabelia* and the existence of several monotypic taxa. We are not wholly comfortable with the delimitation of *Schnabelia*, which analysis 2 weakly suggests is polyphyletic (Fig. 2), but the hypothesis that it is monophyletic is only slightly less parsimonious. The same problem would exist if *Caryopteris aureoglandulosa*, *C. nepetifolia*, and *C. terniflora* were placed in their own new genus. To avoid delimiting a genus of questionable monophyly would require erection of three additional monotypic genera that are marginally distinct from each other. Although our personal bias is to favor phylogenetic over pragmatic concerns in such a conflict, the support for the non-monophyly of *Schnabelia* is too weak to justify it in this case. In general, we suggest that classification should be consistent with the best estimate of phylogeny unless both of the following conditions are met (and both are met in the present example): (1) all possible classifications that are consistent with phylogeny are undesirable from a pragmatic perspective, and (2) the best estimate of phylogeny is poorly supported. If *either* of these conditions does not hold, we would opt for a classification that is consistent with phylogeny (i.e., one in which all supraspecific taxa are either monophyletic or monotypic).

For comparative purposes, we have devised a second classification (Table 3) that follows the conventions of phylogenetic nomenclature (de Queiroz and Gauthier 1992, 1994). In this system, the use of

TABLE 2. Classification of *Caryopteris* and related genera following current rules (ICBN). Asterisk (*) designates new genera and combinations.

Ajugoideae
<i>Caryopteris</i> (7 spp.)
<i>Pseudocaryopteris</i> *
<i>Pseudocaryopteris bicolor</i> *
<i>Pseudocaryopteris foetida</i> *
<i>Pseudocaryopteris paniculata</i> *
<i>Tripora</i> *
<i>Tripora divaricata</i> *
<i>Discretitheca</i> *
<i>Discretitheca nepalensis</i> *
<i>Schnabelia</i>
<i>Schnabelia aureoglandulosa</i> *
<i>Schnabelia nepetifolia</i> *
<i>Schnabelia terniflora</i> *
<i>Schnabelia tetradonta</i>
<i>Schnabelia oligophylla</i>
<i>Rubiteucris</i>
<i>Rubiteucris palmata</i>
<i>Rubiteucris siccanea</i> *
<i>Amethystea</i>
<i>Amethystea coerulea</i>
<i>Trichostema</i> (17 spp.)
<i>Ajuga</i> (40–50 spp.)
<i>Aegiphila</i> , etc. (17 other genera, not of concern here)

ranks is not mandatory, and there is no requirement that a species be referred to a taxon at every level of the hierarchy. Thus, in Table 3, some species are referred only to Teucrioideae (preferable to the name Ajugoideae in a phylogenetic system of nomenclature; see Cantino et al. 1997) and more inclusive taxa such as Lamiaceae that are not shown in Tables 2 and 3, while others are also referred to less inclusive taxa such as *Rubiteucris* and *Caryopteris*. There is no requirement in phylogenetic nomenclature that every clade be named (a common misconception). We have opted to name only those that are both well supported (by reasonably high bootstrap values) and recognizable morphologically; thus they satisfy both the phylogenetic and pragmatic imperatives. Species nomenclature in Table 3 uses hyphenated uninomials (Michener 1964; Cantino 1998), in which the first word of the uninomial is not necessarily the name of a taxon to which the species belongs. This eliminates the need for species-level name changes due to new understanding of interspecific relationships. Italics are used only for species in Table 3 because there are no formal ranks above the species level (e.g., Teucrioideae is not a subfamily, and *Caryopteris* is not a genus; both are simply supraspecific taxa).

When one compares the classifications in Table 2 (following the ICBN) and Table 3 (employing phylogenetic nomenclature), the following similarities

TABLE 3. Classification of *Caryopteris* and related taxa employing the conventions of phylogenetic nomenclature (de Queiroz and Gauthier 1992, 1994) and hyphenated uninomials for species (Michener 1964; Cantino, 1998). See Cantino et al. (1997) for a phylogenetic definition of *Teucrioideae* and explanation of its use in place of the name *Ajugoideae* (the latter is correct according to the ICBN). This classification requires no monotypic taxa or new names. It gives formal recognition to the better supported clades in Figs. 1–3, while declining to name the poorly supported ones. Only species names are italicized (see text).

Teucrioideae (=Ajugoideae in Table 2)

Caryopteris (7 spp.)
Caryopteris-aureoglandulosa
Caryopteris-bicolor
Caryopteris-foetida
Caryopteris-paniculata
Caryopteris-divaricata
Caryopteris-nepalensis
Caryopteris-nepetifolia
Caryopteris-terniflora
Rubiteucris
Rubiteucris-palmata
Caryopteris-siccanea
Schnabelia (2 spp.)
Amethystea-coerulea
Trichostema (17 spp.)
Ajuga (40–50 spp.)
Aegiphila, etc. [17 other taxa (currently genera), not of concern here]

and differences are evident: 1) All supraspecific taxa in both classifications are easily recognizable, thus both satisfy the “pragmatic imperative.” 2) The classification in Table 3 is preferable from a phylogenetic perspective because all supraspecific taxa are well supported clades, whereas one genus in Table 2 (*Schnabelia*) is not. 3) The classification in Table 3 is far preferable from the standpoint of nomenclatural stability, because no new names or name changes are required to accommodate our current knowledge of phylogeny, vs. three new genera and nine new combinations in Table 2. (This assessment assumes that the phylogenetic system was already in use and the hyphenated species names in Table 3 thus already existed). 4) The classification in Table 3 is less cumbersome because it contains no monotypic taxa.

Although we would prefer the classification in Table 3, it deviates from the ICBN in major ways and is presented here only for illustrative purposes. The classification in Table 2 is the best compromise between phylogenetic and pragmatic concerns that we have been able to devise under the ICBN, and the taxonomic changes proposed below are accepted by the authors (i.e., not invalid under ICBN Art. 34.1).

TAXONOMIC CHANGES

In Appendix 1, we provide a key to the genera of the *Caryopteris* complex (as delimited here), a brief synopsis of each, and phylogenetic definitions (de Queiroz and Gauthier 1990) of those that are not monotypic. The new taxa and combinations are described below. Because the traditional circumscriptions of *Caryopteris*, *Rubiteucris*, and *Schnabelia* are substantially altered in this treatment, descriptions of these genera, as delimited here, are also provided below.

Discretitheca P. D. Cantino, *gen. nov.*—TYPE: *D. nepalensis* (Moldenke) P. D. Cantino (*Caryopteris nepalensis* Moldenke).

A *Caryopteris* Bunge inflorescentia bracteata, tubo corollae exannulato, staminibus arcuatis, pollinis granis hexapantocolpatis et spinulosis, lobis styli inaequalibus, et nuculis exalatis differt.

Tall shrub; leaves opposite, petiolate, broadly ovate, dentate. Inflorescence of lax axillary cymes grading into a terminal, paniculiform thyrses. Flowers pedicellate, subtended by small bracts; calyx actinomorphic or nearly so, tube campanulate, broadly so in fruit, lobes 5, lanceolate to triangular; corolla pink, zygomorphic, asymmetrical in bud (expanding abruptly on lower side), tube cylindrical, slightly upturned near base, exannulate, limb 5-lobed, upper and lateral lobes similar, ovate to obovate, \pm erect, lowest lobe larger, reflexed, obovate, concave; stamens 4, didynamous (ventral pair longer), long-exserted, arched, attached in distal third of corolla tube and emerging between upper corolla lobes, filaments pubescent towards base, anther thecae parallel, remaining separate at dehiscence; pollen 6-pantocolpate, tectate-perforate, with supracteal spinules, columellae branched; ovary unlobed, 4-ovuled; style deciduous, glabrous, apex unequally 2-lobed; disc poorly developed or absent. Fruit a dry schizocarp, requiring slight pressure to split into nutlets; nutlets 4, reticulately ridged, minutely appressed-pubescent and glandular, obovoid, obscurely trigonal, outer face convex, 2 inner faces separated by a sharp angle, one face flat, the other concave, attachment scar as long as nutlet. Seeds exalbuminous. Chromosome number unknown. 1 sp., Nepal.

Etymology: The name refers to the complete separation of the anther thecae at dehiscence, the most readily observed distinction from most other genera in this complex (but not from *Caryopteris* s. str.), in which the thecae are confluent at dehiscence.

Pseudocaryopteris (Briq.) P. D. Cantino, *gen. nov.*—

TYPE: *Pseudocaryopteris paniculata* (C. B. Clarke)

P. D. Cantino (*Caryopteris paniculata* C. B. Clarke). *Caryopteris* sect. *Pseudocaryopteris* Briq., in Engl. and Prantl, Nat. Pflanzenfam. 4 (3a): 178. 1895.

A *Caryopteris* Bunge inflorescentia bracteata, tubo corollae exannulato, thecis antherarum divergentibus et confluentibus, pollinis granis verrucatis, et nuculis exalatis differt.

Tall shrubs, often scrambling or spreading, foliage reported to be aromatic; leaves opposite, petiolate, ovate to lanceolate, variously toothed or rarely subentire. Inflorescence of axillary cymes or axillary or terminal paniculiform thyrses. Flowers pedicellate, subtended by small bracts; calyx actinomorphic or nearly so, tube campanulate, broadly so to nearly rotate in fruit, lobes 5–6, lanceolate; corolla white to deep red, purple, or blue, zygomorphic, usually asymmetrical in bud (expanding abruptly on lower side), tube cylindrical, straight, exannulate, limb 5-lobed, upper and lateral lobes similar, obovate to elliptical, \pm erect, lowest lobe larger, spreading, obovate, sometimes slightly concave; stamens 4, didynamous (ventral pair longer) or \pm equal, exserted, arched, attached in throat or near top of corolla tube and emerging between upper corolla lobes, filaments pubescent at base, anther thecae divergent to divaricate, confluent at dehiscence; pollen tricolpate, tectate-perforate, with supratectal verrucae, columellae sparingly branched; ovary unlobed, 4-ovuled; style deciduous, glabrous, apex equally 2-lobed; disc poorly developed. Fruit dry or slightly fleshy (drupaceous), a schizocarp or remaining intact; nutlets or pyrenes 4, boat-shaped (internally concave), smooth or slightly ridged, glabrous or pubescent, attachment scar as long as nutlet. Seeds exalbuminous. $2n = 40, 60$. 3 spp., S China, India, Nepal, Bhutan, Thailand, Myanmar, and Pakistan.

Tripora P. D. Cantino, *gen. nov.*—TYPE: *T. divaricata* (Maxim.) P. D. Cantino (*Caryopteris divaricata* Maxim.).

A *Caryopteris* Bunge habitu herbaceo, inflorescentia bracteata, tubo corollae exannulato, staminibus arcuatis, thecis antherarum divergentibus et confluentibus, pollinis granis triporatis et spinosis, ovario leviter 4-lobato, et nuculis exalatis differt.

Tall herb, foliage strongly ill-scented (like some spp. of *Clerodendrum*); leaves opposite, petiolate,

ovate, dentate to crenate. Inflorescence of lax axillary cymes grading into a terminal, paniculiform thyrses. Flowers pedicellate, subtended by small bracts; calyx actinomorphic, tube campanulate, broadly so in fruit, lobes 5, triangular; corolla purple (but lowest lobe proximally white), zygomorphic, asymmetrical in bud (expanding abruptly on lower side), tube cylindrical, straight, exannulate, limb 5-lobed, upper and lateral lobes similar, broadly obovate to ovate, \pm erect, lowest lobe larger, reflexed, obovate, slightly concave; stamens 4, didynamous (ventral pair longer), long-exserted, arched, attached in distal third of corolla tube and emerging between upper corolla lobes, filaments pubescent towards base, anther thecae divaricate, confluent at dehiscence; pollen triporate, tectate-perforate, with supratectal spines, columellae branched; ovary shallowly 4-lobed, 4-ovuled; style deciduous, glabrous, apex usually unequally 2-lobed; disc moderately well developed. Fruit a dry schizocarp; nutlets 4, obovoid, reticulately-ridged, puberulent, attachment scar 0.5–0.7 \times as long as nutlet. Seeds with a thin layer of endosperm. Chromosome number unknown. 1 sp., China, Japan, Korea.

Etymology: The name refers to the triporate pollen of this genus, apparently unique in the Lamiaceae.

Caryopteris Bunge

Shrubs and subshrubs, foliage strongly aromatic; leaves opposite, petiolate, ovate to lanceolate, elliptical, or suborbicular, variously toothed to entire. Inflorescence of dense axillary and terminal corymboid cymes. Flowers pedicellate, ebracteate; calyx actinomorphic, tube campanulate to tubular-campanulate, lobes 5, lanceolate to deltoid; corolla bluish purple or pale green to yellowish, zygomorphic, \pm symmetrical in bud, tube funnelform, straight, annulate, limb 5-lobed, upper and lateral lobes similar, ovate to oblong, erect, lowest lobe much larger, elliptical to obovate, concave, dentate to fimbriate-laciniate; stamens 4, equal to didynamous (ventral pair longer), long-exserted, straight, divergent, attached in distal half of corolla tube, filaments glabrous above base, anther thecae parallel, remaining separate at dehiscence; pollen tricolpate, tectate-perforate to microreticulate, with or without a supratectal reticulum, columellae sparingly branched; ovary unlobed, 4-ovuled; style deciduous, glabrous, apex equally 2-lobed; disc absent. Fruit a dry schizocarp; nutlets 4, boat-shaped (internally concave) to nearly flat, laterally winged,

usually smooth, glabrous or pubescent, attachment scar as long as nutlet. Seeds with a thin layer of endosperm. $2n = 26, 52, 40?$. 7 spp. and 1 horticultural hybrid, China, Mongolia, Tibet, Taiwan, Korea, Japan.

Rubiteucris Kudo

Rhizomatous perennial herbs; leaves opposite, long-petiolate, simple (broadly ovate), trilobed, or trifoliate, coarsely crenate to dentate. Inflorescence a terminal thyrses. Flowers pedicellate, bracteate; calyx bilabiate, tube broadly campanulate, gaping, gibbous in fruit, lips shallowly lobed, upper lip 3-lobed, lower lip 2-lobed; corolla white, bilabiate with a 2-lobed upper lip and a 3-lobed lower lip or unilabiate with all 5 lobes on lower lip due to a cleft between the upper 2 lobes, asymmetrical in bud (expanding abruptly on lower side), tube cylindrical to funnelform, straight, exannulate, lobes ovate to broadly rounded, the lowest lobe largest, often (always?) concave; stamens 4, didynamous (ventral pair longer), long-exserted, arched, attached at or below middle of corolla tube and emerging between or just beneath upper corolla lobes, filaments glabrous above base, anther thecae divergent to divaricate, confluent at dehiscence; pollen tricolpate, tectate-perforate, with supratectal spinules, columellae branched to granular; ovary unlobed to very shallowly 4-lobed, 4-ovuled; style deciduous, glabrous, apex equally 2-lobed; disc absent. Fruit a dry schizocarp; nutlets 4, broadly obovoid to subglobose, smooth to faintly ridged, glabrous, attachment scar 0.7–1.0x as long as nutlet. Seeds with a thin layer of endosperm. Chromosome number unknown. 2 spp., China, India, Myanmar.

Schnabelia Hand.-Mazz.

Low shrubs and perennial herbs, sometimes prostrate, decumbent or scandent; stems sometimes winged; leaves opposite, petiolate, ovate to triangular or suborbicular, occasionally trilobed, dentate to crenate, sometimes caducous. Inflorescence of axillary, few-flowered cymes, sometimes reduced to solitary flowers. Cleistogamous flowers sometimes present. Chasmogamous flowers pedicellate, bracteate; calyx actinomorphic, tube campanulate to broadly funnelform, lobes 4–5, broadly ovate to linear-lanceolate; corolla white, pink, or purple, zygomorphic, asymmetrical in bud (expanding abruptly on lower side), tube cylindri-

cal, straight, exannulate, limb 5-lobed, sometimes unilabiate due to a cleft between the upper 2 lobes, upper and lateral lobes similar, obovate to ovate, \pm erect, lowest lobe larger, \pm spreading, obovate to oblanceolate, often (always?) concave; stamens 4, didynamous (ventral pair longer), exserted, arched or \pm straight, attached at or above middle of corolla tube and emerging between upper corolla lobes, filaments glabrous or pubescent only at base, anther thecae parallel to divaricate, confluent at dehiscence; pollen tricolpate, tectate-perforate, with supratectal spinules, columellae branched to granular; ovary unlobed to very shallowly 4-lobed, 4-ovuled; style deciduous, glabrous, apex equally to subequally 2-lobed; disc poorly developed or absent. Fruit a dry schizocarp; nutlets 4, obovoid, reticulately-ridged, pubescent, attachment scar 0.5–0.9x as long as nutlet. Chromosome number unknown. 5 spp., China.

New combinations:

Discretitheca nepalensis (Moldenke) P. D. Cantino, comb. nov. *Caryopteris nepalensis* Moldenke, *Phytologia* 7: 77. 1959.

Pseudocaryopteris bicolor (Hardw.) P. D. Cantino, comb. nov. *Volkameria bicolor* Roxb. ex Hardw., *Asiat. Res.* 6: 366. 1799. *Caryopteris bicolor* (Hardw.) Mabb. in Manilal, *Bot. & Hist. Hort. Malab.* 83. 1980. *Volkameria odorata* Roxb., *Hort. Bengal.* 46. 1814 [nomen nudum] *Clerodendrum odoratum* D. Don, *Prodr. Fl. Nepal.* 102. 1825. *Caryopteris odorata* (D. Don) B. L. Rob., *Proc. Am. Acad. Arts* 51: 531. 1916. *Caryopteris wallichiana* Schauer in A. DC., *Prodr.* 11: 625. 1847.

Pseudocaryopteris foetida (D. Don) P. D. Cantino, comb. nov. *Clerodendrum foetidum* D. Don, *Prodr. Fl. Nepal.* 103. 1825. *Caryopteris foetida* (D. Don) Thell., *Vierteljahrsschr. Naturf. Ges. Zürich* 64: 782. 1919.

Pseudocaryopteris paniculata (C. B. Clarke) P. D. Cantino, comb. nov. *Caryopteris paniculata* C. B. Clarke in Hook. f., *Fl. Brit. India* 4: 597. 1885.

Rubiteucris siccania (W. W. Sm.) P. D. Cantino, comb. nov. *Caryopteris siccania* W. W. Sm., *Notes Roy. Bot. Gard. Edinburgh* 10: 18. 1917. *Cardioteucris cordifolia* C. Y. Wu, *Acta Bot. Sin.* 10: 248. 1962.

Schnabelia aureoglandulosa (Vaniot) P. D. Cantino, comb. nov. *Ocimum aureoglandulosum* Vaniot, *Bull. Acad. Int. Geogr. Bot.* 14: 171. 1904. *Caryopteris aureoglandulosa* (Vaniot) C. Y. Wu, *Fl. Yunnan.* 1: 484. 1977.

Schnabelia nepetifolia (Benth.) P. D. Cantino, comb. nov. *Teucrium nepetifolium* Benth. in A.

- DC., Prodr. 12: 580. 1848. *Caryopteris nepetifolia* (Benth.) Maxim., Bull. Acad. Imp. Sci. Saint-Petersbourg [ser. 3] 23: 390. 1877.
- Schnabelia terniflora** (Maxim.) P. D. Cantino, comb. nov. *Caryopteris terniflora* Maxim., Bull. Soc. Imp. Naturalistes Moscou 54: 40. 1879.
- Tripora divaricata** (Maxim.) P. D. Cantino, comb. nov. *Caryopteris divaricata* Maxim., Bull. Acad. Sci. Saint-Petersbourg [ser. 3] 23: 390. 1877. *Caryopteris chosenensis* Moldenke, Phytologia 51: 302. 1982. Note: Although *Caryopteris divaricata* Maxim. was based on the illegitimate name *Clerodendrum divaricatum* Siebold et Zucc. (1846) [not *Clerodendrum divaricatum* Jack (1820)], it is still legitimate (ICBN Art. 58.3); Moldenke's substitute name, *C. chosenensis*, is therefore superfluous.
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- LITERATURE CITED
- ABU-ASAB, M. S., P. D. CANTINO, J. W. NOWICKE, and T. SANG. 1993. Systematic implications of pollen morphology in *Caryopteris* (Labiatae). Systematic Botany 18: 502–515.
- BRIQUET, J. 1895. Verbenaceae. Pp. 132–182 in *Die natürlichen Pflanzenfamilien*, eds. A. Engler and K. Prantl, teil 4, abt. 3a. Leipzig, Germany: W. Engelmann.
- BRUMMITT, R. K. 1997. Taxonomy versus cladonomy, a fundamental controversy in biological systematics. Taxon 46: 723–734.
- and M. S. M. SOSEF. 1998. Paraphyletic taxa are inherent in Linnaean classification—a reply to Freudenstein. Taxon 47: 411–412.
- CAIN, A. J. 1959. The post-Linnaean development of taxonomy. Proceedings of the Linnean Society of London 170: 234–244.
- CANTINO, P. D. 1992. Evidence for a polyphyletic origin of the Labiatae. Annals of the Missouri Botanical Garden 79: 361–379.
- . 1998. Binomials, hyphenated uninomials and phylogenetic nomenclature. Taxon 47: 425–429.
- , R. M. HARLEY, and S. J. WAGSTAFF. 1992. Genera of Labiatae: status and classification. Pp. 511–522 in *Advances in labiate science*, eds. R. M. Harley and T. Reynolds. Kew: Royal Botanic Gardens.
- , R. G. OLMSTEAD, and S. J. WAGSTAFF. 1997. A comparison of phylogenetic nomenclature with the current system: a botanical case study. Systematic Biology 46: 313–331.
- CATALÁN, P., E. A. KELLOGG, and R. G. OLMSTEAD. 1997. Phylogeny of Poaceae subfamily Pooideae based on chloroplast *ndhF* gene sequences. Molecular Phylogenetics and Evolution 8: 150–166.
- CHEN, S.-L. and M. G. GILBERT. 1994. *Caryopteris*. Pp. 43–47 in *Flora of China*, eds. Z.-Y. Wu and P. H. Raven, vol. 17. Beijing: Science Press.
- CRONQUIST, A. 1978. Once again, what is a species? Pp. 3–20 in *Biosystematics in agriculture*, ed. J. A. Romberger. Montclair, New Jersey: Allanheld, Osmun & Co.
- . 1981. *An integrated system of classification of flowering plants*. New York: Columbia Univ. Press.
- . 1987. A botanical critique of cladism. Botanical Review 53: 1–52.
- DAVIS, J. I. 1995. A phylogenetic structure for the monocotyledons, as inferred from chloroplast DNA restriction site variation, and a comparison of measures of clade support. Systematic Botany 20: 503–527.
- DE QUEIROZ, K. 1996. A phylogenetic approach to biological nomenclature as an alternative to the Linnaean systems in current use. In *Proceedings of a mini-symposium on biological nomenclature in the 21st century*, ed. J. L. Reveal [http://www.life.umd.edu/bees/96sym.html].
- . 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. Aliso 15: 125–144.
- . 1998. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. Pp. 57–75, in *Endless forms: species and speciation*, eds. D. J. Howard and S. H. Berlocher. New York: Oxford Univ. Press.
- and J. GAUTHIER. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. Systematic Zoology 39: 307–322.
- and ———. 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23: 449–480.
- and ———. 1994. Toward a phylogenetic system of biological nomenclature. Trends in Ecology and Evolution 9: 27–31.
- DONOGHUE, M. J. and P. D. CANTINO. 1988. Paraphyly, ancestors, and the goals of taxonomy: a botanical defense of cladism. Botanical Review 54: 107–128.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.
- FREUDENSTEIN, J. V. 1998. Paraphyly, ancestors, and classification—a response to Sosef and Brummitt. Taxon 47: 95–104.
- MADDISON, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. Sys-

- tematic Zoology 40: 315–328.
- , M. RUVOLO, and D. L. SWOFFORD. 1992. Geographic origins of human mitochondrial DNA: phylogenetic evidence from control region sequences. *Systematic Biology* 41: 111–124.
- MICHENER, C. D. 1964. The possible use of uninominal nomenclature to increase the stability of names in biology. *Systematic Zoology* 13: 182–190.
- OWENS, S. J. and J. L. ÜBERA-JIMÉNEZ. 1992. Breeding systems in Labiatae. Pp. 257–280 in *Advances in labiate science*, eds. R. M. Harley and T. Reynolds. Kew: Royal Botanic Gardens.
- PEI, C. and S.-L. CHEN. 1982. *Verbenaceae. Flora reipublicae popularis sinicae*, vol. 65 (1). Beijing: Science Press.
- RICE, K. A., M. J. DONOGHUE, and R. G. OLMSTEAD. 1997. Analyzing large data sets: *rbcL* 500 revisited. *Systematic Biology* 46: 554–563.
- RIMPLER, H., C. WINTERHALTER, and U. FALK. 1992. Cladistic analysis of the subfamily Caryopteridoideae Briq. and related taxa of Verbenaceae and Lamiaceae using morphological and chemical characters. Pp. 39–54 in *Advances in labiate science*, eds. R. M. Harley and T. Reynolds. Kew: Royal Botanic Gardens.
- SCHANDER, C. 1998. Mandatory categories and impossible hierarchies—a reply to Sosef. *Taxon* 47: 407–410.
- and M. THOLLESSON. 1995. Phylogenetic taxonomy—some comments. *Zoologica Scripta* 24: 263–268.
- SOSEF, M. S. M. 1997. Hierarchical models, reticulate evolution and the inevitability of paraphyletic supraspecific taxa. *Taxon* 46: 75–85.
- SU, S.-W. 1985. A study on the two types of flowers in *Schnabelia oligophylla*.
- Handel-Mazzetti. *Bulletin of Botanical Research* 5: 109–120.
- SWOFFORD, D. L. 1991. *PAUP: Phylogenetic analysis using parsimony, version 3.1*. Champaign: Illinois Natural History Survey.
- WAGSTAFF, S. J. and R. G. OLMSTEAD. 1997. Phylogeny of Labiatae and Verbenaceae inferred from *rbcL* sequences. *Systematic Botany* 22: 165–179.
- , L. HICKERSON, R. SPANGLER, P. A. REEVES, and R. G. OLMSTEAD. 1998. Phylogeny and character evolution in Labiatae s.l., inferred from cpDNA sequences. *Plant Systematics and Evolution* 209: 265–274.
- WELZEN, P. C. VAN. 1998. Phylogenetic versus Linnaean taxonomy, the continuing story. *Taxon* 47: 413–423.
- WU, C. Y. and S. CHOW. 1962. *Cardioteucris* C. Y. Wu, *Holochaile* (Kudo) S. Chow—duo genera nova labiatarum ex Provincia Yunnan. *Acta Botanica Sinica* 10: 247–252.

APPENDIX 1. Artificial key to the genera (as delimited here) in the *Caryopteris* complex and a synopsis of each, including the type, a species list, geographic distribution, partial synonymy (restricted to well known and/or recent synonyms), and a phylogenetic definition. The definitions are node-based (de Queiroz and Gauthier 1990), employ a wording similar to that of Schander and Thollessen (1995), and are designed to maximize stability of clade membership (Cantino et al. 1997), hence the inclusion of several reference taxa in most definitions.

Key to genera:

1. Anther thecae remaining separate at anthesis, parallel.
 2. Stamens spreading, straight; bracts usually absent; lower corolla lobe dentate to fimbriate-laciniate; corolla tube annulate; pollen tricolpate; stylar lobes equal *Caryopteris* (s. str.)
 2. Stamens parallel, arched; bracts present; lower corolla lobe entire; corolla tube exannulate; pollen hexapantocolpate; stylar lobes unequal *Discretitheca*
1. Anther thecae confluent at anthesis, usually divergent to divaricate.
 3. Leaves entire or rarely a few leaves irregularly few-toothed or lobed; North America *Trichostema*
 3. Leaves regularly toothed, lobed, or both; Asia.
 4. Calyx strongly bilabiate, nutlets subglobose; rhizomatous herbs *Rubiteucris*
 4. Calyx \pm actinomorphic; nutlets obovoid or boat-shaped; herbs or shrubs.
 5. Annual with deeply lobed leaves; stamens 2 *Amethystea*
 5. Perennials with simple (rarely shallowly lobed) leaves; stamens 4.
 6. Tall, spreading shrubs; pollen verrucate; fruit drupaceous or dry, a schizocarp or intact, the nutlets or pyrenes boat-shaped (internally concave), attachment scar as long as nutlet; calyx lobes 5–6 *Pseudocaryopteris*
 6. Herbs or low shrubs; pollen spinulose to spinose; fruit a dry schizocarp, the nutlets obovoid, not concave, attachment scar 0.5–0.9x the nutlet; calyx lobes 4–5.
 7. Flowers in lax, many-flowered axillary cymes, grading into a terminal, paniculiform thyrs; pollen triplicate; tall herb *Tripora*
 7. Flowers solitary or in 3–5 flowered axillary cymes; pollen tricolpate; low herbs or shrubs *Schnabelia*

Synopsis of genera:

Amethystea L., Sp. Pl. 1: 21. 1753.; Gen. Pl. ed. 5: 13. 1754. TYPE.: *A. coerulea* L. Monotypic. Distribution: temperate Asia.

Caryopteris Bunge, *Plantarum Mongolico-Chinensium Decas Prima* 27. 1835. TYPE: *C. mongholica* Bunge. Other species (plus one artificial hybrid): *C. x. clandonensis* A. Simmonds, *C. Forrestii* Diels, *C. glutinosa* Rehder, *C. incana* (Thunb.

APPENDIX 1. Continued.

- ex Houtt.) Miq., *C. jinshajiangensis* Y. K. Yang et X. D. Cong, *C. tangutica* Maxim., and *C. trichosphaera* W. W. Sm. Distribution: China, Mongolia, Tibet, Taiwan, Korea, Japan. PHYLOGENETIC DEFINITION: The least inclusive clade that contains *C. forrestii*, *C. glutinosa*, *C. incana*, and *C. mongholica*.
- Discretitheca* P. D. Cantino, this publication. TYPE.: *D. nepalensis* (Moldenke) P. D. Cantino. Monotypic. Distribution: Nepal.
- Pseudocaryopteris* (Briq.) P. D. Cantino, this publication. TYPE.: *P. paniculata* (C. B. Clarke) P. D. Cantino. Other species: *P. bicolor* (Hardw.) P. D. Cantino, *P. foetida* (D. Don) P. D. Cantino. Distribution: S. China, India, Nepal, Bhutan, Thailand, Myanmar, Pakistan. PHYLOGENETIC DEFINITION: The least inclusive clade that contains *P. foetida* and *P. paniculata*, and also *P. bicolor* if and only if it is more closely related to these two species than to any others.
- Rubiteucris* Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. 2 (2): 297. 1929. *Cardioteucris* C. Y. Wu, Acta Bot. Sin. 10: 247. 1962. TYPE.: *R. palmata* (Benth. ex Hook. f.) Kudo. Other species: *R. siccania* (W. W. Sm.) P. D. Cantino. Distribution: China, India, Myanmar. PHYLOGENETIC DEFINITION: The least inclusive clade that contains *R. palmata* and *R. siccania*.
- Schnabelia* Hand.-Mazz., Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Anz. 58: 92. 1921. *Chienodoxa* Y. Z. Sun, Acta Phytotax. Sin. 1: 22. 1951. TYPE.: *S. oligophylla* Hand.-Mazz. Other species: *S. aureoglandulosa* (Vaniot) P. D. Cantino, *S. nepetifolia* (Benth.) P. D. Cantino, *S. terniflora* (Maxim.) P. D. Cantino, *S. tetradonta* (Y. Z. Sun) C. Y. Wu et C. Chen. Distribution: China. PHYLOGENETIC DEFINITION: The least inclusive clade that contains *S. oligophylla*, *S. tetradonta*, and any of the following three species (*S. aureoglandulosa*, *S. nepetifolia*, and *S. terniflora*) that are more closely related to *S. oligophylla* than to anything outside this set of five species.
- Trichostema* L., Sp. Pl. 2: 598. 1753; Gen. Pl. ed. 5: 260. 1754. *Isanthus* Michx., Fl. Bor.-Amer. 2: 3. 1803. *Eplingia* L. O. Williams, Fieldiana Bot. 36: 18. 1973. TYPE.: *T. dichotomum* L. Other species: *T. arizonicum* A. Gray, *T. austromontanum* F. H. Lewis, *T. brachiatum* L., *T. lanatum* Benth., *T. lanceolatum* Benth., *T. laxum* A. Gray, *T. mexicanum* Epling, *T. micranthum* A. Gray, *T. oblongum* Benth., *T. ovatum* Curran, *T. parishii* Vasey, *T. purpusii* Brandegees, *T. rubisepalum* Elmer, *T. setaceum* Houtt., *T. simulatum* Jeps., *T. suffrutescens* Kearney. Distribution: North America, Bahamas. PHYLOGENETIC DEFINITION: The least inclusive clade that contains *T. arizonicum*, *T. brachiatum*, *T. dichotomum*, *T. lanatum*, *T. lanceolatum*, and *T. purpusii*.
- Tripura* P. D. Cantino, this publication. TYPE.: *T. divaricata* (Maxim.) P. D. Cantino. Monotypic. Distribution: China, Japan, Korea.

APPENDIX 2. Nonmolecular characters used in analyses 1–3. All multistate characters except character 4 were treated as unordered.

- Habit: 0, tree, shrub, or liana; 1, herbaceous perennial; 2, annual or biennial. Subshrubs (woody only at base) are scored as 0/1.
- Branched multicellular trichomes present anywhere on plant: 0, no; 1, yes.
- Anisocytic stomata on leaves: 0, absent; 1, present.
- [ORDERED] Diacytic types of stomata on leaves: 0, absent; 1, diacytic but not diallelocytic stomata present; 2, both diacytic and diallelocytic stomata present.
- Phyllotaxy: 0, opposite; 1, helical (alternate); 2, whorled.
- Leaf structure: 0, simple, unlobed; 1, three-lobed; 2, palmately lobed (more than 3 lobes); 3, pinnately lobed (more than three lobes); 4, ternately compound; 5, palmately compound (more than three leaflets); 6, pinnately compound (more than three leaflets).
- Leaf margins: 0, entire; 1, toothed.
- Inflorescence structure: 0, cymes or thyrses; 1, flowers solitary in axils of foliage leaves or forming racemes or spikes; 2, heads.
- Inflorescence position: 0, axillary only; 1, both axillary and terminal on same plant (e.g., axillary cymes grading into terminal thyrse); 2, terminal only.
- Cymules subtended by bracts that become winglike in fruit: 0, no; 1, yes.
- Calyx symmetry: 0–2, radially symmetrical or nearly so: 0, four-lobed; 1, five lobed; 2, six or more lobes. 3–7, bilaterally symmetrical: 3, three-lobed upper lip and two-lobed lower lip; 4, one-lobed upper lip and two-lobed lower lip; 5, one-lobed upper lip and four-lobed lower lip; 6, one-lobed upper lip and one-lobed lower lip; 7, calyx truncate (unlobed).
- Calyx with a ring of long trichomes in tube: 0, no; 1, yes.
- Lobes of flowering calyx: 0, rounded to obtuse (including rounded and mucronate); 1, acute to attenuate; 2, spine-tipped or aristate; 3, uncinete.
- Fruiting calyx is closed apically by reflexing of one or both lips, enclosing fruit inside: 0, no; 1, yes.
- Fruiting calyx is closed apically by some other method, enclosing fruit inside: 0, no; 1, yes.
- Fruiting calyx greatly inflated, bladderlike: 0, no; 1, yes.
- Fruiting calyx enlarged, broadly funnellform to patelliform: 0, no; 1, yes.
- Fruiting calyx enlarged, with elongate, plumose lobes: 0, no; 1, yes.
- Corolla in bud stalked, expanding abruptly on ventral side only: 0, no; 1, yes.
- Corolla shape: States 0–2 are actinomorphic. 0, limb with four similar lobes; 1, limb with five similar lobes; 2, limb with six or more similar lobes. States 3–6 are zygomorphic but not lipped (i.e., some lobes differ from others in size or shape, but all arise at the same level on the tube). 3, limb with four similar lobes, the fifth (lower) lobe different in shape and usually larger; 4, limb with three similar lobes, the fourth (lower) lobe larger; 5, limb with three similar lobes, the

APPENDIX 2. Continued.

- fourth (upper) lobe larger; 6, lobes of three shapes and/or sizes, the two upper ones of one sort, the two lateral ones of another sort, and the lower lobe of a third sort. States 7–8 are bilabiate (i.e., the sinus separating the two lips is deeper than the sinuses separating the lobes on one or both lips). 7, upper lip two-lobed, lower lip three-lobed; 8, upper lip three-to four-lobed, lower lip one-lobed. States 9 and A are unilabiate. 9, all lobes fall on the lower lip (sometimes seemingly upper by resupination) and are similar in size and shape; A, all lobes fall on lower lip, the middle lobe larger than the other four.
21. Corolla tube gibbous: 0, no; 1, yes.
 22. Corolla tube curved: 0, no; 1, yes.
 23. Interior of corolla: 0, glabrous or nearly so; 1, with an incomplete annulus; 2, with a complete annulus; 3, densely pubescent on most or all of surface.
 24. Lower corolla lobe fimbriate: 0, no; 1, yes.
 25. Corolla persistent, its expanded base forming a sheath covering the fruit: 0, no; 1, yes.
 26. Stamen isomery: 0, stamens fewer than corolla lobes; 1, stamens as many as corolla lobes.
 27. Number of stamens: 0, two or four; 1, five; 2, six or more.
 28. Dorsal pair of stamens reduced to staminodes or absent: 0, no; 1, yes.
 29. Relative length of stamens if at least four fertile stamens present: 0, ventral pair longest; 1, all stamens approximately the same length; 2, dorsal pair longest. If only two fertile stamens present, the character scored as missing.
 30. Ventral stamens dimidiate (i.e., one theca of each stamen consistently aborted): 0, no; 1, yes.
 31. Anther locule confluence at dehiscence: 0, locules fully distinct or stamens dimidiate; 1, locules confluent but recognizable as two; 2, locules totally merged, appearing as one locule.
 32. Anther theca orientation: 0, parallel; 1, divergent. If the locules are fully merged, the character is scored as missing.
 33. Anthers appendaged at base: 0, no; 1, yes.
 34. Anther dehiscence aperture ciliate: 0, no; 1, yes.
 35. Anther dehiscence aperture bordered by one or more small teeth: 0, no; 1, yes.
 36. Anther connective appendaged: 0, no; 1, yes.
 37. Stamen filaments bearded: 0, at base only or not at all; 1, in the middle and/or upper portions of the filament.
 38. Filament extends beyond anther: 0, no; 1, yes.
 39. Number of pollen cells at anthesis: 0, two; 1, three.
 40. Number of pollen apertures: 0, three; 1, six to eight, zonocolpate; 2, six-pantocolpate.
 41. Pollen sculpturing types: 0, psilate, microreticulate to tectate-perforate [tectum relatively even (vs. 1)]; 1, tectate-perforate to microreticulate with muri exhibiting an alternation of distinctly raised and nonraised segments; 2, rugulose; 3, suprareticulate to suprarugulose; 4, verrucate; 5, spinulose; 6, minutely spinulose or granulate (the projections no more than 0.1 μ m long); 7, spinose; 8, suprareticulate and spinose.
 42. Pollen aperture type: 0, colpate; 1, porate.
 43. Pollen colpi operculate: 0, no; 1, yes.
 44. Structure of columellate stratum of exine: 0, with simple columellae; 1, with branched to granular columellae; 2, massive, undifferentiated.
 45. Depth of ovary lobing: 0, unlobed; 1, divided up to three-fourths of the way to the base to form four lobes (disk not elongate); 2, divided more than three-fourths of the way to the base, the style thus gynobasic (disk not elongate); 3, ovary lobes wholly free from each other but laterally attached to an elongate upward extension of the disk that terminates between them.
 46. Nectary disk below ovary: 0, absent or poorly developed; 1, well developed.
 47. Vertically elongate lobes on nectary disk: 0, absent (or no disk); 1, present.
 48. Style persists after abscission of corolla: 0, no; 1, yes.
 49. Style pubescence: 0, entirely glabrous; 1, pubescent, at least in part.
 50. Relative length of unlobed versus lobed portion of style: 0, unlobed portion more than three times the length of the lobes; 1, unlobed portion not more than three times the length of the lobes.
 51. Relative length of stylar lobes: 0, lobes equal or nearly so; 1, lobes distinctly unequal; 2, unlobed.
 52. Shape of embryo sac: 0, micropylar lobe no longer than but up to twice as broad as the chalazal lobe; 1, micropylar lobe no longer than but more than twice as broad as the chalazal lobe; 2, micropylar lobe both longer and broader than the chalazal lobe.
 53. Fruit type: 0, indehiscent capsule; 1, drupe with more than four one-seeded pyrenes; 2, drupe with one four-seeded pyrene (or fewer seeds by ovule abortion); 3, drupe with four one-seeded pyrenes (or fewer pyrenes by ovule abortion); 4, fruit separates into four fleshy, one-seeded mericarps (or fewer by ovule abortion); 5, fruit separates into four dry, one-seeded mericarps ("nutlets") (or fewer by ovule abortion). Taxa with fruits that split into mericarps only with pressure are scored as intermediate between 0 and 5 or between 3 and 4.
 54. Mericarp or pyrene attachment scar length: 0, as long as mericarp; 1, shorter than mericarp. If the fruit is a capsule or a drupe with only one pyrene, the character is scored as state 0.
 55. Surface of pericarp (if dry) or pyrene (if drupaceous) ridged, the ridges often forming a reticulum: 0, no; 1, yes.
 56. Surface of pericarp (if dry) or pyrene (if drupaceous) with tuberculate or elongate outgrowths: 0, no; 1, outgrowths tuberculate, papilliform or verrucate; 2, outgrowths greatly elongate, usually plumose, developing during fruit maturation from papilliform outgrowths on ovary.

APPENDIX 2. Continued.

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57. Pericarp pubescence: 0, glabrous; 1, puberulent to pubescent.
 58. Mericarp shape: 0, obovoid to obloid; 1, quarter-sphere; 2, boat-shaped; 3, nearly flat; 4, subspherical to spherical; 5, clavate; 6, trigonal; 7, boomerang-shaped (abruptly bent); 8, ovoid; 9, lenticular; A, half-sphere. If the fruit is not a schizocarp, the character scored as missing.
 59. Mericarps with lateral wings: 0, no; 1, yes. If the fruit is not a schizocarp, the character scored as missing.
 60. Moistened pericarp produces mucilage (myxocarpy): 0, no; 1, yes.
 61. Endosperm: 0, absent; 1, present.
 62. Embryo shape: 0, spatulate, straight or slightly curved; 1, abruptly bent but not doubled over; 2, doubled over on itself; 3, investing.
 63. Allenic component (probably laballenic acid) present in the seed oils: 0, no; 1, yes.
 64. Plant produces rosmarinic acid: 0, no; 1, yes.