PHYLOGENY AND PHYLOGENETIC TAXONOMY OF DIPSACALES, WITH SPECIAL REFERENCE TO *SINADOXA* AND *TETRADOXA* (ADOXACEAE)

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Abstract. To further clarify phylogenetic relationships within Dipsacales, we analyzed new and previously published *rbc*L sequences, alone and in combination with morphological data. We also examined relationships within Adoxaceae using *rbc*L and nuclear ribosomal internal transcribed spacer (ITS) sequences. We conclude from these analyses that Dipsacales comprise two major lineages: Adoxaceae and Caprifoliaceae (*sensu* Judd et al., 1994), which both contain elements of traditional Caprifoliaceae. Within Adoxaceae, the following relationships are strongly supported: (*Viburnum* (*Sambucus* (*Sinadoxa* (*Tetradoxa*, *Adoxa*)))). Combined analyses of Caprifoliaceae yield the following: (Caprifolieae (Diervilleae (Linnaeeae (Morinaceae (Dipsacaceae (*Triplostegia*, Valerianaceae)))))). On the basis of these results we provide phylogenetic definitions for the names of several major clades. Within Adoxaceae, Adoxina refers to the clade including *Sinadoxa*, *Tetradoxa*, and *Adoxa*. This lineage is marked by herbaceous habit, reduction in the number of perianth parts, nectaries of multicellular hairs on the perianth, and bifid stamens. The clade including Morinaceae, Valerianaceae, *Triplostegia*, and Dipsacaceae is here named Valerina. Probable synapomorphies include herbaceousness, presence of an epicalyx (lost or modified in Valerianaceae), reduced endosperm, and distinctive chemistry, including production of monoterpenoids. The clade containing Valerina plus Linnaeeae we name Linnina. This lineage is distinguished by reduction to four (or fewer) stamens, by abortion of two of the three carpels, and possibly by supernumerary inflorescences bracts.

Keywords: Adoxaceae, Caprifoliaceae, Dipsacales, ITS, morphological characters, phylogeny, phylogenetic taxonomy, phylogenetic nomenclature, *rbc*L, *Sinadoxa*, *Tetradoxa*.

Several studies of Dipsacales phylogeny have appeared in recent years, based on both morphological and molecular evidence (Donoghue, 1983; Donoghue et al., 1992; Judd et al., 1994; Backlund and Donoghue, 1996; Backlund and Bremer, 1997; Pyck et al., 1999; Pyck and Smets, 2000; Olmstead et al., 2000). These have concluded that *Viburnum* is related to *Sambucus* plus *Adoxa* and that the remainder of the traditional Caprifoliaceae are more closely related to Morinaceae, Valerianaceae, and Dipsacaceae. Furthermore, these studies have supported the monophyly of Caprifolieae, Diervilleae, and Linnaeeae (all of traditional Caprifoliaceae), and the view that Linnaeeae are more closely related to Morinaceae, Valerianaceae, and Dipsacaceae. However, support for these clades has not been uniformly strong, and the exact placement of several key taxa (*Heptacodium*, *Sinadoxa*, *Tetradoxa*, *Triplostegia*) remains uncertain.

Here we present an expanded analysis of chloroplast DNA *rbc*L sequences for Dipsacales, and a combined analysis of *rbc*L with morphological characters. We focus special attention on phylogenetic relationships within Adoxaceae, based on a combination of nuclear ribosomal internal transcribed spacer (ITS) and *rbc*L sequences. Of special interest is the placement of the two rare and morphologically bizarre Chinese species, *Sinadoxa corydalifolia* and *Tetradoxa omeiensis*. The recent rediscovery of these species allows us to present molecular evidence on their relationships.

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On the basis of these findings we contrast a phylogenetic nomenclatural system for Dipsacales with a traditional Linnaean taxonomic treatment, and present phylogenetic definitions for the names of several major clades.

MATERIALS AND METHODS

Taxa

Our *rbc*L analyses included 30 species of traditional Dipsacales, covering all major lineages (Table 1). We also included *Columellia* and *Desfontainia*, which may be closely related to, or possibly even nested within, Dipsacales (Backlund and Donoghue, 1996; Backlund and Bremer, 1997). Previous analyses have shown that Dipsacales belong within Asteridae (Olmstead et al., 1992, 1993; Chase et al., 1993; Backlund and Bremer 1997), where they are related to Apiales and Asterales within a "euasterid II" clade (APG, 1998). Here we have included published *rbc*L sequences from four species of Apiales (*Coriandrum*, *Griselinia*, *Hedera*, *Pittosporum*), and four species of Asterales (*Barnadesia*, *Boopis*, *Campanula*, *Menyanthes*). In addition, we added *Gentiana* and *Nicotiana* as representatives of the "euasterid I" clade (APG, 1998), and *Cornus* of Cornales. On the basis of all previous phylogenetic analyses, our trees were rooted along the branch connecting *Cornus*.

Our ITS analyses included new sequences from *Tetradoxa* and *Sinadoxa* (Table 1), along with five sequences from *Sambucus* (Eriksson and Donoghue, 1997) and five from *Viburnum* (Donoghue and Baldwin, 1993; Baldwin et al., 1995; see also Eriksson and Donoghue, 1997). Sequences of *Diervilla* and *Weigela* (Diervilleae), obtained from Genbank (Kim and Kim, 1999), were included for rooting purposes.

Sequencing

Of the 43 *rbc*L sequences included in our analyses, 27 were obtained from the authors of previous studies or from Genbank (Table 1) and 16 are reported here for the first time. The new sequences were obtained using standard protocols and primers (see, e.g., Olmstead et al., 1992, 1993). ITS sequences for *Sinadoxa* and *Tetradoxa* were obtained using protocols described elsewhere (Eriksson and Donoghue, 1997); however, we used a different 5' primer (ITS-I of Urbatsch et al., 2000), and reads were long enough that internal primers were not needed. All sequences reported here were proofread using sequences of both DNA strands. ITS sequences were edited using the Staden package (Staden, 1996) under the Linux operating system.

Alignment

*rbc*L nucleotide sequence data were aligned manually using the editor in PAUP* (Swofford, 2001); no indels were recorded. The *rbc*L data matrix contained 2% "missing data" for the 43 taxa, reflecting uncertainty in base-calling. Primer positions 1–26 were excluded from the analyses. Of the remaining 1402 characters, 230 were parsimony informative.

ITS nucleotide sequences from 15 taxa were aligned manually using the Se-Al alignment editor (Rambaut, 1996), resulting in 679 aligned positions. Positions 414–482 were removed from parsimony analyses owing to difficulties in alignment. Indels were treated as "uncertain" in the matrix, and 21 parsimony-informative indels (positions 47, 48, 53, 92, 111–112, 129, 166, 203, 210–212, 216, 221, 222, 235, 372, 375, 405, 572, 581, 607–608, 609, and 631) were coded as binary presence/absence characters and added to the end of the matrix. Our ITS matrix contained 6.2% uncertain data: 0.4% due to uncertain scorings, 2.8% to implied indels, and 3.0% to filling in unsequenced portions of the 5.8S gene in several species. In total, our ITS matrix contained 181 parsimony-informative characters.

Combining Data

We analyzed five datasets. Three of these focused on Dipsacales: (1) *rbc*L alone for Dipsacales and outgroups, (2) *rbc*L plus morphological data from Judd et al. (1994), and (3) *rbc*L plus morphological data from Backlund and Donoghue (1996). All data from the morphological studies were added without changes in the characters or in taxon scoring; both datasets also included chromosome and secondary chemical characters. Two additional datasets focused on Adoxaceae: (4) ITS alone for Adoxaceae and outgroups, and (5) ITS plus *rbc*L. Here we describe assembly of the combined datasets (2, 3, and 5).

The Judd et al. (1994) morphological analysis included a subset of the taxa in our *rbc*L matrix. From our *rbc*L dataset we omitted 12 outgroup taxa not present in Judd et al., keeping only *Pittosporum* for rooting purposes. Judd et al. included Alseuosmiaceae, but these are probably not closely related to Dipsacales (Gustafsson et al., 1996) and have been omitted here. We also omitted *rbc*L sequences for those Dipsacales not represented in Judd et al.: *Heptacodium*, *Morina*, *Sinadoxa*, *Tetradoxa*, and *Triplostegia*. Judd et al. lumped *Weigela* and *Diervilla* together, and also *Kolkwitzia* and *Abelia*, because these scored identically for their 35 (25 binary, 10 multistate) morphological characters. In our analysis each of these pairs was separated into two taxa, which were scored identically for all morphological characters. Several taxa in Judd et al. were represented by two or more *rbc*L sequences in our matrix. Using the "merge taxa" function in MacClade (Maddison and Maddison, 1992), we merged the sequences of our two *Sambucus* species into a single sequence with six polymorphic positions. Similarly, we merged sequences of *Viburnum* (three species), *Lonicera* (two species), Dipsacaceae (three species), and Valerianaceae (five species), resulting in 28, 55, 40, and 100 polymorphic positions, respectively. The resulting combined matrix contained 16 taxa and 1437 characters (after excluding primer sites 1–26); there were 93 parsimony-informative characters.

The Backlund and Donoghue (1996) dataset contained many more taxa (58) and characters (109). However, owing to differences in taxon sampling, we removed 9 outgroup taxa from our *rbc*L dataset (*Barnadesia*, *Boopis*, *Campanula*, *Coriandrum*, *Cornus*, *Gentiana*, *Hedera*, *Menyanthes*, and *Nicotiana*). Likewise, from the morphological dataset we removed 12 Dipsacales and 16 outgroup taxa. *Sambucus*, *Viburnum*, and *Lonicera* sequences were merged as described above. The combined dataset contained 30 taxa and 1511 characters (after excluding primer sites 1–26); there were 236 parsimony-informative characters.

The combined analysis of Adoxaceae used the intersection of all available ITS and *rbc*L sequences. It contained 10 taxa and 2012 characters (after excluding primer sites 1–26 and 69 ITS sites in a region of ambiguous alignment); there were 229 parsimony-informative characters.

All of our data matrices, and the trees reported here, are available in TreeBASE (http://treebase.org).

Phylogenetic Analyses

Parsimony analyses were conducted using PAUP* (Swofford, 2001). For datasets 1 and 3 (see above), we carried out heuristic searches (1000 random addition sequence starting trees, TBR branch swapping, saving all most parsimonious trees); branch-and-bound searches were possible for datasets 2, 4, and 5. All characters were weighted equally, and indels were treated as described above. MacClade and PAUP* were used for the output of trees, character optimizations, and so on.

Measures of Support

Decay indices (Bremer, 1988; Donoghue et al., 1992) were calculated using AutoDecay (Eriksson, 1999) and PAUP*. The converse constraint runs in PAUP* were performed using branch-and-bound searches when possible; otherwise, heuristic searches were conducted with 100 random addition sequence starting trees, TBR branch swapping, and saving all most parsimonious trees. Bootstrap analyses (Felsenstein, 1985) were carried out using 500 replications with simple addition sequence, TBR branch swapping, and saving all most parsimonious trees in each replicate.

Results

Parsimony analysis of our *rbc*L matrix (analysis 1) resulted in four minimum-length trees of 996 steps (CI = 0.521; CI excluding uninformative = 0.404; RI = 0.593); these differ only in whether *Symphoricarpos* or *Triosteum* is more closely related to *Lonicera* (Fig. 1). This result supports many previous conclusions. Dipsacales are seen to be monophyletic with *Columellia* and *Desfontainia* as their sister group. This is in contrast to several previous reports that *Columellia* and *Desfontainia* may be nested within the group (e.g., Backlund and Donoghue, 1996; Backlund and Bremer, 1997; see discussion). We find little support for a connection between Adoxaceae and Araliales (Backlund and Bremer, 1997); forcing these taxa together adds a minimum of five steps. The traditional Dipsacaceae and Valerianaceae are both monophyletic, show internal relationships largely consistent with previous results (but see Caputo and Cozzollino, 1994, on Dipsacaceae), and are weakly united with *Triplostegia*. In our *rbc*L analysis, it is equally parsimonious to place *Triplostegia* as the sister group of Valerianaceae (as in previous studies: Backlund and Donoghue, 1996; Backlund and Bremer, 1997; see discussion) or Dipsacaceae. *Morina* (Morinaceae) is sister to the Dipsacaceae-*Triplostegia*-Valerianaceae clade.

Caprifoliaceae, in the traditional sense, are clearly not monophyletic. *Viburnum* and *Sambucus* are united with *Adoxa* and its rela-

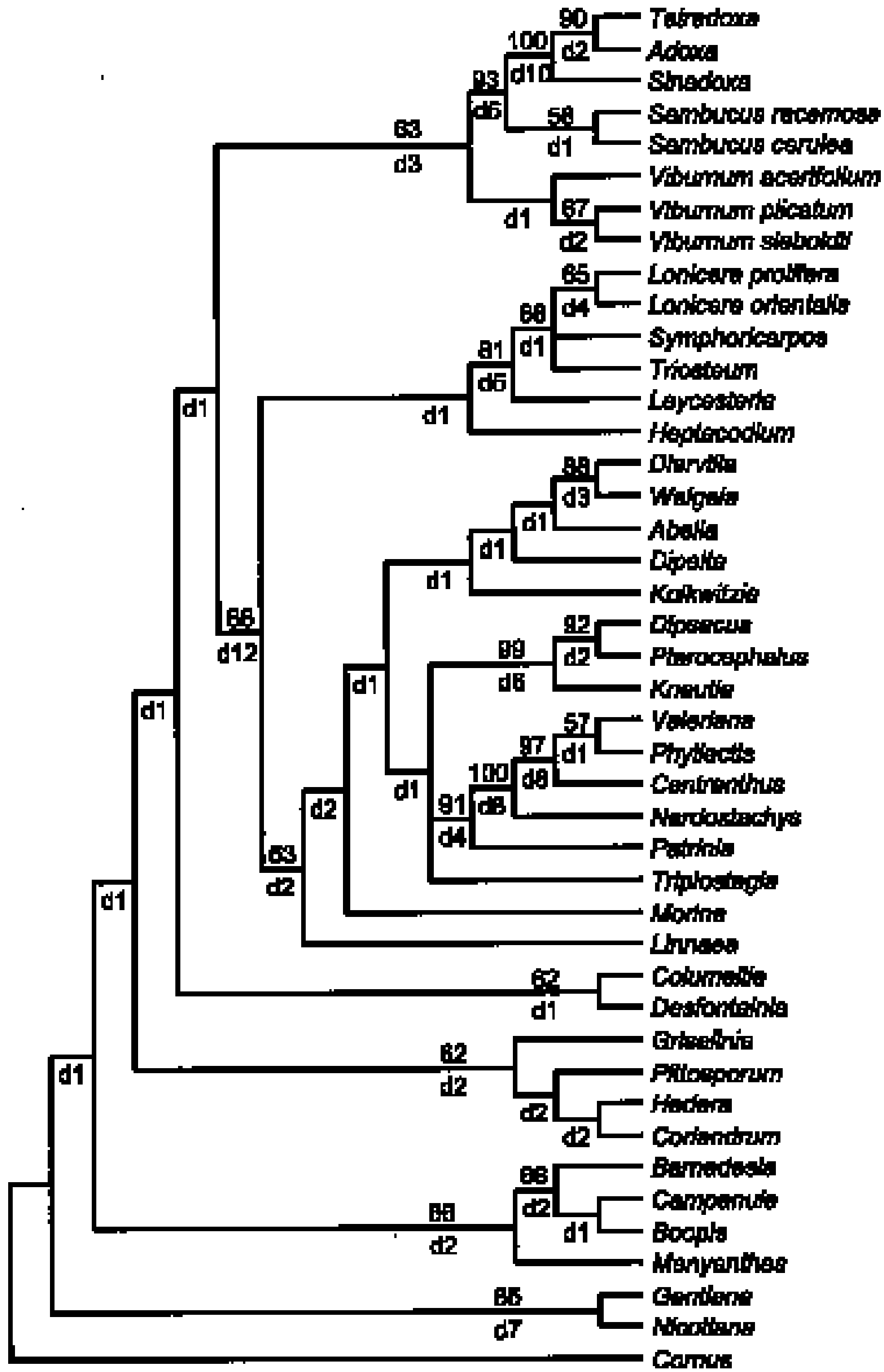

FIGURE 1. Strict consensus of four most parsimonious trees resulting from the analysis of *rbc*L sequence data alone (analysis 1); length=996 steps; consistency index (CI), excluding uninformative characters=0.40; retention index (RI)= 0.59. Bootstrap values greater than 50% are indicated above the branches and decay indices below.

tives, with *Sinadoxa* seen to be the sister group of *Adoxa* plus *Tetradoxa*. Caprifolieae, Diervilleae, and Linnaeeae, of the traditional Caprifoliaceae, are more closely related to the Morinaceae-Dipsacaceae-*Triplostegia*-Valerianaceae clade. Caprifolieae are monophyletic, with *Leycesteria* the sister group of a clade including *Symphoricarpos*, *Triosteum*, and *Lonicera*. This clade is in turn weakly united with *Heptacodium*. Diervilleae (*Diervilla*, *Weigela*) are also monophyletic. However, in contrast with previous analyses, Linnaeeae do not form a clade in this analysis. *Linnaea* is separated from *Abelia*, *Dipelta*, and *Kolkwitzia*, which are in turn paraphyletic in relation to Diervilleae. Branch lengths in this portion of the tree are especially short (Fig. 2), implying that other arrangements may be nearly as parsimonious. Trees constrained to unite *Abelia*, *Dipelta*, and *Kolkwitzia* are only two steps longer than our shortest trees; however, linking *Linnaea* to this group, in a monophyletic Linnaeeae, yields trees that are five steps longer.

Parsimony analyses of *rbc*L sequences combined with morphological characters yield several important insights. Combining *rbc*L with the Judd et al. (1994) morphological dataset (analysis 2) yielded five trees of 258 steps (Fig. 3; CI = 0.767; CI excluding uninformative = 0.657; RI = 0.757). These trees are entirely congruent with those obtained by Judd et al. (1994) using morphology alone, and in almost every respect they are also congruent with the *rbc*L trees discussed above. However, in contrast to results from analyses using *rbc*L sequences alone, the Linnaeeae form a weakly supported clade, which is separated from Diervilleae and instead united directly with Dipsacaceae and Valerianaceae.

Combining *rbc*L with the Backlund and Donoghue (1996) morphological characters (analysis 3) yielded 12 trees of 861 steps (Fig. 4; CI = 0.569; CI excluding uninformative = 0.478; RI = 0.689). Almost all of the clades in these trees correspond with those found using morphological characters alone, *rbc*L sequences alone, and *rbc*L plus the Judd et al. morphological characters. The main difference is between this combined analysis and the *rbc*L sequences analyzed separately. Although support values are not high, here again the combined data yield a monophyletic Linnaeeae, which is separated from Diervilleae and united with a clade including Morinaceae, Valerianaceae, *Triplostegia*, and Dipsacaceae. The combined analysis also united *Triplostegia* with Valerianaceae, instead of with Dipsacaceae as in the *rbc*L analysis.

Our analysis of Adoxaceae based on ITS sequences alone (analysis 4) resulted in two trees of 347 steps (Fig. 5; CI = 0.784; CI excluding uninformative = 0.750; RI = 0.864). As in previous analyses (Donoghue, 1983; Donoghue et al., 1992; Judd et al., 1994; Backlund and Donoghue, 1996), *Viburnum* appears to be the sister group of a clade containing *Sambucus* and *Adoxa*. The significant new result is strong support for the placement of *Sinadoxa* and *Tetradoxa* in relation to *Adoxa*. As in the *rbc*L analyses just discussed, *Sinadoxa* is the sister group of a *Tetradoxa*-*Adoxa* clade (also see Backlund and Donoghue, 1996). As expected, the combined analysis of ITS and *rbc*L sequences for Adoxaceae (analysis 5) yielded a single tree of 395 steps (CI = 0.858; CI excluding uninformative = 0.828; RI = 0.881) with remarkably high support values for all clades (Fig. 6).

Discussion

Phylogenetic Relationships

With the availability of one or more *rbc*L sequences for all of the standardly recognized genera of the traditional Caprifoliaceae (*Zabelia*, a segregate of the traditional *Abelia*, is not included here), and a reasonable sample of Valerianaceae and Dipsacaceae, many aspects of the phylogeny of Dipsacales are now established with considerable certainty. Most importantly, it is clear, as highlighted by Donoghue (1983), that the traditional circumscription of Caprifoliaceae must be abandoned (also see Donoghue et al., 1992; Judd et al., 1994; Backlund and Donoghue, 1996; and later authors). *Viburnum* and *Sambucus* are more closely related to *Adoxa* and its relatives than they are to the other traditional Caprifoliaceae. Caprifolieae, Diervilleae, and Linnaeeae, of the traditional Caprifoliaceae, are more closely related to Morinaceae, Valerianaceae, *Triplostegia*, and Dipsacaceae than they are to *Viburnum* and *Sambucus*. Of these groups, Linnaeeae appear to be more closely related to the Morinaceae-Valerianaceae-*Triplostegia*-Dipsacaceae clade than to Caprifolieae or Diervilleae.

For purposes of the remaining discussion we will adopt the names for the two major clades of Dipsacales suggested by Judd et al. (1994).

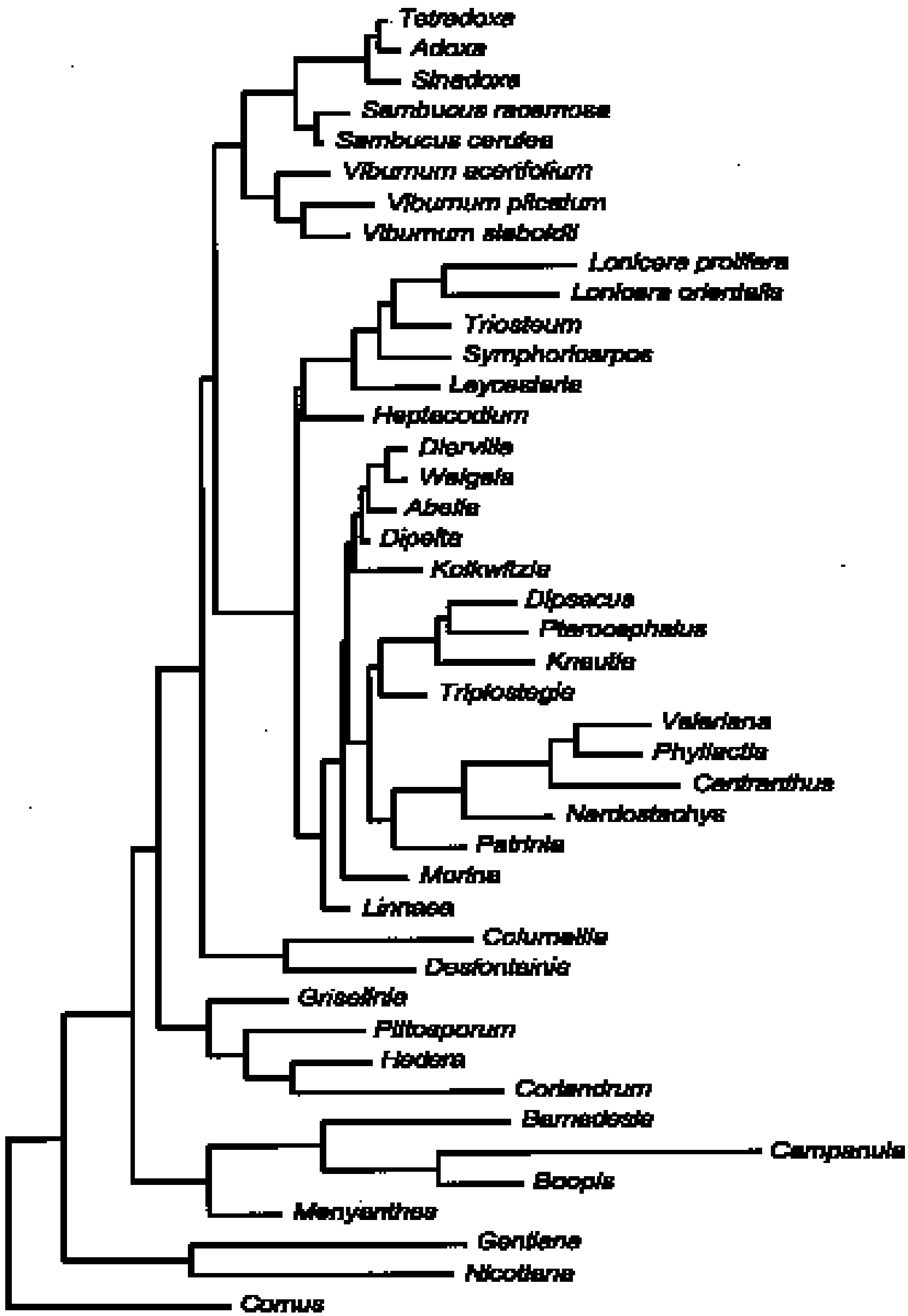

FIGURE 2. Phylogram from the *rbc*L analysis; branch lengths scaled to the number of inferred state changes.

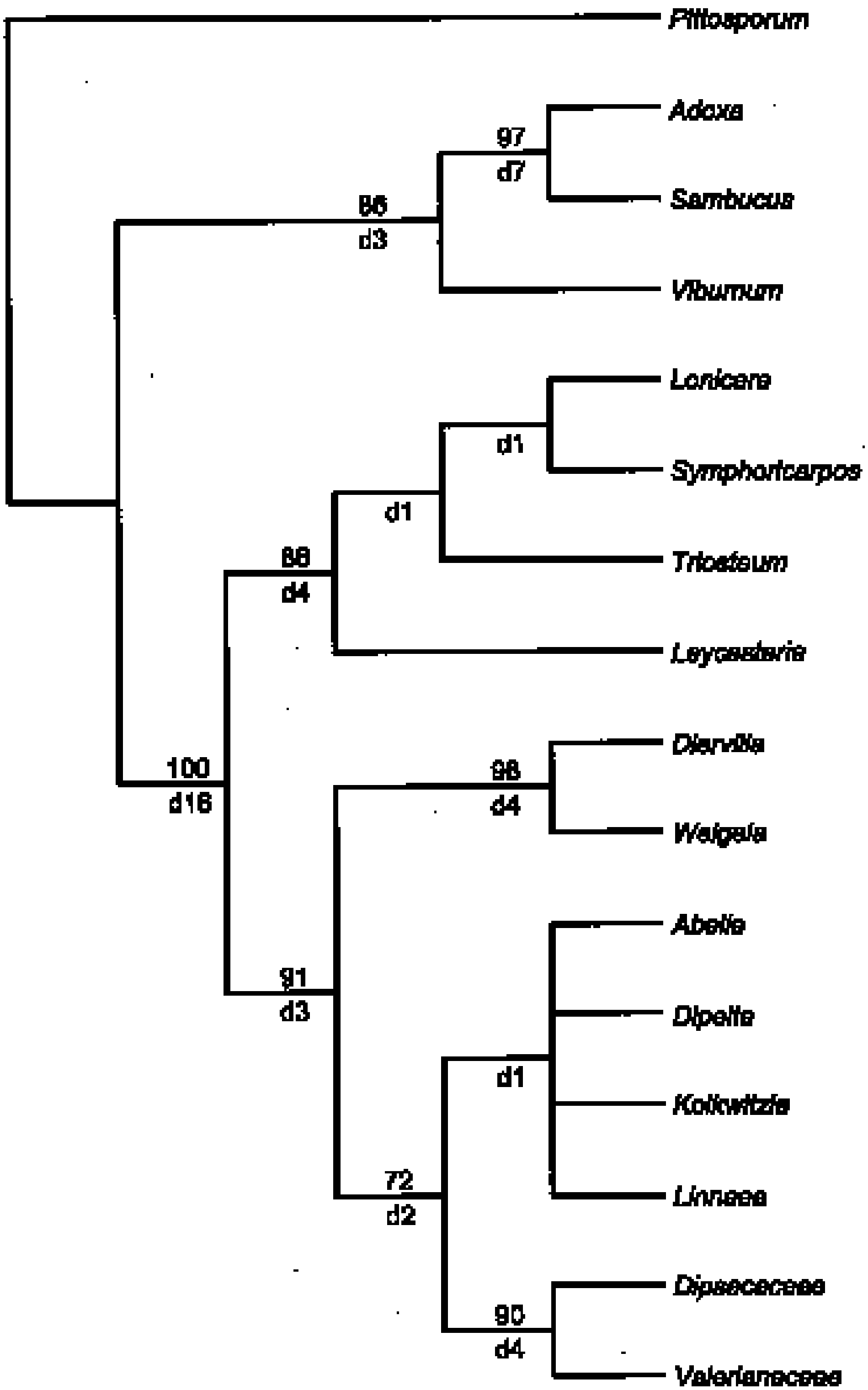

FIGURE 3. Strict consensus of five most parsimonious trees resulting from the analysis of *rbc*L sequence data combined with the morphological characters from Judd et al. (1994) (analysis 2); length=258 steps; consistency index (CI), excluding uninformative characters=0.66; retention index (RI)= 0.76. Bootstrap values greater than 50% are indicated above the branches and decay indices below.

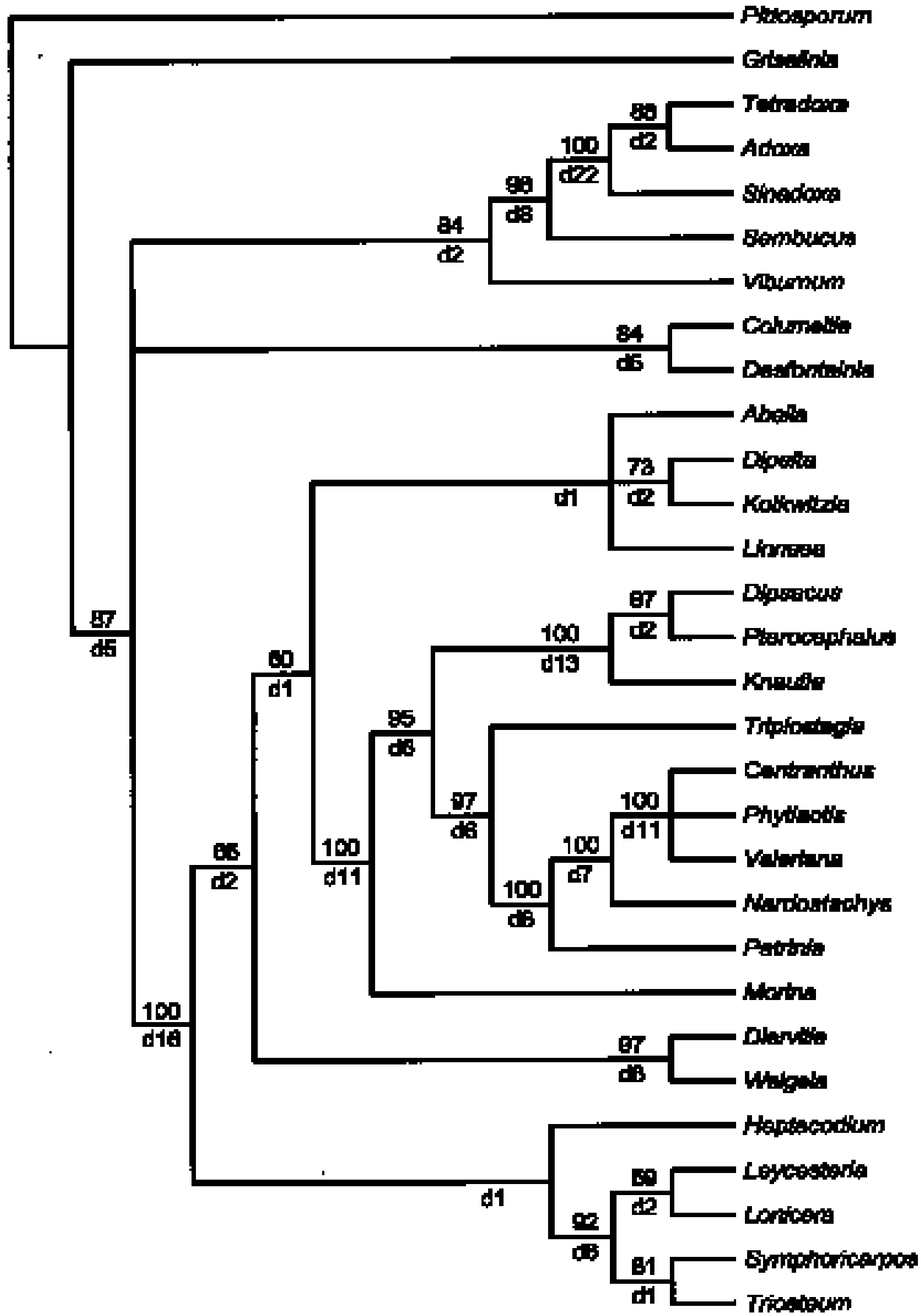

FIGURE 4. Strict consensus of 12 most parsimonious trees resulting from the analysis of *rbc*L sequence data combined with the morphological characters from Backlund and Donoghue (1996) (analysis 3); length=861 steps; consistency index (CI), excluding uninformative characters=0.48; retention index (RI)=0.69. Bootstrap values greater than 50% are indicated above the branches and decay indices below.

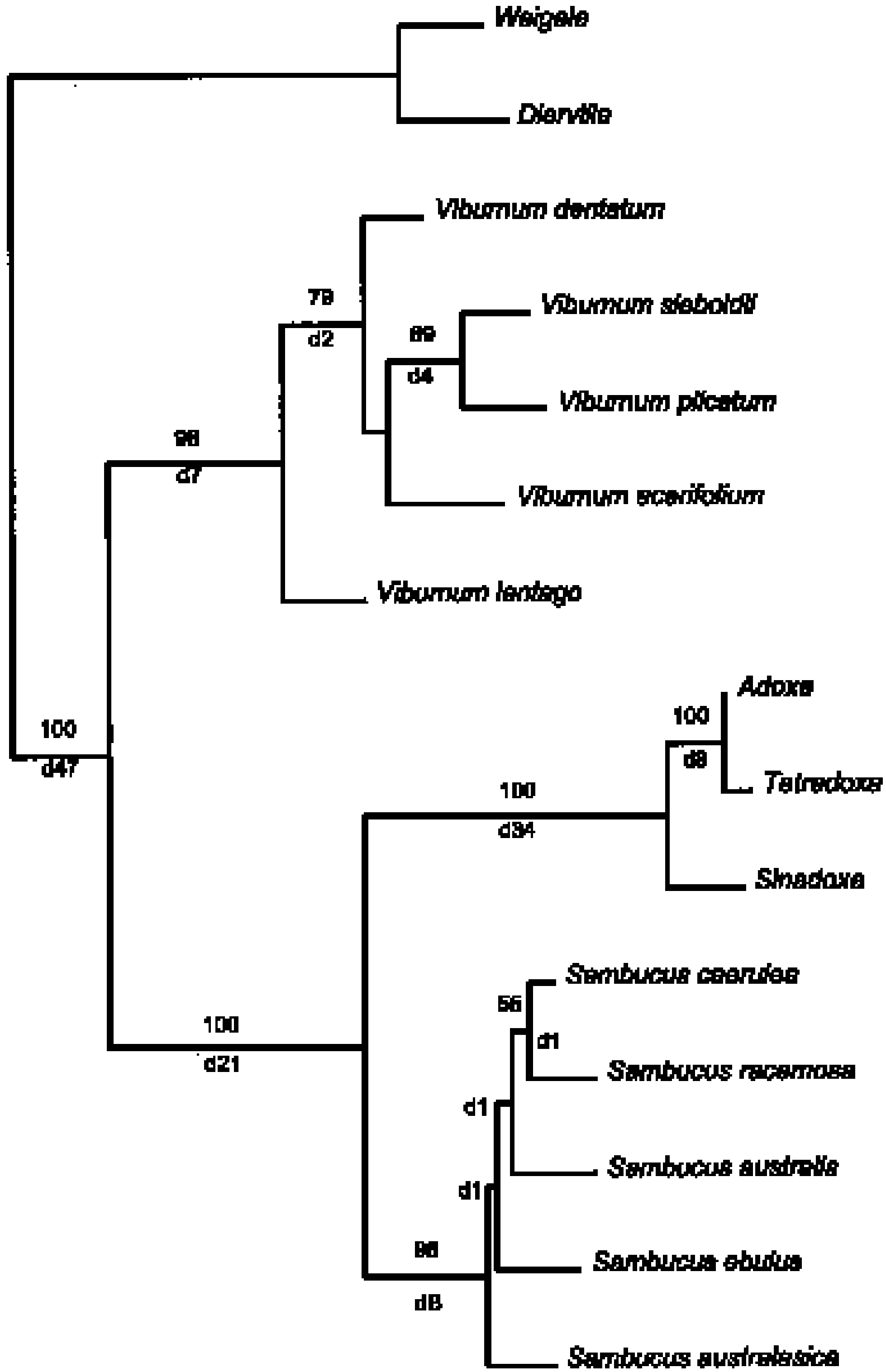

FIGURE 5. Phylogram of one of the two most parsimonious trees resulting from the analysis of Adoxaceae based on ITS sequences (analysis 4); length=347 steps; consistency index (CI), excluding uninformative characters=0.75; retention index (RI)=0.86. Bootstrap values greater than 50% are indicated above the branches and decay indices below. Branch lengths scaled to the number of inferred state changes.

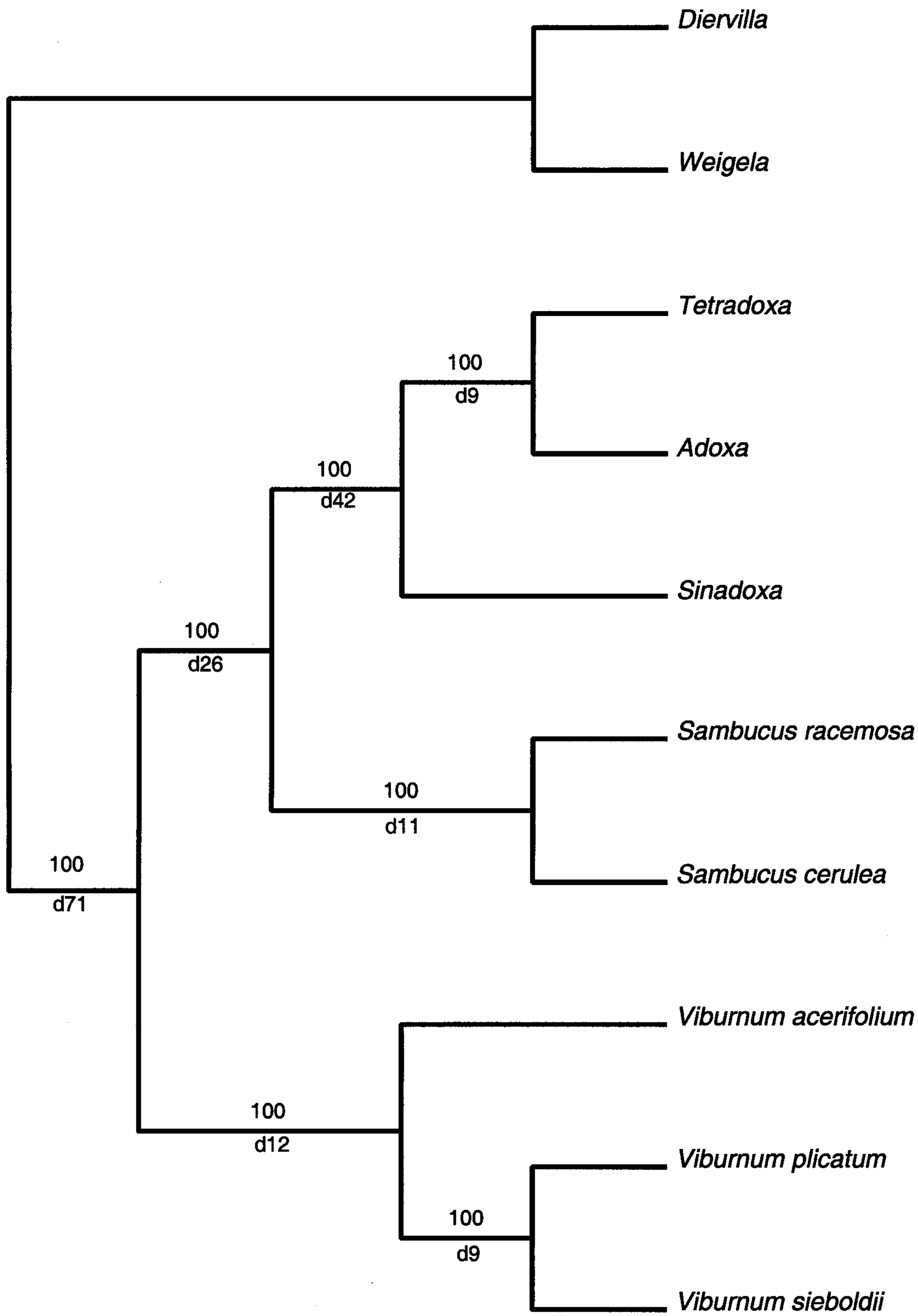

FIGURE 6. The single most parsimonious trees resulting from the analysis of Adoxaceae based on *rbc*L and ITS sequences (analysis 5); length=395 steps; consistency index (CI), excluding uninformative characters=0.83; retention index (RI)=0.88. Bootstrap values greater than 50% are indicated above the branches and decay indices below.

Adoxaceae will refer to the clade including *Viburnum*, *Sambucus*, *Sinadoxa*, *Tetradoxa*, and *Adoxa*. Caprifoliaceae will refer to the clade including Caprifolieae, Diervilleae, and Linnaeeae (of traditional Caprifoliaceae), plus Morinaceae, Valerianaceae, *Triplostegia*, and Dipsacaceae. Note especially that Caprifoliaceae *sensu* Judd et al. (1994) includes several taxa traditionally treated as families (e.g., Dipsacaceae, Valerianaceae), whose names we retain here (see below under "Phylogenetic Taxonomy"). Adoxaceae, Caprifoliaceae, and the names of other major clades are given formal phylogenetic definitions below.

Relationships and evolution in Adoxaceae.

Relationships within Adoxaceae now seem firmly established. *Sambucus* and *Adoxa* have previously been united on the basis of morphological characters (Donoghue, 1983; Judd et al., 1994; Backlund and Donoghue, 1996), *rbc*L sequences (e.g., Donoghue et al., 1992; Chase et al., 1993; Backlund and Bremer, 1997), and ITS sequences (Eriksson and Donoghue, 1997). The relationships of *Sinadoxa* and *Tetradoxa* have, however, received rather little attention, owing in large part to the rarity of these plants and, therefore, the limited material available for study (but see Liang, 1997). These taxa were both described from China in 1981—*Sinadoxa* by Wu et al. (1981) from limestone outcrops near Nangqen in the southeast corner of Qinghai province, and *Tetradoxa* by Hara (1981; Wu, 1981) from Mt. Omei in Sichuan province. Relocating these plants has proven difficult, however, and few additional specimens have come to light. In 1995 an expedition organized by Dr. In Kaipu of the Chengdu Botanical Institute was successful in rediscovering *Tetradoxa* on Mt. Omei. Later that summer, *Sinadoxa* was recollected in southern Qinghai on an expedition jointly organized by the Xining Botanical Institute, the Beijing Botanical Institute, and the Arnold Arboretum of Harvard University. Both species appear to be extremely rare, but sufficient material was obtained to conduct the sequencing reported here (Table 1).

Several authors have argued that *Adoxa* and *Sinadoxa* are directly related, with *Tetradoxa* more distant and retaining the largest number of ancestral features (Wu, 1981; Liang and Zhang, 1986; Liang, 1997). These three taxa formed a clade in the morphological analysis of Backlund and Donoghue (1996), but relationships among them were unresolved. All of our molecular analyses, based on *rbc*L alone, ITS alone, and the two combined, support the *Sinadoxa*-*Tetradoxa*-*Adoxa* clade, with bootstrap values of 100% in each case, and decay values of 10 for *rbc*L, 34 for ITS, and 42 for the combined data. These analyses also support the conclusion that *Adoxa* and *Tetradoxa* are more closely related to one another than either is to *Sinadoxa*. Bootstrap and decay values are high for the *Tetradoxa*-*Adoxa* clade: 89% and decay = 2 for *rbc*L alone, 100% and decay = 8 for ITS alone, and 100% and decay = 9 for the combined analysis.

These results bear importantly on our interpretation of character evolution in Adoxaceae. The first split, between *Viburnum* and the *Sambucus*-*Adoxa* clade (Adoxoideae *sensu* Thorne, 1992; Eriksson and Donoghue, 1997) is marked by several morphological changes. Abortion of two of the three carpels and displacement of the remaining fertile ovule into a sterile carpel (Wilkinson, 1948, 1949; Fukuoka, 1972) presumably evolved along the *Viburnum* branch (Donoghue, 1983); the resulting one-seeded drupe is also probably a *Viburnum* synapomorphy. The Adoxoideae are marked by the evolution of pinnately compound (or deeply dissected) leaves, simple vessel perforations, extrorse anthers (at least at maturity; see Erbar, 1994), vestigial archesporial tissue (Erbar, 1994), *Adoxa*-type embryo sac development, and possibly by several chemical characters, including production of alkaloids (Donoghue, 1983; Judd et al., 1994; Backlund and Donoghue, 1996; Eriksson and Donoghue, 1997).

Within Adoxoideae, exactly which morphological changes mark the *Sambucus* branch remains uncertain, though candidate synapomorphies include crystal sand in cortical cells and apical opening of the endocarp (see Eriksson and Donoghue, 1997). In contrast, the *Sinadoxa*-*Tetradoxa*-*Adoxa* clade is well marked by the evolution of the herbaceous habit, with rhizomes and a basal rosette of deeply lobed leaves; reduction of the perianth parts to four or fewer in at least some flowers; nectaries of multicellular hairs positioned on the perianth parts (see Wagenitz and Laing, 1984; Erbar, 1994); bifid stamens (arising from a single primordium) in which the filaments are more or less deeply split and the monothecous anthers are therefore widely separated; separate styles with small stigmas; and fruits that are more-or-less dry at maturity (possibly dispersed by ants). These plants may also have a distinctive chemistry, including loss of valerianic acid and the production of coumarins, though this has not been studied in *Sinadoxa* and *Tetradoxa*. It is noteworthy that several of these features appear to have evolved independently within *Sambucus*, including herbaceousness, reduction in the number of perianth parts, and a tendency toward splitting of the stamens and styles (Eriksson and Donoghue, 1997).

Within the *Sinadoxa-Tetradoxa-Adoxa* clade, *Sinadoxa* is unique by virtue of its spikelike inflorescence structure (with scattered clusters of three to five flowers), extreme variation and reduction in the number of perianth parts, and especially by the reduction to just a single carpel and the production of fruits with calyx-derived carnose sacs (which may facilitate water dispersal). The *Tetradoxa-Adoxa* clade is characterized by smaller plants with leaves that are trifoliate or ternately lobed. In *Tetradoxa*, the perianth parts are acuminate at the apex (as they also are in several *Sambucus* species, including *S. ebulus*; Eriksson and Donoghue, 1997); fusion of filament-halves at the base (i.e., separation of filaments above the middle) may also be an apomorphy of this species. The elongate inflorescence of *Tetradoxa*, with flowers on distinct pedicels, may represent the ancestral condition from which the headlike inflorescence of *Adoxa* was derived by "compression." Although most *Tetradoxa* flowers are 4-merous, they show considerable variation in merousness along the inflorescence axis (Liang and Zhang, 1986)**;** in *Adoxa*, the four lateral flowers in the cubelike head are typically five-merous (usually with only three sepals developed), and the terminal flower is four-merous (see Erbar, 1994).

Liang (1997) showed that *Tetradoxa* and *Sinadoxa* have simpler floral vasculature than either *Adoxa moschatellina* or *A. orientalis* (Nepomnyashchaya, 1984) and suggested that *Tetradoxa*, in particular, had retained the ancestral characteristics (see also Liang and Zhang, 1986). Our results suggest that elongate inflorescences may have been ancestral, but it is possible that the T-shaped stamens of *Tetradoxa* were derived from an ancestor with the completely bifid condition, as seen in the other species. Inclusion of *Sinadoxa* and *Tetradoxa* in developmental studies will be necessary to determine the generality of many other unusual characteristics seen in *Adoxa* (Erbar, 1994), such as "lobelioid" orientation of the five-merous flowers (also see Donoghue et al., 1998), loss of early corolla ring primordium, and reduced vestigial archesporium.

Relationships and evolution in Caprifoliaceae. Comparison of our separate and combined analyses shows that, although these generally yield similar results, morphological characters are important in resolving a number of relationships. Perhaps most importantly, morphological data tend to unite the genera of Linnaeeae, greatly increase support for the Morinaceae-Valerianaceae-*Triplostegia*-Dipsacaceae clade, and link these two clades directly together. They also seem to link *Triplostegia* with Valerianaceae, as opposed to Dipsacaceae.

Linnaeeae were united by supernumerary inflorescence bracts (see Fukuoka, 1969; Weberling, 1989) in Judd et al. (1994). However, it is perhaps more likely that this feature is characteristic of Linnaeeae plus the Morinaceae-Valerianaceae-*Triplostegia*-Dipsacaceae clade. Under this view, supernumerary bracts were modified and fused to form the characteristic epicalyx seen in Morinaceae and Dipsacaceae (Hofmann and Göttmann, 1990; Manchester and Donoghue, 1995; Roels and Smets, 1996; Backlund and Donoghue, 1996). This scenario would, however, require the addition of a second epicalyx in *Triplostegia* and the loss of epicalyx in Valerianaceae (or perhaps its modification to form fruit wings, as in *Patrinia*). It is possible that Linnaeeae are distinguished by supervolute leaf vernation and by contraction of the chloroplast DNA inverted repeat, but data are still too limited to be certain (Backlund and Donoghue, 1996). The best support for the monophyly of Linnaeeae comes from analyses of *ndh*F and other chloroplast genes. Studies by Pyck et al. (1999), Pyck and Smets (2000), and Bell et al. (2001) all support Linnaeeae as a clade.

Morphological data provide more convincing support for the Morinaceae-Valerianaceae-*Triplostegia*-Dipsacaceae clade, which is only weakly supported in *rbc*L analyses. A number of characters reflect a shift to herbaceousness in this group, including the presence of a taproot and persistent basal leaves (in addition to cauline leaves), the absence of bud scales, and a tendency toward simple perforation plates in the vessels (especially in Valerianaceae). Possible reproductive synapomorphies include the presence of an epicalyx (though, as noted above, this would require loss in Valerianaceae), reduction of the calyx lobes or modification into persistent bristles or pappus (more "normal" lobes are seen in Morinaceae and in *Nardostachys* of Valerianaceae), and reduction in endosperm, culminating in complete loss in Valerianaceae. Finally, the Morinaceae-Valerianaceae-*Triplostegia*-Dipsacaceae clade is characterized by distinctive chemistry, including the presence of alkaloids, cathecolic tannins, and monoterpenoids.

The link between the Linnaeeae and the Morinaceae-Valerianaceae-*Triplostegia*-Dipsacaceae clade is also supported by several rather clear-cut morphological features, as highlighted by Judd et al. (1994). Stamen number is reduced from five to four, which then may be didynamous in arrangement. During ovary development two of the three carpels abort, leaving a single-seeded carpel occupying half of the ovary. Wilkinson (1949), in particular, stressed the great similarity of this condition in Linnaeeae and Valerianaceae, along with the similar median position and compound vasculature of the ovule (also see Fukuoka, 1972). Similar carpel abortion occurs in Morinaceae and in *Triplostegia*. Under the view that this characterizes the entire clade, the loss of a clear sign of aborted carpels in Dipsacaceae is interpreted as a further modification. Finally, the ovary in all of these plants matures into an achene.

These results have especially important implications for our understanding of ovary and fruit evolution. Trees based on *rbc*L sequences alone indicate that Linnaeeae are not monophyletic and that Diervilleae were, in effect, derived within Linnaeeae. Such trees imply that the bi-carpellate, many-seeded, elongate capsules characteristic of the Diervilleae were derived from the tri-carpellate, one-seeded, achene fruits seen in Linnaeeae, Morinaceae, *Triplostegia*, Valerianaceae, and, probably ancestrally, in Dipsacaceae. As we have noted, this result is not upheld in combined analyses with morphological characters; Linnaeeae are instead linked with the Morinaceae-Valerianaceae-*Triplostegia*-Dipsacaceae clade. Support for this result is not especially strong, but it certainly yields a simpler scenario for fruit evolution. Specifically, our combined trees imply that abortion of two carpels and achene fruits evolved once, at the base of the Linnaeeae-Morinaceae-Valerianaceae *Triplostegia*-Dipsacaceae clade, and did not secondarily give rise to bi-carpellate capsules.

Triplostegia has sometimes been linked with Valerianaceae and sometimes with Dipsacaceae (see Backlund and Bremer, 1998). In an earlier *rbc*L study (Backlund and Bremer, 1998) the position of *Triplostegia* was poorly resolved; successive-approximations weighting weakly linked it with Valerianaceae. In our *rbc*L analysis it is weakly linked with Dipsacaceae instead. Taking morphological characters into account (Backlund and Donoghue, 1996), *Triplostegia* is linked with both Valerianaceae and Dipsacaceae on the basis of simple perforation plates (or nearly so), further reduction of the calyx lobes, several pollen characters, and the presence of chlorophyllous embryos (Yakovlev and Zhukova, 1980). Within this clade, *Triplostegia* is united with Valerianaceae on the basis of pollen morphological characters, including apertures with a distinctive "halo" (Backlund and Nilsson, 1997); endosperm reduction in *Triplostegia* (Peng et al., 1995) or complete loss in Valerianaceae; and chemical characters, especially the presence of valepotriate iridoid compounds (Backlund and Moritz, 1996).

Dipsacales monophyly.

Several phylogenetic problems are not convincingly resolved by our analyses, most notably the question of the monophyly of traditional Dipsacales (Donoghue, 1983), including just Adoxaceae and Caprifoliaceae *sensu* Judd et al. (1994). In most previous molecular studies, this clade has been recovered (Chase et al., 1993; Olmstead et al., 1992, 1993; Rice et al., 1997), though with only weak support. Donoghue et al. (1992) and Downie and Palmer (1992) found alternative arrangements, sometimes including Araliaceae, but taxon sampling was limited in these studies. The main alternative was suggested by *rbc*L analyses conducted by Bremer et al. (1994), which implied that *Desfontainia* may be closely related to, or even nested within, Dipsacales. Outgroups were too poorly sampled by Judd et al. (1994) to provide a critical test using morphological data. However, the Backlund and Donoghue (1996) morphological analysis, as well as their combined analysis with *rbc*L, showed *Columellia* and *Desfontainia* to be nested within Dipsacales as the sister group(s) of the Caprifoliaceae clade.

In our *rbc*L analysis the monophyly of Dipsacales was supported, but only weakly (bootstrap $<50\%$; decay = 1); it requires just a single extra step to move the *Columellia-Desfontainia* clade within the group. With the addition of the Backlund and Donoghue (1996) morphological characters, trees of both types are equally parsimonious, that is, with *Columellia* and *Desfontainia* as the sister group of Dipsacales and with these taxa nested within Dipsacales as the sister group of Caprifoliaceae.

The original Backlund and Donoghue (1996) analysis, which included a broader sample of outgroups, appeared to show much better support for the inclusion of *Columellia* and *Desfontainia* within Dipsacales. However, on closer inspection, this is not the case. Both the clade containing the traditional Dipsacales plus *Columellia* and *Desfontainia*, and the branch linking *Columellia* and *Desfontainia* with Caprifoliaceae, were very weakly supported (bootstraps <50%; decay = 1). Furthermore, reexamination of the morphological characters optimized as changing along these branches (referred to below by character numbers used in Backlund and Donoghue, 1996) shows that most of these do not provide unequivocal support. The branch including traditional Dipsacales plus *Columellia* and *Desfontainia* is marked by 12 morphological changes in Backlund and Donoghue (1996). Two of these are unknown in *Columellia* and *Desfontainia*—iridoids (character 87) and saponins (95)—and for 7 others the presumed derived state is not present in *Columellia* and/or *Desfontainia*: leaves are evergreen in *Columellia* and *Desfontainia* (4); leaf margins in Dipsacales are very rarely spiny, as in *Columellia* and *Desfontainia* (11); leaf vernation is conduplicate in *Columellia* and *Desfontainia* (15); *Desfontainia* has perforation plates with many cross bars (24); rotate corollas are not found in *Columellia* and *Desfontainia*, or in Caprifoliaceae (42); stamens are clearly fused to the corolla in *Columellia* and *Desfontainia*, as in Caprifoliaceae (50); chromosome numbers are X = 7 in both, not X = 8 as in Dipsacales (103). This leaves tenuinucellate ovules (65), opposite leaves (5), and petals fused into a tube (40), all of which are widespread among asterids, such that the location of character changes are heavily dependent on which outgroups are included in an analysis.

The branch linking *Columellia* and *Desfontainia* with Caprifoliaceae is marked by changes in 14 characters in Backlund and Donoghue (1996). However, 4 of these characters are unknown in *Columellia* and *Desfontainia* (93, ellagic acid; 104, chromosome size; 106, structural rearrangement of the chloroplast inverted repeat; 108, size of the inverted repeat), and *Columellia* or *Desfontainia* lack the presumed derived state of 5 others (27, superficial phellogen is not present in *Desfontainia*; 37, three vascular traces are not present in the calyx lobes of *Columellia*; 46, corolla vasculature is not laterally connected in *Columellia*; 59, stigmas are bilobed, not capitate, in *Columellia*, and are polymorphic in *Desfontainia*; 69, the tapetum is glandular, not amoeboid, in *Desfontainia*). Of the remaining 5 characters, vascular cylinder (21) was scored incorrectly for *Viburnum* and *Sambucus* (they do have cylinders); well-developed corolla tubes (42) and stamens attached within (50) appear to be directly correlated and are widespread among asterids; corolla zygomorphy (43) is polymorphic in most genera of Caprifoliaceae s.s.; and the production of cathecolic tannins (99) is poorly known and highly variable among possible outgroups and must also be homoplastic within Dipsacales.

We conclude from this analysis that molecular *and* morphological evidence is unconvincing that *Columellia* and *Desfontainia* are united with, or nested within, Dipsacales. These taxa may be linked with Dipsacales on the basis of opposite leaves, fused petals, and tenuinucellate ovules, and they may specifically be united with Caprifoliaceae on the basis of elongate corolla tubes bearing the stamens. However, these characters each show high levels of homoplasy among asterids, and there are obvious conflicting characters. Unlike traditional Dipsacales, *Columellia* and *Desfontainia* have spiny, evergreen leaves, bi-carpellate ovaries that are half inferior in *Columellia* and fully superior in *Desfontainia*, solanad embryogeny, and base chromosome numbers of X = 7. Placement within Dipsacales also seems odd from a biogeographic standpoint; traditional Dipsacales are basically Northern Hemisphere in distribution,with greatest diversity in eastem Asia, whereas *Columellia* and *Desfontainia* are centered in South America. Finally, traditional Dipsacales do share a number of possible apomorphies, which may not have been correctly represented in prior analyses, for example, the widespread occurrence of aborted ovules or vestigial archesporial tissue in the upper portion of the ovary (see Erbar, 1994). Depending on details of broader relationships, cellular endosperm development, asterad and related forms of embryogeny, and 3- to 5-carpellate gynoecia may also be synapomorphies of traditional Dipsacales.

Phylogenetic Taxonomy

It is possible to reflect our current understanding of Dipsacales phylogeny using traditional Linnaean nomenclature; that is, using standard ranks such as family, tribe, and so on. This approach has been taken by the Angiosperm Phylogeny Group (APG, 1998), which recognized six families within an Order Dipsacales that excludes Adoxaceae (which APG left unassigned within their "euasterid II" clade): (1) Caprifoliaceae (restricted to the former Caprifolieae), (2) Diervillaceae (for the former Diervilleae; Backlund and Pyck, 1998), (3) Linnaeaceae (for the former Linnaeeae; Backlund and Pyck, 1998), (4) Morinaceae, (5) Dipsacaceae, and (6) Valerianaceae (presumably including *Triplostegia*; Backlund and Bremer, 1998). Note that in this system old names are applied to clades that already have names (e.g., Caprifoliaceae for Caprifolieae; Dipsacales for Caprifoliaceae *sensu* Judd et al., 1994), new names are introduced for clades that already have names that are in wide use (Diervillaceae for Diervilleae, Linnaeaceae for Linnaeeae), and, ironically, no new names are introduced to reflect widely accepted knowledge of phylogenetic relationships among these groups (e.g., the link between Morinaceae, Valerianaceae, and Dipsacaceae, or between this clade and Linnaeeae).

Phylogenetic nomenclature (*sensu* de Queiroz and Gauthier, 1992, 1994; see also Hibbett and Donoghue, 1998), without ranks, deals with this problem more efficiently (Fig. 7). The names Caprifolieae, Diervilleae, Linnaeeae, Dipsacaceae, and Valerianaceae are simply retained for their respective clades; renaming these can only cause confusion. Following Judd et al. (1994), the name Caprifoliaceae is applied to the clade including all of these taxa. Likewise, the name Adoxaceae is used for the clade including *Viburnum*, *Sambucus*, and *Adoxa*, and Adoxoideae is used for the clade including *Sambucus* and *Adoxa* (Donoghue, 1983; Thorne, 1992; Eriksson and Donoghue 1997). On the basis of arguments presented above, the name Dipsacales is retained for the clade that includes Adoxaceae and Caprifoliaceae. Although we consider it doubtful on present evidence, we recognize the possibility that the least inclusive clade including Adoxaceae and Caprifoliaceae might also include *Columellia* and *Desfontainia*.

With phylogenetic nomenclature, new names are given only to clades that have not previously been named. Within Adoxaceae, we here propose the name Adoxina for the clade including *Sinadoxa*, *Tetradoxa*, and *Adoxa*. Within Caprifoliaceae we propose the name Valerina for the clade including Morinaceae, Dipsacaceae, *Triplostegia*, and Valerianaceae, and the name Linnina is applied to the clade including Valerina plus Linnaeeae. Formal phylogenetic definitions of these clades are presented in Table 2.

Conclusions

Previous phylogenetic conclusions are largely confirmed by our analyses. Caprifoliaceae in the traditional sense are not monophyletic, and there are two major lineages within Dipsacales: (1) Adoxaceae, including *Viburnum*, *Sambucus*, *Sinadoxa*, *Tetradoxa*, and *Adoxa*; and (2) Caprifoliaceae, including Caprifolieae, Diervilleae, Linnaeeae, Morinaceae, Valerianaceae, *Triplostegia*, and Dipsacaceae. Within Adoxaceae we conclude that *Sinadoxa* and *Tetradoxa* are linked with *Adoxa*, in Adoxina. Within Caprifoliaceae our combined analyses support Valerina, including Morinaceae, Dipsacaceae, *Triplostegia*, and Valerianaceae, and Linnina, including Valerina plus Linnaeeae. Each of these clades is marked by morphological synapomorphies.

Additional data are needed to test the monophyly of Linnaeeae, as well as to clarify the relationships of Diervilleae (whether with Caprifolieae or with Linnina). Although *Heptacodium* appears to be related to Caprifolieae (rather than Linnaeeae), and *Triplostegia* may be weakly united with Valerianaceae (rather than Dipsacaceae), we look forward to additional evidence on these issues. Relationships within Diervilleae have recently been analyzed (Kim and Kim, 1999), but relationships within Caprifolieae and Linnaeeae remain poorly resolved. Finally, the question of the monophyly of Dipsacales, whether including or excluding *Columellia* and *Desfontainia*, needs further attention.

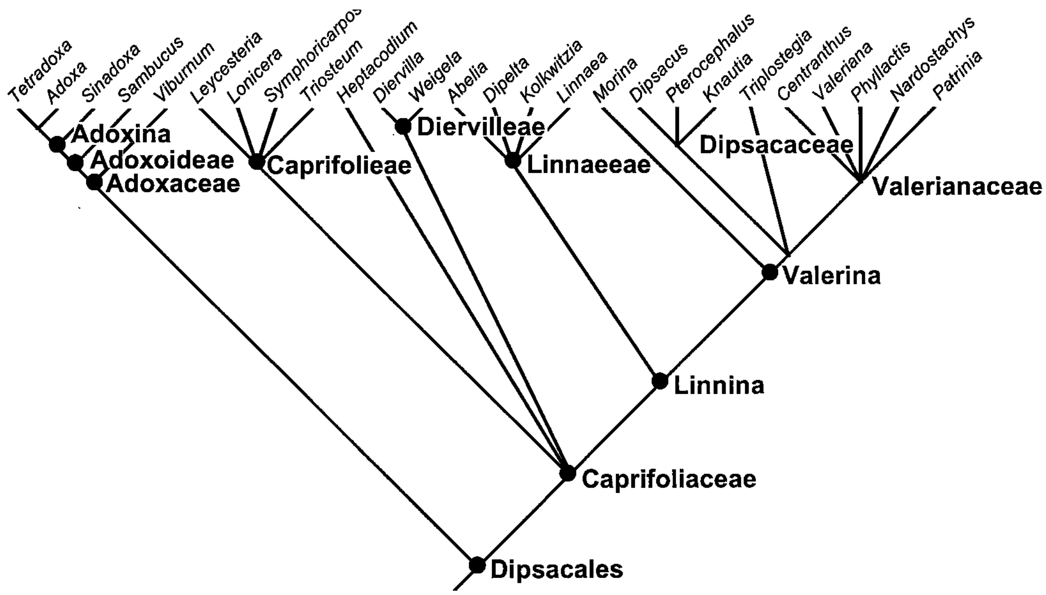

FIGURE 7. Summary Dipsacales phylogeny showing the proposed application of names to clades. Phylogenetic definitions are provided in Table 2 for those clades marked with a dot.

TABLE 1. Voucher information and GenBank accession numbers for species used in the *rbc*L and ITS analyses.

SPECIES	REFERENCE OR VOUCHER	GENBANK NO.
Abelia x *grandiflora* Rehder	Cult. Univ. Arizona, Tucson, 1993; Donoghue, voucher lacking	AJ420875
Adoxa moschatellina L.	*rbc*L: Donoghue et al., 1992 ITS: Eriksson and Donoghue, 1997	L01884 U88194
Barnadesia caryophylla (Vell.) S. F. Blake	Olmstead et al., 1992	L01887
Boopis anthemoides Juss.	Olmstead et al., 1993	L13860
Brunia albiflora Phillips	Backlund and Bremer, 1997	Y10674
Campanula ramulosa Wall.	Olmstead et al., 1992	L13861
Centranthus ruber (L.) DC.	Cult. Univ. Arizona, Tucson, 1993; Donoghue, voucher lacking	AJ420879
Columellia oblonga Ruiz & Pav.	Backlund and Bremer, 1997	Y10675
Coriandrum sativum L.	Olmstead et al., 1992	L11676
Cornus kousa Hance	Olmstead et al., 1993	L14395
Desfontainia spinosa Ruiz & Pav.	Bremer et al., 1994	Z29670
Diervilla sessilifolia Buckley	*rbc*L: Bremer et al., 1994 ITS: Kim and Kim, 1999	Z29672 AF078703
Dipelta floribunda Maxim.	Cult. Arnold Arboretum, 14514-B; *Kelly and Buckland 32*	AJ420876
Dipsacus sativus (L.) Honck.	Olmstead et al., 1992	L13864
Gentiana procera Holm	Olmstead et al., 1993	L14398
Griselinia lucida G. Forst.	Xiang et al., 1993	L11225
Hedera helix L.	Olmstead et al., 1992	L01924
Heptacodium miconioides Rehder	Cult. Arnold Arboretum 1549-80-D; *Koller s.n.*, 12 Oct. 1984 (A)	AJ420873
Knautia intermedia Pernh. & Wettst.	Backlund and Bremer, 1997	Y10698
Kolkwitzia amabilis Graebn.	Cult. Arnold Arboretum 18090; *Elsik and Siegel 1558* (A)	AJ420877
Leycesteria formosa Wall.	Cult. Kew Botanic Gardens, UK, 1990; Donoghue, voucher lacking	AJ420872
Linnaea borealis L.	Door County, WI, 1990; Donoghue, voucher lacking	AJ420878
Lonicera orientalis Lam.	Gustafsson et al., 1996	X87389
Lonicera prolifera (G.Kirchn.) Rehder	Cult. Arnold Arboretum, 870-74-A; voucher lacking	AJ420870
Menyanthes trifoliata L.	Olmstead et al., 1993	L14006
Morina coulteriana Royle	Backlund and Bremer, 1997	Y10706
Nardostachys jatamansii (D. Don) DC.	Backlund and Bremer, 1997	Y10705

TABLE 1. (CONT.)

SPECIES	REFERENCE OR VOUCHER	GENBANK NO.
Nicotiana tabacum L.	Lin et al., 1986	
Patrinia rupestris (Pall.) Dufr.	Backlund and Bremer, 1997	Y10704
Phyllactis bracteata Wedd.	Backlund and Bremer, 1997	Y10703
Pittosporum japonicum Hort. ex C. Presl.	Morgan and Soltis, 1993	L11202
Pterocephalus lasiospermus Link ex Buch	Backlund and Bremer, 1997	Y10702
Sambucus australasica (Lindl.) Fritsch	ITS: Eriksson and Donoghue, 1997	U41381
Sambucus australis Cham. & Schltdl.	ITS: Eriksson and Donoghue, 1997	U88196
Sambucus caerulea Rafinesque	*rbc*L: vic. Tucson,Arizona, 1993; Donoghue, voucher lacking	AJ420867
	ITS: Eriksson and Donoghue, 1997	U88197
Sambucus ebulus L.	ITS: Eriksson and Donoghue, 1997	U88200
Sambucus racemosa L.	*rbc*L: Donoghue et al., 1992 ITS: Eriksson and Donoghue, 1997	L14066 U88207
Sinadoxa corydalifolia C. Y. Wu, Z. L. Wu & R. F. Huang	*rbc*L: *Boufford et al. 26555* (A) ITS: *Boufford et al. 26555* (A)	AJ420866 AJ419711
Symphoricarpos albus (L.) S. F. Blake	Olmstead et al., 1992	L11682
Tetradoxa omeiensis (H. Hara) C. Y. Wu	*rbc*L: *Donoghue et al. 4000* (A) ITS: *Donoghue et al. 4000* (A)	AJ420865 AJ419710
Triosteum perfoliatum L.	vic. Madison, WI, 1990; Donoghue, voucher lacking	AJ420870
Triplostegia glandulifera Wall. ex DC.	Backlund and Bremer, 1997	Y10700
Valeriana officinalis L.	Olmstead et al., 1992	L13934
Viburnum acerifolium L.	*rbc*L: Olmstead et al., 1992 ITS: Cult. Arnold Arboretum 1505-67; *Elsik 2102* (A)	L01959 AJ420923 AJ420924
Viburnum dentatum L.	ITS: Eriksson and Donoghue, 1997	U88552 U88553
Viburnum lentago L.	ITS: Eriksson and Donoghue, 1997	U88554 U88555
Viburnum plicatum Thunb.	*rbc*L: Cult. Arnold Arboretum 1050-67-A; *Dwyer et al., 4354* (A) ITS: Cult. Arnold Arboretum 1050-67-A; *Dwyer et al., 4354* (A)	AJ420868 AJ420925 AJ420926
Viburnum sieboldii Miq.	*rbc*L: Cult. Arnold Arboretum 616-6-B; *Elsik et al. 2640* (A) ITS: Eriksson and Donoghue, 1997	AJ420869 U88556 U88557
Weigela hortensis (Sieb. & Zuck.) C. A. Mey.	*rbc*L: Cult. Arnold Arboretum 1897-77-A; *Kelly and Buckland 28* (A) ITS: Kim and Kim, 1999	AJ420874 AF078713

TABLE 2. Phylogenetic definitions for clade names in Fig. 7.

Clade	Definition[1]	Notes
Dipsacales	*Dipsacus fullonum* L. *Linnaea borealis* L. *Lonicera caprifolium* L. *Viburnum lantana* L.	*Sensu* Donoghue (1983) and Judd et al. (1994)
Adoxaceae	*Viburnum lantana* L. *Sambucus nigra* L. *Adoxa moschatellina* L.	*Sensu* Donoghue (1983) and Thorne (1983); defined phylogenetically by Judd et al. (1994)
Adoxoideae	*Sambucus nigra* L. *Adoxa moschatellina* L.	*Sensu* Thorne (1983)
Adoxina	*Adoxa moschatellina* L. *Tetradoxa omeiensis* (H. Hara) C. Y. Wu *Sinadoxa corydalifolia* C.Y. Wu, Z. L. Wu & R. F. Huang	New clade name
Caprifoliaceae	*Lonicera caprifolium* L *Diervilla lonicera* Miller *Linnaea borealis* L. *Valeriana pyrenaica* L. *Dipsacus fullonum* L.	Defined phylogenetically by Judd et al. (1994); Dipsacales *sensu* APG (1998)
Caprifolieae	*Lonicera caprifolium* L. *Symphoricarpos orbiculata* Moench *Leycesteria formosa* Wall.	Caprifoliaceae *sensu* Backlund and Pyck (1998) and APG (1998)
Diervilleae	*Diervilla lonicera* Miller and *Weigela japonica* Thunb.	Diervilliaceae *sensu* Backlund and Pyck (1998) and APG (1998)
Linnina	*Abelia chinensis* R. Brown *Linnaea borealis* L. *Morina persica* L. *Valeriana pyrenaica* L. *Dipsacus fullonum* L.	New clade name
Linnaeeae	*Abelia chinensis* R. Brown *Linnaea borealis* L. *Kolkwitzia amabilis* Graebner and *Dipelta floribunda* Maxim.	Linnaeaceae *sensu* Backlund and Pyck (1998) and APG (1998)
Valerina	*Morina persica* L. *Valeriana pyrenaica* L. *Dipsacus fullonum* L.	New clade name

[1] All of the definitions are "node-based" (de Queiroz and Gauthier, 1992, 1994; see the PhyloCode at http://www.ohiou.edu/phylocode/); each name is defined as the least-inclusive clade containing the taxa listed.

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