

The Phylogenetic Relationships of *Viburnum*

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Introduction

"It is legitimate . . . to formulate and test alternative hypotheses of relationship within the context of a larger hypothesis which is accepted for the sake of analysis. How could it be otherwise? . . . We must assume we have gotten somewhere during the last few hundred years of research in systematics."

(Eldredge, 1979:171)

Plant systematists are attempting to decipher the evolutionary history of the angiosperms and to reflect their understanding of phylogenetic relationships in a classification. This is a formidable undertaking and there are many areas of uncertainty, as well as disagreements over particular relationships and, more importantly, over general approaches to phylogeny reconstruction and classification. In recent years Takhtajan (1969, 1980), Cronquist (1968, 1981), Thorne (1968, 1976), and Dahlgren (1975, 1980) have

outlined their views on the relationships among angiosperm families and orders. Although these "systems" have much in common, they differ markedly in the circumscription and placement of some families. These areas of disagreement often are the result of differing interpretations of the relationships of pivotal genera that share traits with two or more dissimilar constellations of genera.

As I show below, the genus *Viburnum* is one such pivotal genus and its placement greatly affects hypotheses of relationships at several levels. It shares some traits with *Sambucus* and some with the ten other genera that are usually placed in the Caprifoliaceae and in this way appears to provide a "link" between two otherwise dissimilar elements. Indeed, if *Viburnum* did not exist it is unlikely that *Sambucus* would be allied with the Caprifoliaceae *sensu stricto*.

If a taxon shares traits with two distinct groups, how are we to interpret the phylogenetic relationships of the taxa involved? Is there necessarily a relationship between them, and is it possible to determine the phylogenetic relationships of the pivotal taxon? Hennig (1966) developed a logic by which to assess phylogenetic (cladistic) relationships. He emphasized the importance of distinguishing between ancestral (primitive or plesiomorphic) character states and derived (advanced or apomorphic) states, because, at any particular level, only shared derived character states (synapomorphies) are informative about cladistic relationships; shared ancestral states (symplesiomorphies) do not provide evidence of common ancestry.

In general, determining the evolutionary polarity of character states requires an initial hypothesis of the phylogenetic relationships of the organisms under study, since ancestral and derived conditions are relative to particular ancestors (see below). Since for many groups of angiosperms we presently lack well-corroborated hypotheses of phylogenetic relationship, it appears to be impossible to proceed with the assessment of character state polarities and, in turn, with cladistic analysis.

The case of *Viburnum* provides a good example of this dilemma. In order to assess its cladistic relationships we have to determine whether the character states it shares with other genera are ancestral or derived. However, to determine these polarities requires a prior understanding of the more inclusive cladistic relationships of these groups. Unfortunately, these broader relationships are very uncertain, and thus we appear to be faced with a paradox: until we know more about the overall cladistic relationships among angiosperms it is impossible to proceed with the cladistic analysis of particular groups. In what follows, I consider the phylogenetic relationships of *Viburnum* and outline a general approach to this problem of equivocal outgroups that clarifies the relationships between a "phenetic groping" phase and a cladistic phase of phylogenetic analysis.

In my opinion, much of the confusion surrounding the relationships of *Viburnum* (and, in fact, of many other taxa) is not that there are insufficient data but rather that a rigorous logic for translating character-state distributions into hypotheses of cladistic relationship has not been applied to the available data. Therefore, the emphasis throughout this paper is on the logic of phylogenetic analysis of character data rather than on the characters themselves. Ultimately, of course, our understanding of evolution rests on a thorough understanding of the characters of organisms. Hopefully the hypotheses generated in the present analysis will help to focus attention on the characters and, in turn, this will stimulate new and improved hypotheses of relationship.

Previous Treatments

In Table 10.1 I have summarized the placement of *Viburnum* in the principal angiosperm classifications of the last 150 years. The taxa in which *Viburnum* is placed in these classifications are listed on the left, and to the right are the other taxa included in each category. In this section I compare and contrast these previous treatments, paying

Table 10.1
History of the classification of *Viburnum*

Reference	Rank ^a	Viburnum	Caprifoliaceae <i>sensu stricto</i>									Miscellaneous included taxa ^b
			Sambucus	Triosteum	Diervillaeae Lonicereae Linnaeae	Adoxa	Valerianaceae and Dipsacaceae	Rubiaceae	Cornaceae	Araliaceae		
Candolle (1830)	F	Caprifoliaceae	+	+	+							
	T	Sambuceae	+									
Hooker (1873)	S	Inferae	+	+	+	+	+	+				CAR (in RUB), CAL, oth
	O	Rubiales	+	+	+	+		+				
	F	Caprifoliaceae	+	+	+	+						ALS, <i>Microsphenium</i>
	T	Sambuceae	+			+						
Fritsch (1891)	SC	Sympetalae	+	+	+	+	+	+				CAR (in RUB), CAL, oth
	F	Caprifoliaceae	+	+	+							ALS
	T	Viburneae		+								
Engler (1898)	SC	Sympetalae	+	+	+	+	+	+				CAR (in RUB), CAL, oth
	O	Rubiales	+	+	+	+	+	+				
	F	Caprifoliaceae	+	+	+							ALS(?)
	T	Viburneae										
Wagenitz (1964)	SC	Sympetalae	+	+	+	+	+	+				CAL, oth
	O	Dipsacales	+	+	+	+	+					
	F	Caprifoliaceae	+	+	+							CAR, ALS(?)
	T	Viburneae		+								
Hutchinson (1967, 1973)	O	Araliales	+	+	+					+	+	oth
	F	Caprifoliaceae	+	+	+							ALS
	T	Viburneae										CAR
Thorne (1976)	SO	Corniflorae	+	+	+	+	+			+	+	oth
	O	Dipsacales	+	+	+	+	+					CAL, MOR
	F	Caprifoliaceae	+	+	+							
	SF	Sambucoideae	+									
Dahlgren (1980)	SO	Corniflorae	+	+	+	+	+			+		ALS, oth
	O	Dipsacales		+	+		+					CAL, MOR, TRI
	F	Viburnaceae										
Takhtajan (1980)	SC	Asteridae	+	+	+	+	+	+		+		CAL, oth
	O	Dipsacales	+	+	+	+	+					MOR
	F	Caprifoliaceae	+	+	+							CAR
	SF	Viburnoideae										
Cronquist (1981)	SC	Asteridae	+	+	+	+	+	+		+		oth
	O	Dipsacales	+	+	+	+	+					CAL
	F	Caprifoliaceae	+	+	+							CAR

^aSC = Subclass; S = Series; SO = Superorder; O = Order; F = Family; SF = Subfamily; T = Tribe.

^bALS = Alseuosmiaceae (*Alseuosmia*, *Memecylanthus*, *Periomphale*); CAR = Carlemanniaceae (*Carlemannia*, *Silvianthus*); CAL = Calyceraceae; RUB = Rubiaceae; MOR = Morinaceae and TRI = Triplotegiaceae, segregates of Dipsacaceae; oth = others.

particular attention to *Viburnum*, *Sambucus*, and *Adoxa*, which figure prominently in the analysis which follows. I also discuss the circumscriptions and presumed relationships of the Caprifoliaceae *sensu stricto* (s.s.) and the Dipsacales (Table 10.2), and the reasons for not considering the relationships between *Viburnum* and several genera which have occasionally been allied with it (i.e., the Carlemanniaceae and Alseuosmiaceae).

VIBURNUM, SAMBUCUS, AND ADOXA

Although once divided into five genera (Oersted, 1861), *Viburnum sensu lato* (s.l.) is characterized by several unique (and very probably derived) traits, especially the structure and development of the ovary and the construction of the fruits (Fukuoka, 1972; Wilkinson, 1948b, 1949). *Viburnum* is placed in the Caprifoliaceae in all of the classifications in Table I except that of Dahlgren (1980), who (taking up the suggestion of Norn, 1978) placed it in its own family, the Viburnaceae, which he allied with the Caprifoliaceae s.s. in the order Dipsacales. The name Viburnaceae was first proposed by Dumortier (1829), who also included *Sambucus* in that family.

Owing to its unique combination of character states, *Viburnum* is placed by some authors in its own tribe (Engler, 1898; Fukuoka, 1972) or subfamily (Takhtajan, 1980) within the Caprifoliaceae. But relationships to *Sambucus* (Candolle, 1830; Thorne, 1976) and *Adoxa* (Hooker, 1873) have been suggested. Fritsch (1891) proposed a relationship between *Viburnum* and *Triosteum* which was taken up by Wagenitz (1964). However, this suggestion has been convincingly rejected on the basis of differences in habit, inflorescence, calyx, floral symmetry, style, floral anatomy, and chromosome number and morphology (Fukuoka, 1972; Lewis and Fantz, 1973), and is again rejected below.

As is evident from Table 10.1, *Sambucus* is most often placed by itself in a tribe or subfamily of the Caprifoliaceae or is allied with *Viburnum*. A close relationship to other genera in the Caprifoliaceae has never been suggested. Owing mostly to its compound leaves and extrorse anthers, *Sambucus* is sometimes treated as a separate family (Airy Shaw, 1973; Dahlgren, 1975, 1980; Höck, 1892; Link, 1829).

The monotypic genus *Adoxa*¹ has been placed in the Araliaceae (Candolle, 1830), in the Saxifragaceae (Hutchinson, 1973; Warming and Möbius, 1929; see also Sprague, 1927), and in the Caprifoliaceae (Eichler, 1875; Hooker, 1873). However, most authors put *Adoxa* in its own family, which is usually allied with the Caprifoliaceae in the Dipsacales (Table 10.1), although Dahlgren (1975, 1980) placed the Adoxaceae (along with the Sambucaceae) in his Cornales. Several authors have commented on the close relationship of *Adoxa* to *Sambucus* (Eichler, 1875; Takhtajan, 1980); Hallier (1912:224) stated that "*Adoxa* n'est à vrai dire qu'un *Sambucus* réduit." For reasons discussed below, in portions of the analysis which follows I consider *Adoxa* to be a member of the Caprifoliaceae s.l.

The genus *Sinadoxa* (containing a single species) has recently been described from China and placed in the Adoxaceae (Wu et al., 1981). I have not had access to living or herbarium material, but judging from its description and an accompanying line drawing, it appears to be a distinct taxon that is similar in many ways to *Adoxa*. However, considering the paucity of information about this new taxon it has not been possible to include it in the present analysis. If it were included, the hypothesized relationship between *Adoxa* and *Sambucus* presented below might be changed, because *Sinadoxa*

¹Most authors have maintained that there is only a single species of *Adoxa* (*A. moschatellina* L.), which is circumboreal in distribution and highly variable in morphology. Recently, a second species (*A. omeiensis* Hara) was described from central China (Hara, 1981), and was subsequently given generic status (*Tetradoxa* C. Y. Wu, 1981). The status of the unusual collections from this area is unclear at present; however, even if they do represent a distinct species, the following analysis would not be significantly affected.

might appear as the sister group of *Adoxa*. However, the addition of *Sinadoxa* would probably not affect the position of *Viburnum*, at least in relation to *Sambucus*.

THE CAPRIFOLIACEAE S.S.

Ten genera (and genera sometimes segregated from these) form the core of the Caprifoliaceae (Table 10.2). With the exception of *Leycesteria*, which was originally placed in the Rubiaceae (tribe Hamelieae), these genera have always been considered members of the Caprifoliaceae. However, the monophyly of this group of genera (the Caprifoliaceae s.s.), as evidenced by synapomorphy, has never been established (see below).

Usually the genera of Caprifoliaceae s.s. are placed in three or four tribes. *Leycesteria*, which Airy Shaw (1932) considered the most primitive genus in the family, is generally allied with *Lonicera* (in the tribe Lonicereae), since both have 2- to 5-loculate ovaries without sterile locules, berry fruits, racemose inflorescences, and a tendency to produce perfoliate leaves.

Symphoricarpos, *Linnaea*, *Dipelta*, *Kolkwitzia*, and *Abelia* (including the segregate *Zabelia*; Ikuse and Kurosawa, 1954) have been united by most authors as the tribe

Table 10.2

Taxa referred to in text

Caprifoliaceae (12 genera in 6 tribes; modified from Fukuoka, 1972; subfamilies after Thorne, 1976)
Subfamily Caprifolioideae
Tribe Lonicereae R. Brown ex DC.
<i>Heptacodium</i> Rehder
<i>Leycesteria</i> Wail.
<i>Lonicera</i> L.
Tribe Linnaeae Fritsch
<i>Abelia</i> R. Brown, including <i>Zabelia</i> (Rehder) Makino ex Hisauchi and Hara
<i>Dipelta</i> Maxim.
<i>Kolkwitzia</i> Graebner
<i>Linnaea</i> L.
<i>Symphoricarpos</i> Duhamel
Tribe Diervilleae C. A. Meyer
<i>Diervilla</i> Miller, including <i>Calyptristigma</i> Trautv. and Mey., <i>Macrodiervilla</i> Nakai, and <i>Weigela</i> Thunberg
Tribe Triosteae Hutchinson
<i>Triosteum</i> L.
Subfamily Sambucoideae
Tribe Viburneae Fritsch
<i>Viburnum</i> L.
Tribe Sambuceae HBK ex DC.
<i>Sambucus</i> L.
Caprifoliaceae sensu lato (s.l.)
Caprifoliaceae plus <i>Adoxa</i>
Caprifoliaceae sensu stricto (s.s.) (10 genera in 4 tribes)
Caprifoliaceae minus <i>Viburnum</i> and <i>Sambucus</i>
Dipsacales
Caprifoliaceae s.l.
Dipsacaceae
Valerianaceae
Dipsacales sensu stricto (s.s.)
Dipsacales minus the Caprifoliaceae s.l.

Linnaeae, because of the reduction in the number of fertile locules in the ovary (from five to three, except four in *Symphoricarpos*), in the number of seeds (from many to one or two), and in stamen number (from five to four).

Diervilla (including *Calyptrostigma*, *Macrodiervilla*, and *Weigela*; see Nakai, 1936; Schneider, 1930) is usually placed in a separate tribe because of its elongate, bilocular ovary which develops into a many-seeded capsule.

The relationship of *Triosteum* is questionable. In addition to its placement with *Viburnum* (see above), it has been placed in a separate tribe because of its herbaceous habit, floral anatomy (Wilkinson, 1949), and unusual fruits (Fukuoka, 1972; Hutchinson, 1967). However, it has also been allied with the Lonicereae (Lewis and Fantz, 1973; Troll and Weberling, 1966).

The position of *Heptacodium* is also unclear. Metcalfe (1952) presented anatomical evidence for its inclusion in the Caprifoliaceae. Rehder (1916) noted its similarity to *Lonicera* and *Linnaea*, and Weberling (1966a) placed it with *Lonicera* on the basis of inflorescence structure.

OTHER GENERA

Several other genera have been placed in the Caprifoliaceae, but these appear to be unrelated to any member of the family and are best accommodated elsewhere. Hooker (1873) put *Microsplenium* Hook. f. in the Caprifoliaceae, but this taxon (as the genus *Machaonia* Knuth) belongs in the Rubiaceae (Baillon, 1881). The relationships of several other genera are more problematical.

Carlemannia Benth. and *Silvianthus* Hook. f. are sometimes included in the Caprifoliaceae (Table 10.1; see also Kern and Van Steenis, 1951), but relationships with the Rubiaceae, Valerianaceae, Gesneriaceae, Verbenaceae, and Saxifragaceae have also been suggested. Bremekamp (1939, 1966) considered them best allied with the Caprifoliaceae, but possibly as a separate family. However, Airy Shaw (1965b) concluded that they should definitely not be placed in the Caprifoliaceae; instead he proposed that they be placed in a separate family, the Carlemanniaceae. These plants are perennial herbs, with uni- or bilocular ovaries containing numerous ovules, two stamens with anthers connivent around the style, and elongate, asymmetrical calyx lobes. In addition, in stem anatomy, pollen morphology, and stomata they are unlike any member of the Caprifoliaceae. These characters exclude them from the Caprifoliaceae in any sense. Hutchinson's (1967) suggestion that they are closely related to *Viburnum* is unfounded, since these genera have virtually nothing in common (Fukuoka, 1972). For this reason *Carlemannia* and *Silvianthus* are not discussed further here.

Three small genera native to New Zealand, New Caledonia, and Australia—*Alseuosmia* A. Cunn., *Periomphale* Baill. (including *Pachydiscus* Gilg and Schltr.), and *Mecyclyanthus* Gilg and Schltr.—have sometimes been assigned to the Caprifoliaceae (Schlechter and Gilg, 1907), especially in older treatments. More recently they have often been segregated as the family Alseuosmiaceae (Airy Shaw, 1965a) and allied with the woody Saxifragales or Rosales (e.g., Escalloniaceae or Pittosporaceae; Gardner, 1978). Hutchinson (1967) noted a resemblance between *Alseuosmia* and "certain Vacciniaceae." Recently (Donoghue and Stevens, unpubl.) a relationship has been proposed between *Alseuosmia* and the problematical genus *Wittsteinia* F. Muell., which has been considered a monotypic subfamily of the Ericaceae (Stevens, 1971). These two genera are very similar in their flowers, leaves, trichomes, and pollen grains, and they differ markedly from the Caprifoliaceae in having alternate leaf arrangement, valvate corolla lobe aestivation, and sometimes hypogynous flowers, and in pollen morphology (Cronquist, 1968; Gardner, 1978). In any case, there is no evidence of a relationship between these genera and *Viburnum*, and, therefore, they will not be discussed further.

OTHER FAMILIES

In most modern treatments the Caprifoliaceae are allied with the Valerianaceae and Dipsacaceae. However, Hutchinson (1973) placed the herbaceous families in a separate division. The Caprifoliaceae are generally considered the primitive member of the Dipsacales from which the herbaceous groups were presumably derived (Cronquist, 1968). In particular, the Valerianaceae are thought to be derived from the Linnaeae through an ancestor similar to *Nardostachys* DC. (Valerianaceae). This hypothesis is supported by studies of floral morphology and anatomy (Wilkinson, 1945, 1948a, 1949). The Valerianaceae and Dipsacaceae are very closely related (so much so that they might be united by the criteria of Thorne, 1958, 1973), with the Dipsacaceae thought to be the more derived of the two (Cronquist, 1968). Sometimes the Morinaceae and/or Triplotegiaceae are segregated from the Dipsacaceae.

The Calyceraceae are frequently placed with the Dipsacales (Cronquist, 1968; Dahlgren, 1980; Thorne, 1976), but they are sometimes allied with the Campanulaceae on account of their specialized pollen presentation mechanism. They are also out of place in the Dipsacales because of their binucleate pollen, alternate leaves, and centripetal (racemose) inflorescences. In any case, there is no evidence of a relationship of Calyceraceae to *Viburnum*, and hence they are not discussed further.

There is no agreement concerning the relationships of the Caprifoliaceae and Dipsacales to other families. Most authors have allied these groups with the Rubiaceae. In fact, it has been suggested that the Caprifoliaceae should be submerged in the Rubiaceae (Baillon, 1881; McAtee, 1921). Among the modern systems, Takhtajan (1980) and Cronquist (1968, 1981), following Bessey (1915), place the Dipsacales and the Rubiaceae in their Asteridae and discuss their close relationship to one another. Cronquist (1968) indicated a direct derivation of the Dipsacales from the Rubiales. These authors place the Cornaceae and Araliaceae in their subclass Rosidae, but discuss the possibility of a common origin of the Dipsacales with the Cornales and Rubiaceae.

On the other hand, Hutchinson (1973), Thorne (1976), and Dahlgren (1980) ally the Caprifoliaceae with the Cornaceae and/or Araliaceae, and consider any similarity to the Rubiaceae to be incidental and not indicative of close relationship.

Several authors have proposed relationships between the Caprifoliaceae and the Staphyleaceae (Airy Shaw, 1973; Linden, 1966), and even the Loranthaceae (Wight, 1846), but these suggestions are based on superficial resemblances; there are no shared derived character states that could constitute evidence for a close cladistic relationship.

Character-State Distributions in the Caprifoliaceae s.l.

In Tables 10.3 and 10.4 I have recorded the distribution of character states (for 19 characters) among the genera of the Caprifoliaceae s.l. (Table 10.2). This information was obtained from my observations on living plants and herbarium specimens and/or from the literature (see footnote to Tables 10.3 and 10.4 for references). I have listed only those characters that vary among taxa, because characters for which a single state is shared by all members are uninformative about relationships within the group (for these "ubiquitous characters" see Table 10.5). For the same reason, I have not tabulated characters with states distributed so that all taxa but one share a single state; some of these "unique characters" are discussed below. Character-state polarities are not indicated in Tables 10.3 and 10.4. The task of assessing polarities is taken up in the next section.

The character-state distributions fall basically into two patterns, which together demonstrate the pivotal position occupied by *Viburnum*, and hence the confusion surrounding its relationships. In the first pattern (Table 10.3), *Viburnum*, *Sambucus*, and *Adoxa*

(with exceptions as noted and discussed below) are united by one state and the four tribes of the Caprifoliaceae s.s. by the opposite state. On the basis of these characters alone, *Viburnum* appears to be related to *Sambucus* and *Adoxa*. In the second pattern (Table 10.4) *Viburnum* is united with the Caprifoliaceae s.s. and not with *Sambucus* and *Adoxa*, which (as in Table 10.3) continue to share the same state for each character. There are no known character states that unite only *Viburnum* and *Triosteum*, and, hence, the contention that they are closely related is unfounded.

In terms of overall similarity (assuming that characters are not differentially weighted) *Viburnum* clusters with *Sambucus* and *Adoxa*, but in sharing character states with the Caprifoliaceae s.s. it "links" *Sambucus* and *Adoxa* to them. This linkage has, in fact, deterred most authors from removing *Sambucus* from the Caprifoliaceae. *Sambucus* is sometimes placed in its own family, but the character data suggest that even on phenetic grounds alone, if *Sambucus* is removed, *Viburnum* should be removed along with it. These data also clearly demonstrate that *Sambucus* and *Adoxa* have much in common. Previous authors have been reluctant to place them together, however, because *Adoxa* has many unique features and hence is phenetically removed from *Sambucus*.

Assessing the Polarity of Character States

Botanical systematists have become increasingly interested in applying cladistic methods (Bremer and Wanntorp, 1977; Funk and Stuessy, 1978, and references therein, and *Systematic Botany* 3(2):1978, and 5(2):1980), but, unfortunately, emphasis has largely been placed (especially in the United States) on computer methods of cladogram con-

Table 10.3
Character-state distributions in the Caprifoliaceae *sensu lato*: pattern I*

Characters and States	Caprifoliaceae <i>sensu stricto</i> (10 genera)						
	Lonicereae	Linnaeae	Diervilleae	Triosteae	<i>Viburnum</i>	<i>Sambucus</i>	<i>Adoxa</i>
(1) Corolla							
large, tubular, zygomorphic (-)	-	-	-	-	+	+	+
small, rotate, actinomorphic (+)							
(2) Style							
long (-)	-	-	-	-	+	+	+
short (+)							
(3) Stigma							
capitate (-)	-	-	-	-	+	+	+
lobed (+)							
(4) Flower anatomy							
lateral and dorsal carpel	-	-	-	-	+	+	-
traces not extensive (-)							
extensive (+)							
(5) Ovary							
fully inferior (-)	-	-	-	-	+	+	+
$\frac{3}{4}$ inferior (+)							

Characters and States	Caprifoliaceae <i>sensu stricto</i> (10 genera)						
	Lonicereae	Linnaceae	Diervilleae	Triosteae	<i>Viburnum</i>	<i>Sambucus</i>	<i>Adoxa</i>
(6) Fruit							
berry, capsule, or nutlet (-)	-	- ^a	-	- ^b	+	+	+
drupe (+)							
(7) Pollen size							
large (-)	-	- ^c	-	-	+	+	+
small (ca. 1/2 times smaller) (+)							
(8) Pollen exine							
tectate-imperforate (-)	-	-	-	-	+	+	+
semitectate, reticulate (+)							
(9) Tapetum							
ameboid (-)	-	-	-	-	+	+	-
glandular (+)							
(10) Chromosomes							
small (-)	-	-	-	-	+	+	+
large (2 to 4 times longer) (+)							
(11) Inflorescence							
not umbel-like (-)	-	-	-	-	+	+	+
umbel-like (+)							
(12) Stipules							
absent (-)	- ^e	-	-	-	+	+	-
present in some (+)							
(13) Flavonoids							
flavones predominate (-)	-	-	+	-	+	+	nk
flavonols predominate (+)							

*The literature for morphological characters 1, 2, 3, 6, 12, 15, 17, and 19 includes general treatments of the family (Airy Shaw, 1973; Eichler, 1875; Ferguson, 1966a; Fritsch, 1891; Fukuoka, 1972; Hooker, 1873; Hutchinson, 1967, 1973; Lawrence, 1951; Metcalfe and Chalk, 1950; Nakai, 1931; Wagenitz, 1964) and treatments of *Abelia* (Graebner, 1900; Ikuse and Kurosawa, 1954), *Adoxa* (Sprague, 1927; Sturm, 1910), *Diervilla* (Nakai, 1936; Schneider, 1930), *Heptacodium* (Metcalfe, 1952; Weberling, 1966a), *Kolkwitzia* (Weberling, 1966b), *Leycesteria* (Airy Shaw, 1932), *Linnaea* (Graebner, 1900), *Lonicera* (Rehder, 1903), *Sambucus* (Schwerin, 1909, 1920), *Symphoricarpos* (Jones, 1940), and *Viburnum* (Oersted, 1861; Rehder, 1908, 1940). Information on other characters was obtained from the following sources: (1) floral anatomy, characters 4 and 5 (Fukuoka, 1972; Horne, 1914; Wilkinson, 1945, 1949); (2) pollen, characters 7 and 8 (Basset and Crompton, 1970; Donoghue, 1982; Erdtman, 1966; Punt et al., 1974; Reitsma and Reuvers, 1975); (3) embryology, characters 9 and 14 (Davis, 1966; Maheshwari, 1946, 1950; Moissl, 1941; Sunesson, 1933); (4) chromosomes, characters 10 and 16 (Bolkhovskakh et al., 1969; Egolf, 1962; Lewis and Fantz, 1973; Ourbeck, 1970; Sax and Kribs, 1930); (5) inflorescence, character 11 (Sprague, 1927; Troll and Weberling, 1966; Weberling, 1957); (6) flavonoid chemistry, character 13 (Bohm and Glennie, 1971; Gornall et al., 1979); and (7) wood anatomy, character 18 (DeVos, 1951; Metcalfe and Chalk, 1950).

^aThe fruit of *Symphoricarpos* is a drupe.

^bThe fruit of *Triosteum* is a "dry drupe."

^cThere are two pollen sizes in *Symphoricarpos* (Basset and Crompton, 1970).

^dThe inflorescence of *Adoxa* is much reduced (Sprague, 1927).

^eSome species of *Leycesteria* and *Lonicera* have stipules.

Table 10.4
Character-state distributions in the Caprifoliaceae *sensu lato*; pattern II*

Characters and States	Caprifoliaceae <i>s.s.</i>						
	Lonicereae ^d	Linnaeae	Diervilleae	Triosteae	Viburnum	Sambucus	Adoxa
(14) Embryo sac <i>Polygonum</i> type (-) <i>Adoxa</i> type (+)	-	-	-	-	- ^a	+	+
(15) Anthers introrse (-) extrorse (+)	-	-	-	-	-	+	+
(16) Chromosome number $x = (8)9$ (-) $x = 18$ (+)	-	- + ^b	-	-	-	+	+
(17) Habit woody (-) herbaceous (+)	-	-	-	+	-	- +	+
(18) Vessel element perforations scalariform (-) simple (+)	-	-	-	-	-	+	- +
(19) Leaves simple (-) compound (+)	-	-	-	-	-	+	+

* See footnote to Table 10.3.

^a Some *Viburnum* species may have *Allium*-type embryo sac development (Sunesson, 1933).

^b In *Symphoricarpos* $x = 9$, *Abelia* $x = 16$ and 18, remainder $x = 16$.

struction, and not enough attention has been paid to the logic of cladistics and the character level of analysis (Coombs et al., 1981).

Recently, considerable attention has been devoted to the criteria by which the evolutionary polarity of the character states in a transformation series can be determined (Arnold, 1981; Crisci and Stuessy, 1980; Jong, 1980; Lundberg, 1972; Stevens, 1980; Watrous and Wheeler, 1981). Although a number of criteria have been used, most of these are either fraught with practical difficulties (e.g. fossil data), are logically unjustifiable (e.g., ingroup common is primitive), or logically reduce to outgroup analysis (Lundberg, 1972; Stevens, 1980, 1981; Watrous and Wheeler, 1981; Wheeler, 1981). Knowledge of ontogenetic trajectories (which is often very limited) can be used, even in the absence of a hypothesis of relationships, to establish the polarity of the states in an ontogeny, or the polarity of compared ontogenetic sequences (Nelson, 1978b). However, a hypothesis of relationships can readily reverse a parsimony decision concerning the polarity of compared ontogenetic sequences that was based on ontogenetic data alone. If it is possible (as it surely is in most cases) to narrow down the broader cladistic relationships of a study group (even to a set of possible outgroups, as in the present example), then this information should be added to the analysis to yield the best possible parsimony decision concerning polarity (Donoghue and Maddison, unpubl.).

Unfortunately, the problem of determining character-state polarities has received insufficient attention in actual applications of cladistics to plant groups, and the ingroup method (see Stevens, 1980; and Watrous and Wheeler, 1981. for a description and

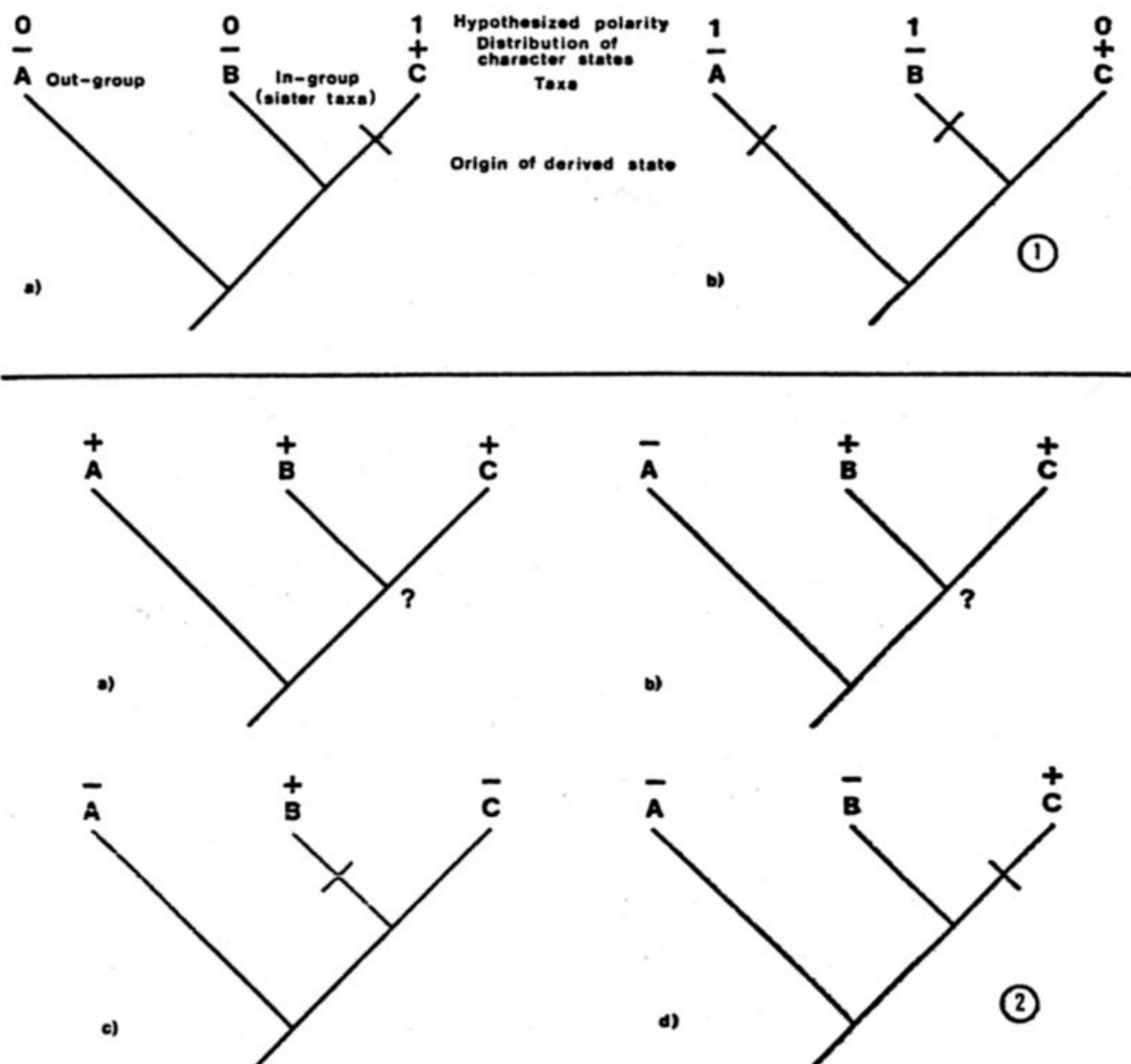
critique of this approach) has been applied without considering its important and potentially misleading consequences (cf. Estabrook and Anderson, 1978; Gardner and LaDuke, 1978). In the present study I employ exclusively the outgroup method of assessing character-state polarities. Although this method has been described in some detail (see especially Stevens, 1980; Watrous and Wheeler, 1981), a thorough understanding of the logic of outgroup comparison is critical to an understanding of the approach used in this paper, and, therefore, I briefly outline this logic here.

Determining polarity by the outgroup method requires some initial understanding of the cladistic relationships of a group. Specifically, to assess whether a character state possessed by the members of a group is ancestral or derived, its sister group and at least one group cladistically basal to these two groups must be known or hypothesized (Fig. 10.1). The underlying principle of the outgroup method is parsimony. The simplest hypothesis, the one which makes the fewest assumptions (requires the fewest character-state transformations) to account for the available evidence, is preferred. For this reason the cladogram in Figure 10.1a is preferred over that in Figure 10.1b.

Additional character-state distributions are considered in Figure 10.2. If all three taxa share a state (Fig. 10.2a) the character is uninformative about character-state polarity or about relationships among the taxa. If the sister groups B and C share a state not possessed by their outgroup A (Fig. 10.2b), this is still uninformative about polarity because it is effectively a two-taxon statement (A versus B and C), and an effective three-taxon statement is a requisite of the outgroup method. Figure 10.2c-d is informative about character-state polarity and hence can provide evidence of the monophyly of particular taxa. These cladograms have in common variation among the sister taxa B and C, with A being similar to *either* B *or* C. The condition in Figure 10.2c provides evidence of the monophyly of taxon B, while that in Figure 10.2d provides evidence of the monophyly of taxon C. Note that it is not possible to establish that a taxon in the position of A has a derived character state. To determine this, outgroups of the clade A, B, C are required.

Although the character-state distributions in Figure 10.2c-d are sufficient for assessing character-state polarity by the outgroup method, it should be clear that other information can and will bear on the choice of the most parsimonious hypothesis of polarity. For example, an additional outgroup corroborates the hypothesis if it possesses the same state as the first outgroup, but it makes a parsimony assessment impossible if it differs in state from the first outgroup. In this latter instance yet another outgroup is required to reach a decision. By an extension of this logic, the more outgroups that are known, and the more of them that share the same character state with the closest outgroup, the more confident we can be that our parsimony decision will not be reversed.

In the analyses below I employ the outgroup method by hypothesizing a series of three-taxon statements. I attempt to find shared derived character states and consider these to be *prima facie* evidence of monophyly. In order to proceed I have had to make assumptions about monophyly and outgroups. Since there are no well-corroborated hypotheses of the broader cladistic relationships of the groups under consideration, I provisionally accept the beliefs of the majority of angiosperm phylogenists, i.e., that the Caprifoliaceae *s.l.* and the Dipsacales are both monophyletic groups. With these assumptions the polarities of character states within the Caprifoliaceae *s.l.* can be determined. Next, I consider the character states that unite the Caprifoliaceae *s.l.* and whether or not, and under what circumstances, they could be considered autapomorphies. Because there is no clear evidence that the Caprifoliaceae *s.l.* is monophyletic, I consider the alternatives, namely, that it is paraphyletic or polyphyletic. In this procedure I have assumed that angiosperm phylogenists have suggested the close relatives of the genera under consideration, and I use these putative relatives, either one at a time or in various combinations, as the outgroups. In these latter instances I have not performed complete



Figs. 10.1–10.2. Logic of the outgroup method of assessing character-state polarity; – and + do not designate polarity; 1 = derived (apomorphic), 0 = ancestral (plesiomorphic). 10.1. In the absence of other information, the interpretation in cladogram (a) is preferred over that in cladogram (b); see text for discussion. 10.2. Character-state distributions on a cladogram of three taxa (A, B, C); (a) and (b) are uninformative about polarity. In (c) the state of B (+) is hypothesized to be derived. In (d) the state of C (+) is hypothesized to be derived.

cladistic analyses but, instead, have sought those character-state distributions which bear directly on the placement of *Viburnum*, and in particular on its placement with *Sambucus* and *Adoxa*.

The Relationships of *Viburnum*, *Sambucus*, and *Adoxa* if the Caprifoliaceae s.l. and the Dipsacales Are Monophyletic

If we assume that the Caprifoliaceae s.l. is a monophyletic family within a monophyletic order Dipsacales (Fig. 10.3a–d), it is possible to establish the polarity of any character with states which vary within the Caprifoliaceae s.l. by referring to the out-group(s) (i.e., the Dipsacales s.s.). For purposes of the analysis I assume that the Dipsacales s.s. is monophyletic, or paraphyletic in a manner which does not affect the analysis (dotted lines in Fig. 10.3). If a state is found in the Dipsacales s.s. and in some

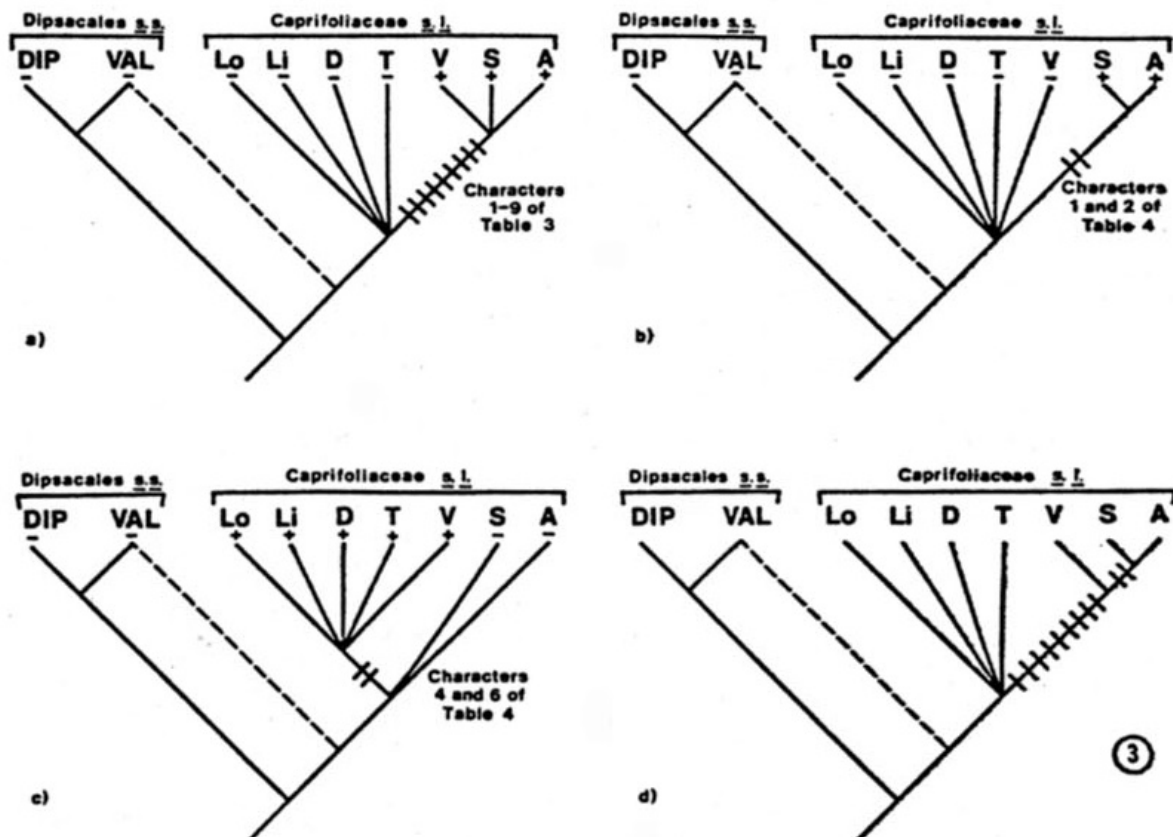


Fig. 10.3. Cladograms of the Dipsacales, with Caprifoliaceae *s.l.* and Dipsacales both assumed to be monophyletic, Dipsacales *s.s.* either monophyletic or paraphyletic (dotted line). DIP = Dipsacaceae; VAL = Valerianaceae; Lo = Lonicereae; Li = Linnaeae; D = Diervilleae; T = Triosteae; V = *Viburnum*; S = *Sambucus*; A = *Adoxa*. a. Synapomorphies of V, S, and A. b. Synapomorphies of S and A. c. Synapomorphies of Lo, Li, D, T, and V. d. Most parsimonious cladogram based on (a), (b), and (c) together.

members of the Caprifoliaceae then it can be considered ancestral. Hence, by determining the states of the characters in Tables 10.3 and 10.4 that occur in the Dipsacales *s.s.*, polarity within the Caprifoliaceae *s.l.* can be determined.²

For characters 1 through 9 in Table 10.3, the states that unite *Viburnum*, *Sambucus*, and *Adoxa* are derived. These synapomorphies suggest that together these genera form a monophyletic group within the Caprifoliaceae *s.l.* (Fig. 10.3a). Characters 14 and 15 in Table 10.4 support a hypothesis that *Sambucus* and *Adoxa* form a monophyletic group (Fig. 10.3b). There is little support for the monophyly of the Caprifoliaceae *s.s.* or of the Caprifoliaceae *s.s.* together with *Viburnum* (Table 10.4, characters 17 and 19; Fig. 10.3c). Hence, the most parsimonious hypothesis is that *Viburnum* is cladistically related to *Sambucus* and *Adoxa* (Fig. 10.3d).

We can conclude, then, that if the Caprifoliaceae *s.l.* is considered monophyletic within a monophyletic Dipsacales, there can be little doubt that *Viburnum*, *Sambucus*, and *Adoxa* form a monophyletic group within the family. Therefore, under these assumptions, the classification of *Viburnum* with *Triosteum* (Fritsch, 1891; Wagenitz, 1964) or with any other genus of the Caprifoliaceae *s.s.* is unjustified. Placement of *Viburnum* in its own tribe (Engler, 1898; Hutchinson, 1973) or subfamily (Takhtajan, 1980) is justifiable. Placement of *Viburnum* with *Sambucus* but excluding *Adoxa* (Candolle, 1830;

²In addition to the standard references on the characters of angiosperm families listed in the footnote to Tables 10.3 and 10.4, I also consulted Ferguson (1965), Patel and Skvarla (1979), and Cronquist (1981) for information on the Valerianaceae and Dipsacaceae.

Thorne, 1976) creates a paraphyletic taxon, but recognizes the relationships of *Sambucus* and *Viburnum* within the Caprifoliaceae as traditionally defined. Placing *Viburnum* in its own family (Dahlgren, 1980) is not justified unless it is allied with *Sambucus* and *Adoxa* at the next higher level. Hooker's (1873) placement of *Viburnum*, *Sambucus*, and *Adoxa* in the same subfamily within the Caprifoliaceae s.l. is supported by this analysis; however, it should be noted that Hooker did not directly relate the Valerianaceae and the Dipsacaceae to the Caprifoliaceae.

Some angiosperm phylogenists would probably be ill at ease with the assumptions made in this section (i.e., the general relationships shown in Fig. 10.3a-d), because the opinion has been expressed (e.g., Cronquist, 1968) that the Valerianaceae and Dipsacaceae are derived relative to the Caprifoliaceae s.l. In particular, their close relationship to, and possible derivation from, the tribe Linnaeae has been suggested (e.g., Wilkinson, 1948a, 1949). But if these suggestions are taken at face value the Caprifoliaceae must be a paraphyletic group. This possibility is considered in more detail below (Figs. 10.5, 10.6).

One of the most striking features of Tables 10.3 and 10.4 is that *Sambucus* and *Adoxa* share the same state for nearly every character. Relative to the rest of the Dipsacales, characters 14 and 15 (at least) in Table 10.4 are synapomorphies for these two genera. But regardless of the outgroup, the fact that *Sambucus* and *Adoxa* both possess the *Adoxa*-type embryo sac argues very strongly for their having shared an immediate common ancestor (Wagenitz, 1977).

In the *Adoxa* type of embryo sac development, all four megaspore nuclei undergo a mitotic division to form an 8-nucleate embryo sac with an egg apparatus, three antipodals, and two polar nuclei (Maheshwari, 1950).

Maheshwari (1946) thoroughly reviewed the occurrence of this kind of development and showed that, although it was once considered widespread among angiosperms, there are "only five genera in which its occurrence is a more or less regular feature: *Adoxa*, *Sambucus*, and some species of *Erythronium*, *Tulipa*, and *Ulmus*" (Maheshwari, 1950:122).³ The very limited occurrence of the *Adoxa*-type embryo sac (in angiosperm genera that are not believed to be primitive) suggests that it is a derived state. That its occurrence is scattered among presumably distantly related groups (Liliaceae, *Ulmus*, and *Sambucus* and *Adoxa*) suggests that it has arisen independently at least three times. It is possible that it arose independently in *Sambucus* and *Adoxa*, but considering the large number of character states that these taxa share, it is most parsimonious to assume that it arose just once in an immediate common ancestor of the two genera. Therefore, in the following analyses *Sambucus* and *Adoxa* together are considered a monophyletic group.

The Monophyly of the Caprifoliaceae s.l. and of the Dipsacales

In the preceding analysis the Caprifoliaceae s.l. was assumed to be monophyletic. This seems a reasonable first assumption, because it has been recognized as a distinct family by nearly all angiosperm phylogenists. However, several authors (e.g., Dahlgren, 1980) have suggested that it is a paraphyletic or polyphyletic group. If the Caprifoliaceae s.l. were paraphyletic or polyphyletic this might greatly affect the hypothesized relationships of *Viburnum*. Therefore, in this section I consider the evidence that the Caprifoliaceae s.l. is monophyletic.

In Table 10.5 I have listed 15 character states shared by all (or nearly all) members

³In *Erythronium* and *Ulmus* species that have been investigated, development is sometimes of the *Adoxa* type and sometimes of the *Fritillaria* type. *Tulipa* species exhibit either an unusual form of *Adoxa*-type development or the *Fritillaria* or *Drusa* type (Maheshwari, 1950).

Table 10.5

Character states that unite members of the Caprifoliaceae *s.l.*, and their distributions among putatively related families

Character State	Valerianaceae	Rubiaceae	Cornaceae	Araliaceae
(1) Flowers 5(4)-merous	+	+	+	+(-)
(2) Flowers perfect	+(-)	+	+(-)	+(-)
(3) Stamens alternate with the petals or corolla lobes	+	+	+	+
(4) Pistil 1	+	+	+	+
(5) Ovary $\frac{3}{4}$ or fully inferior	+	+	+	+
(6) Ovules pendulous	+	+ -	+	+
(7) Embryo small and straight	+	+	+	+
(8) Leaves opposite	+	+	+(-)	-
(9) Pollen trinucleate	+	+ -	-	+
(10) Style 1	+	+	+(-)	-(+)
(11) Ovules unitegmic	+	+	+	-
(12) Endosperm copious	-	+(-)	+	+
(13) Corolla sympetalous	+	+	-	-
(14) Corolla lobes (or petals) imbricate	+	+ -	-(+)	-(+)
(15) Stamens epipetalous	+	+	-	-

of the Caprifoliaceae *s.l.* I have also indicated the distribution of these character states among the families that have traditionally been considered close relatives of the Caprifoliaceae *s.l.* (Table 10.1).⁴ It is clear that none of these character states is restricted in occurrence to the Caprifoliaceae *s.l.* Character states 3, 5, 7, 9, 11, 13, and 14 occur in all of the other families, while the remaining states are found in two or more of them.

On the basis of these data it is not possible to assess whether or not the Caprifoliaceae *s.l.* is monophyletic. Although no single character state is restricted to the Caprifoliaceae *s.l.*, one or more of the character states in Table 10.5 might still be an autapomorphy for the group. It is possible, however, to determine the relationships which would have to obtain in order for any of these character states to provide evidence of monophyly. For example, in order for sympetaly (character state 2) to be an autapomorphy of the Caprifoliaceae *s.l.*, we would have to assume that the ancestors of the Caprifoliaceae *s.l.* were polypetalous (Fig. 10.4a). Therefore, if any of the putative relatives are actual relatives, the Cornaceae and/or Araliaceae must have shared an immediate common ancestor with the Caprifoliaceae *s.l.* We must further assume that the Caprifoliaceae *s.l.* are not the sister group of either the Valerianaceae or the Rubiaceae. This cladogram requires the parallel evolution of numerous other character states (including at least states 1, 4, 6, and 8 in Table 10.3).

⁴In addition to the standard references on the characters of angiosperm families listed in the footnote to Tables 10.3 and 10.4, I also consulted Ferguson (1966b), Graham (1966), Brewbaker (1967), and Cronquist (1981) for information on the Araliaceae, Cornaceae, and Rubiaceae.

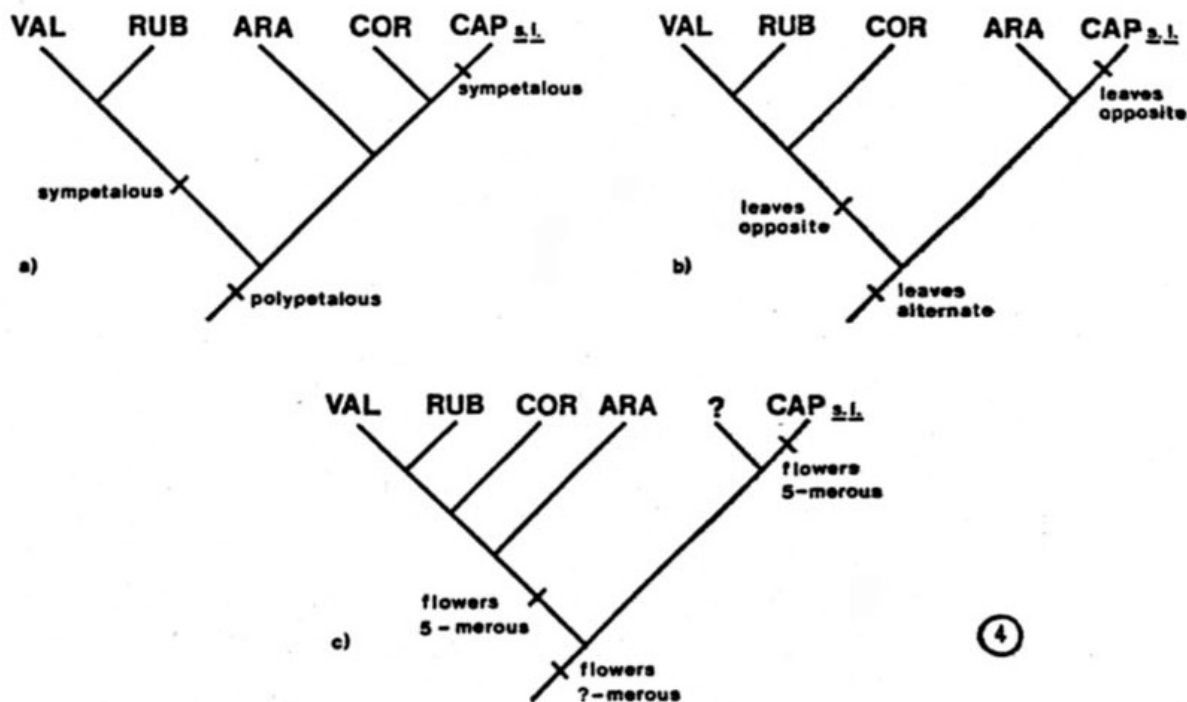


Fig. 10.4. Hypothetical cladograms of Caprifoliaceae *sensu lato* (CAP *s.l.*) and putatively related families. VAL = Valerianaceae, RUB = Rubiaceae; ARA = Araliaceae; COR = Cornaceae. a. Sympetaly as an autapomorphy of the Caprifoliaceae *s.l.* b. Opposite leaves as an autapomorphy. c. 5-merous flowers as an autapomorphy.

The cladograms that allow character states that are more widespread among the related families to be autapomorphies for the Caprifoliaceae *s.l.* are even more limited. Consider opposite leaves (character state 1); if we assume that the putatively related families are actual relatives, the cladogram in Figure 10.4b would allow opposite leaves to be an autapomorphy of the Caprifoliaceae *s.l.* As in Figure 10.4a, this cladogram entails considerable homoplasy.

For a character state that occurs in all of the putatively related families to be an autapomorphy of the Caprifoliaceae *s.l.*, we have to assume that it is *not* the sister group of any of its putative relatives. For example, the cladogram in Figure 10.4c would allow 5-merous flowers (character state 3) to be an autapomorphy of the Caprifoliaceae *s.l.* This cladogram requires that the Caprifoliaceae *s.l.* be cladistically more closely related to some group of plants not previously suggested by angiosperm phylogenists, and would again require parallelism in many characters.

Although no character state is restricted to the Caprifoliaceae *s.l.*, this cannot be taken as evidence of the paraphyly or polyphyly of the group. However, for any widespread character state to be an autapomorphy requires restricted sets of cladograms on which presumably related families are separated from the Caprifoliaceae. On such cladograms homoplasy is great. Therefore, an alternative explanation, i.e., that the Caprifoliaceae *s.l.* is not a monophyletic group, is considered in the following analyses.

This same kind of argument can easily be extended to the Dipsacales to show that, likewise, no character state is restricted to it, either among angiosperms generally or among its putative relatives. Therefore, I also consider the possibility that the order is polyphyletic, and that the Caprifoliaceae *s.l.*, or portions of it, are cladistically most closely related to other families.

Other Possible Outgroups

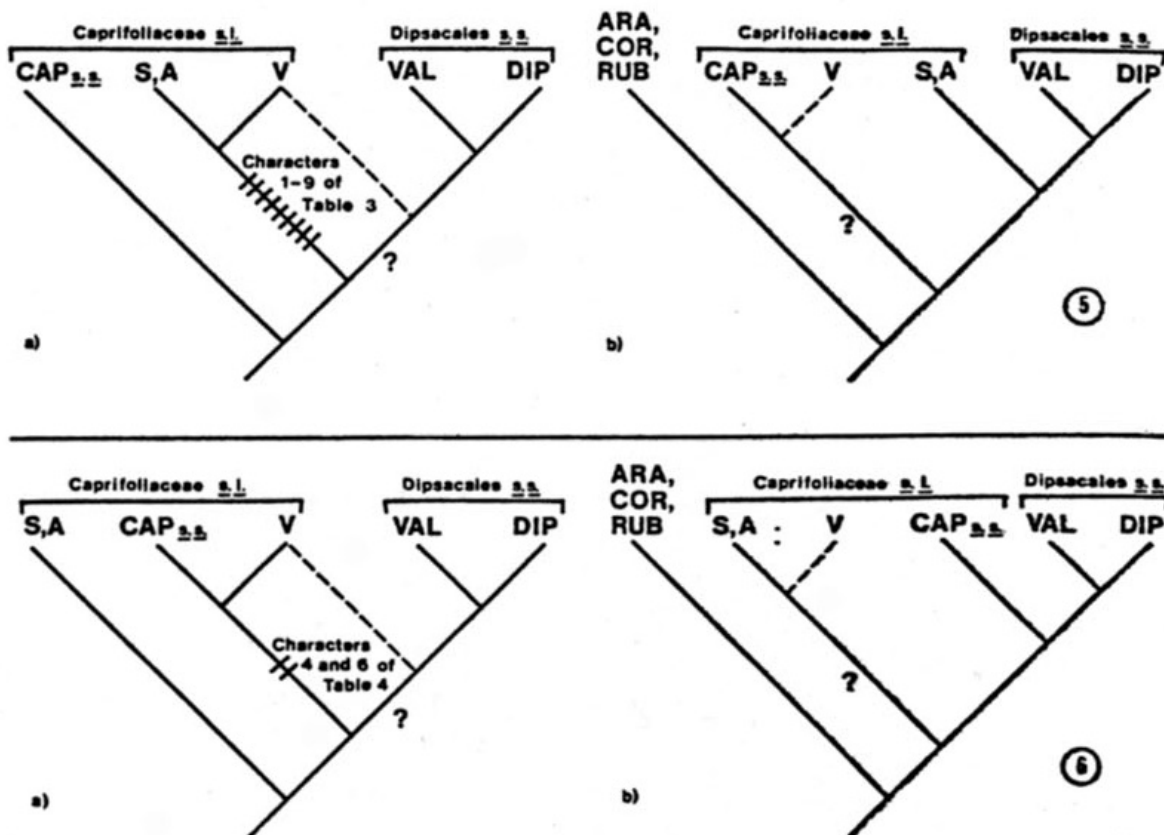
Inasmuch as the Caprifoliaceae *s.l.* and the Dipsacales may not be monophyletic groups, it is necessary to consider what claims can be made about the relationships of *Viburnum* if those taxa are paraphyletic or polyphyletic. In the following analyses I suppose particular arrangements of taxa (which have, in fact, been suggested by previous workers) and consider under which circumstances it is possible (with presently available data) to assess the relationships of *Viburnum*. If it is not possible to do so, I specify the additional information necessary.

DIPSACALES MONOPHYLETIC, CAPRIFOLIACEAE *S.L.* PARAPHYLETIC

There are several ways in which the Caprifoliaceae *s.l.* could be paraphyletic within the Dipsacales. In order to proceed with the analysis I assume that *Sambucus* and *Adoxa* form a monophyletic group (see above), and that the Caprifoliaceae *s.s.*, Valerianaceae, and Dipsacaceae are each monophyletic or are paraphyletic in a way that does not affect the argument (e.g., dotted lines in Fig. 10.3). *Viburnum* is not assumed to be related either to *Sambucus* and *Adoxa* or to the Caprifoliaceae *s.s.*, and an effort is made to find synapomorphies with both of these groups.

In the first case (Fig. 10.5) *Sambucus* and *Adoxa* are the sister group of the Dipsacales *s.s.*, and the Caprifoliaceae *s.s.* are the basal group within the order. Under these circumstances it is possible to determine the polarity of character states that vary within the group which includes *Sambucus*, *Adoxa*, and the Dipsacales *s.s.* by using the Caprifoliaceae *s.s.* as the outgroup. If *Viburnum* belongs in a monophyletic group with *Sambucus*, *Adoxa*, and the Dipsacales *s.s.*, there is abundant evidence that it is cladistically related to *Sambucus* and *Adoxa* (Fig. 10.5a). In fact, all of the character states in Table 10.3 that unite *Viburnum* with *Sambucus* and *Adoxa*, and which were determined to be derived within a monophyletic Caprifoliaceae *s.l.*, would also be derived character states within the group *Sambucus*, *Adoxa*, and Dipsacales *s.s.* It is not possible to find derived character states to support a hypothesis that *Viburnum* is cladistically related to the Caprifoliaceae *s.s.* (a proposition for which there is little evidence, Fig. 10.3c) without looking to additional outgroups (Fig. 10.5b). Using any one of the plausible (previously suggested) outgroups (Araliaceae, Cornaceae, and/or Rubiaceae), I am unable to find a character-state distribution that provides evidence of the monophyly of *Viburnum* and the Caprifoliaceae *s.s.* (i.e., a character in which one state is shared by all members of the outgroup and by *Sambucus*, *Adoxa*, and the Dipsacales *s.s.* and the alternate state is possessed by the Caprifoliaceae *s.s.* and *Viburnum*). All character-state distributions are either uninformative, as in Figure 10.2a or 10.2b, or the character is variable within the outgroup. For example, *Sambucus*, *Adoxa*, and the Dipsacales *s.s.* have compound leaves, the Caprifoliaceae *s.s.* and *Viburnum* have simple leaves, and the Araliaceae have both simple and compound leaves. Under these circumstances polarity cannot be assessed until the ancestral condition in the Araliaceae is established, which requires additional outgroups.

A second way in which the Caprifoliaceae *s.l.* could be paraphyletic within the Dipsacales is shown in Figure 10.6. In this case the Caprifoliaceae *s.s.* are the sister group of the Dipsacales *s.s.*, and *Sambucus* and *Adoxa* are the basal clade in the order. If *Viburnum* is hypothesized to belong to a monophyletic group with the Caprifoliaceae *s.s.* and the Dipsacales *s.s.*, then we can assess its relationships within that group by using *Sambucus* and *Adoxa* as the outgroup. In particular we can assess whether *Viburnum* shares derived character states with the Caprifoliaceae *s.s.* (Fig. 10.6a). When this is done only one derived character state unites these taxa, i.e., simple leaves (Table 10.4, character state 19). Another possible synapomorphy of *Viburnum* and the Capri-



Figs. 10.5–10.6. Cladograms of the Dipsacales, with Dipsacales monophyletic, Caprifoliaceae *s.l.* paraphyletic. 10.5. Caprifoliaceae *s.s.* (CAP *s.s.*) as the basal clade. a. Synapomorphies of *Viburnum* (V), *Sambucus* (S), and *Adoxa* (A) using CAP *s.s.* as the outgroup; b. No synapomorphies are known for V with CAP *s.s.* using Araliaceae (ARA), Cornaceae (COR), and/or Rubiaceae (RUB) as outgroups. 10.6. *Sambucus* and *Adoxa* as the basal clade. a. Synapomorphies of V with CAP *s.s.* using S and A as the outgroup. b. No synapomorphies are known for V with S and A using ARA, COR, and/or RUB as outgroups.

foliaceae *s.s.* under these conditions is the woody habit. Most *Sambucus* species are woody but this could perhaps be interpreted as a secondary acquisition of woodiness independent of *Viburnum* and the Caprifoliaceae *s.s.* If we assume, then, that the ancestors of the Dipsacales possessed compound leaves (and were herbaceous?), *Viburnum* and the Caprifoliaceae *s.s.* would be united by the derived state(s).

To determine if *Viburnum* shares derived states with *Sambucus* and *Adoxa* when the latter are the basal group, additional outgroups are necessary (Fig. 10.6b). Again, using the Araliaceae, Cornaceae, and/or Rubiaceae as outgroups, I have been unable to find character-state distributions to support or refute a cladistic relationship of *Viburnum* with *Sambucus* and *Adoxa*.

DIPSACALES POLYPHYLETIC, CAPRIFOLIACEAE *s.l.* MONOPHYLETIC

If the Caprifoliaceae *s.l.* is monophyletic but unrelated to the Valerianaceae or Dipsacales, and instead is related most directly to, and derived from, either the Araliaceae, Cornaceae, or Rubiaceae, the cladogram in Figure 10.7 is obtained. For each outgroup we should be able to determine whether *Viburnum* shares derived states with the Caprifoliaceae *s.s.* or with *Sambucus* and *Adoxa*. However, in each case I can find no evidence of a cladistic relationship of *Viburnum* to either the Caprifoliaceae *s.s.* or to *Sambucus* and *Adoxa*. There is, however, abundant evidence that the Caprifoliaceae *s.s.* is monophyletic. The reason for these results is that (1) it is not possible to assess

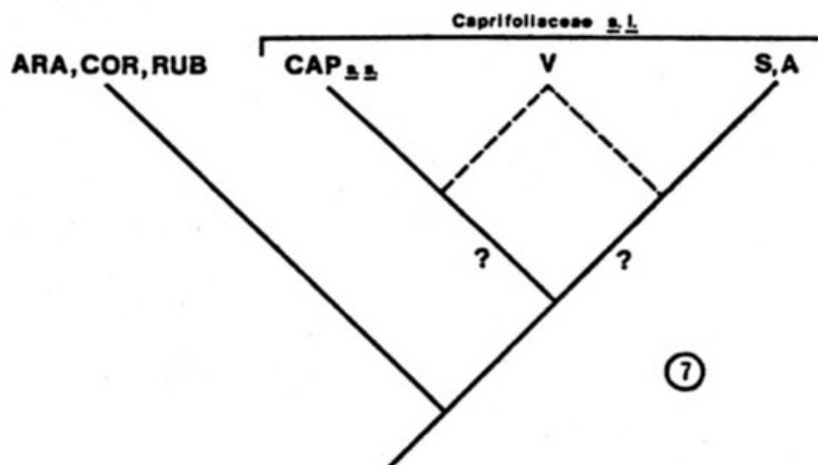


Fig. 10.7. Dipsacales polyphyletic, Caprifoliaceae *s.l.* monophyletic. No synapomorphies are known for V with either CAP *s.s.* or S and A using Araliaceae (ARA), Cornaceae (COR), and/or Rubiaceae (RUB) as outgroups.

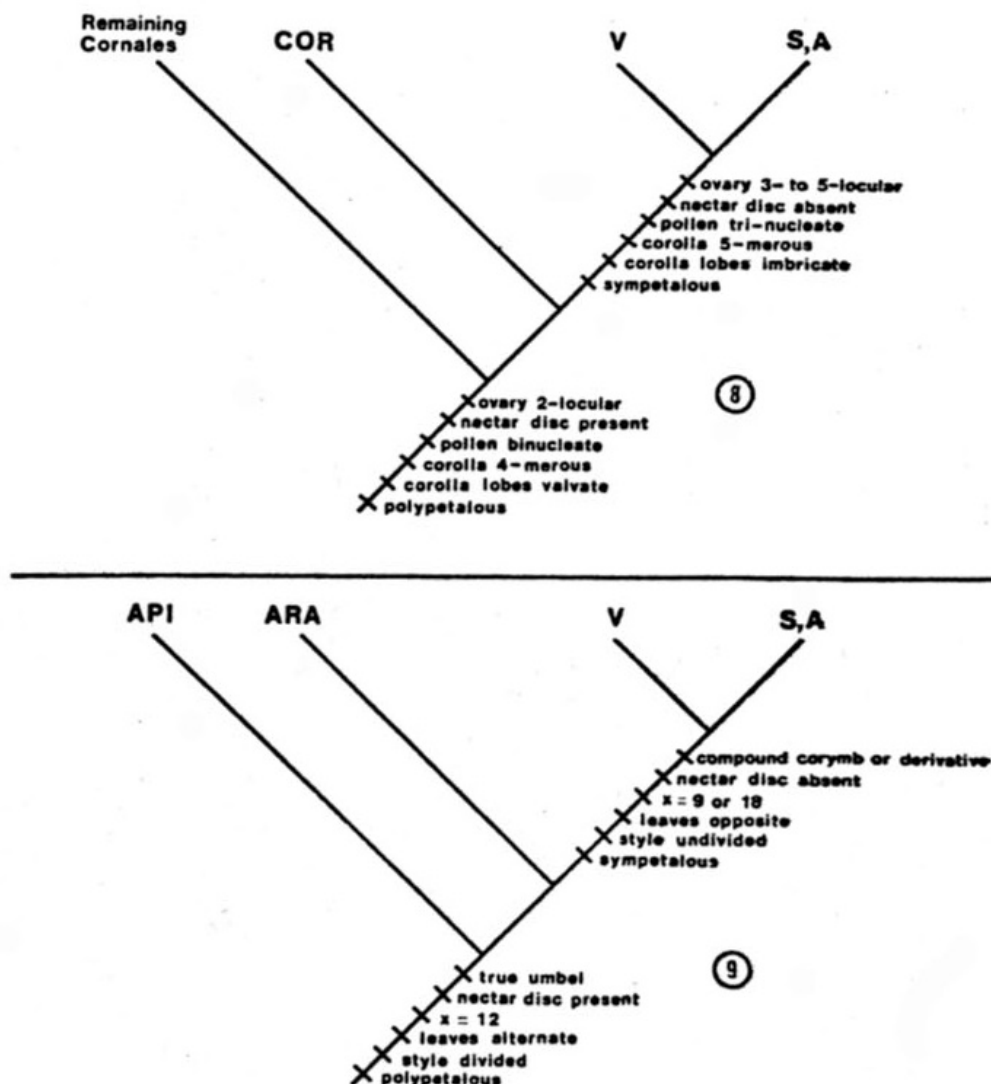
character-state polarities with the available data (i.e., additional outgroups are necessary for a resolution of relationships within an immediate outgroup), or (2) *Viburnum* is united to other groups only by ancestral states.

DIPSACALES POLYPHYLETIC, CAPRIFOLIACEAE *s.l.* POLYPHYLETIC

It has been suggested that *Viburnum*, *Sambucus*, and *Adoxa* (together or in various combinations) are not closely related either to the Caprifoliaceae *s.s.* or to other members of the Dipsacales but instead are more directly related to, and derived relative to, some other family. The Cornaceae has been most often mentioned as a possibly related family, but the Araliaceae must also be considered. *Viburnum*, *Sambucus*, and *Adoxa* have not been directly related by any phylogenist to the Rubiaceae, unless they are allied with the Caprifoliaceae *s.s.* For this reason the Rubiaceae is not here considered a possible outgroup of *Viburnum*, *Sambucus*, and *Adoxa*; however, if it were, *Viburnum*, *Sambucus*, and *Adoxa* would be united by several derived character states (e.g., cellular endosperm, the absence of alkaloids, and 3–5 carpellate ovaries).

In Figure 10.8 I hypothesize that *Sambucus* and *Adoxa* are the sister group of the Cornaceae and that the outgroup to these taxa is the remainder of the Cornales. These remaining families (Alangiaceae, Davidiaceae, Garryaceae, Nyssaceae, and Rhizophoraceae) are those which appear (as families or subfamilies) in the Cornales of both Cronquist (1981) and Thorne (1976). If *Viburnum* is assumed to be a member of a monophyletic group with the Cornaceae and *Sambucus* and *Adoxa*, there are at least six derived states which unite it with *Sambucus* and *Adoxa* (shown in Fig. 10.8). I am unable to find derived states which unite it with the Cornaceae; however, if we accept parsimony as a criterion, in order to prefer a hypothesis that *Viburnum* is more closely related to the Cornaceae than to *Sambucus* and *Adoxa*, we would have to find more than six derived states that it shares with members of the Cornaceae.

In Figure 10.9 I hypothesize that *Sambucus* and *Adoxa* are the sister group of the Araliaceae *s.s.* and that the remaining Araliales (the Apiaceae) are the outgroup. If *Viburnum* is hypothesized to be a member of a monophyletic group with the Araliaceae and *Sambucus* and *Adoxa*, then at least six derived states unite it with *Sambucus* and *Adoxa* (shown in Fig. 10.9). Again, I have not performed a complete cladistic analysis on the group Araliaceae, *Viburnum*, *Sambucus*, and *Adoxa*, and the evidence that *Viburnum* belongs with *Sambucus* and *Adoxa* might be outweighed by evidence supporting



Figs. 10.8–10.9. Dipsacales and Caprifoliaceae *s.l.* both polyphyletic. 10.8. Synapomorphies of *Viburnum*, *Sambucus*, and *Adoxa* using the Cornaceae as their sister group and the remaining families of the Cornales (see text) as the outgroup. 10.9. Synapomorphies of *Viburnum*, *Sambucus*, and *Adoxa* using the Araliaceae as their sister group and the Apiaceae as the outgroup.

a closer relationship to the Araliaceae. Again, however, more than six derived character states are required to change the outcome.

It might be objected that the relationships proposed in the preceding analysis are unreasonable and that, instead, *Sambucus* and *Adoxa* should be the basal group (Fig. 10.10). If *Sambucus* and *Adoxa* are the basal group, then in order to find evidence of a cladistic relationship between *Viburnum*, *Sambucus*, and *Adoxa*, additional outgroups are necessary. Although the relationships of the Araliales are controversial, some workers have allied it with the Cornales (e.g., Thorne, 1976). If the Cornales are used as the outgroup (Fig. 10.10b), then *Viburnum*, *Sambucus*, and *Adoxa* are still united by the character states common to Figures 10.8 and 10.9 (i.e., sympetaly and the absence of a nectar disc). If the positions of the Cornales and the Araliales are reversed on this cladogram (Fig. 10.10c), the same results are obtained. Hence there is support for a cladistic relationship of *Viburnum* to *Sambucus* and *Adoxa* if these genera are related most directly to the Cornales and/or the Araliales. The possibility that *Viburnum* is more closely related to some other genera within these orders than it is to *Sambucus* and *Adoxa* cannot be ruled out but appears unlikely.

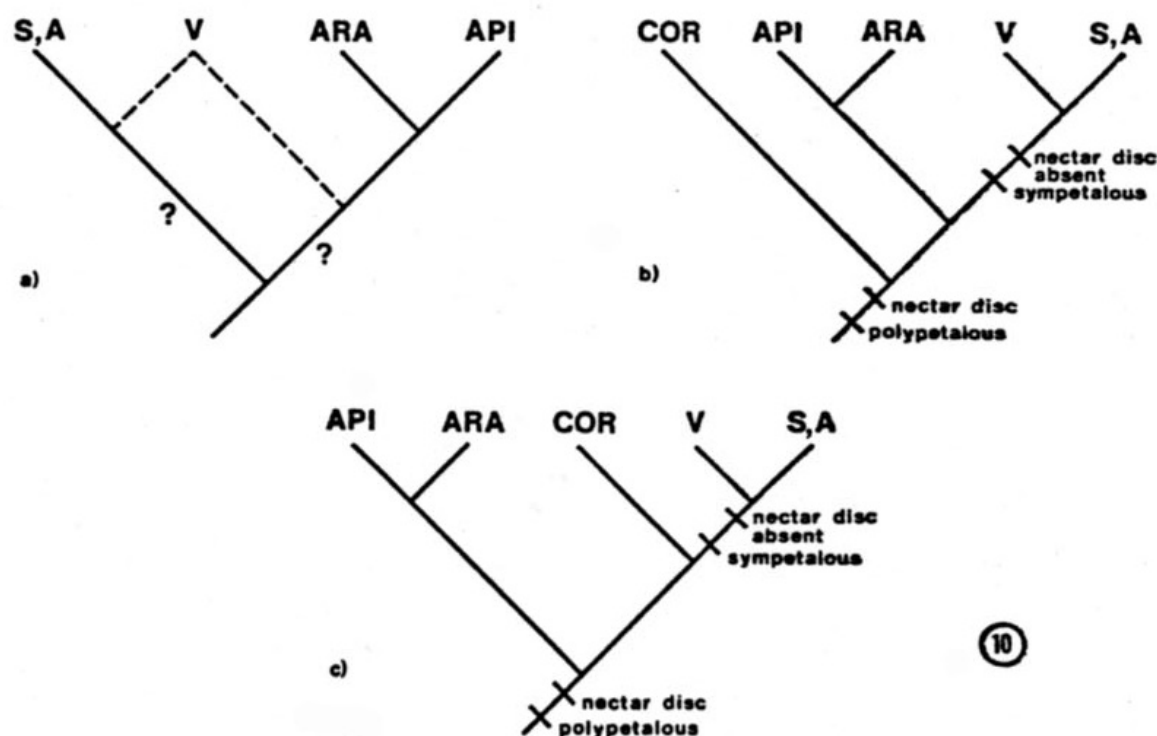


Fig. 10.10. Dipsacales and Caprifoliaceae *s.l.* both polyphyletic. a. *Sambucus* and *Adoxa* as the sister group of the Araliales—Araliaceae (ARA) and Apiaceae (API). b. Synapomorphies of *Viburnum*, *Sambucus*, and *Adoxa* using the Araliales as their sister group and the Cornales as the outgroup. c. The Cornales as the sister group and the Araliales as the outgroup.

Conclusions and Discussion

THE PHYLOGENETIC RELATIONSHIPS AND CLASSIFICATION OF *VIBURNUM*

The following conclusions can be drawn from the arguments presented above. (1) *Viburnum* has seemed to occupy a pivotal position because it shares some character states with *Sambucus* and *Adoxa* and others with the 10 genera of the Caprifoliaceae *s.s.* (2) If most modern angiosperm classifications are "correct" and the Caprifoliaceae *s.l.* and the Dipsacales are both monophyletic groups, then the character data support the hypothesis that *Viburnum* is the sister group of *Sambucus* and *Adoxa*. (3) There is no character state that is restricted to the Caprifoliaceae *s.l.*, and this severely limits the circumstances under which it could be considered monophyletic; therefore, the possibility that it is not monophyletic must be seriously entertained. (4) If the Dipsacales is monophyletic and the Caprifoliaceae *s.l.* is paraphyletic within it, then there is ample evidence for a cladistic relationship of *Viburnum* to *Sambucus* and *Adoxa*, if the Caprifoliaceae *s.s.* is the basal taxon in the order. However, if *Sambucus* and *Adoxa* are the basal group, I find no evidence for this relationship. (5) If the Dipsacales is polyphyletic and the Caprifoliaceae *s.l.* is monophyletic and cladistically related to (and derived relative to) the Araliaceae, Cornaceae, or Rubiaceae, I find no evidence for or against a relationship of *Viburnum* to *Sambucus* and *Adoxa*. (6) If the Caprifoliaceae *s.l.* is polyphyletic, and *Viburnum*, *Sambucus*, and *Adoxa* are most closely related to the Araliaceae or Cornaceae, I find evidence which supports the hypothesis that *Viburnum*, *Sambucus*, and *Adoxa* form a monophyletic group. However, it must be emphasized that in these latter instances I have not sought character-state distributions which would "falsify" this hypothesis, i.e., lead us to prefer an alternative hypothesis (Cartmill, 1981). To do so would require a cladistic analysis using an unbiased sample of characters of each group (including *Viburnum*, *Sambucus*, and *Adoxa*).

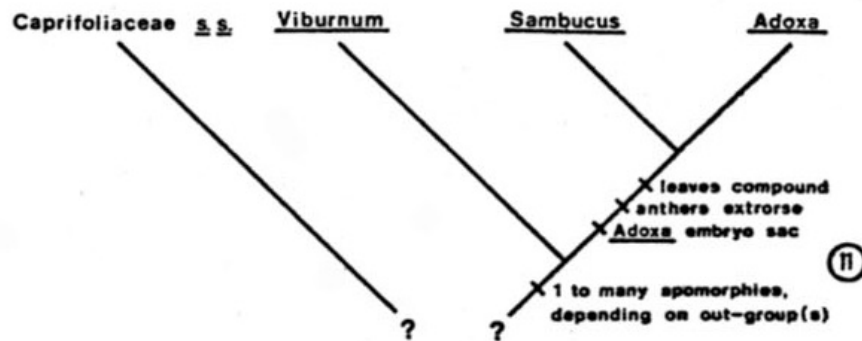


Fig. 10.11. The hypothesized phylogenetic relationships of *Viburnum*, showing three synapomorphies of *Sambucus* and *Adoxa*. The relationships of *Viburnum*, *Sambucus*, and *Adoxa* and of the Caprifoliaceae s.s. (to one another and to other groups) are uncertain.

It should be evident from this analysis that the nature and strength of any statement about the relationships of *Viburnum* depends on the assumptions we make about its broader relationships. The hypothesis that *Viburnum* is phylogenetically related to *Sambucus* and *Adoxa*, and not to the Caprifoliaceae s.s., is well supported under some hypotheses of the broader relationships of these groups, but with other outgroups and assumptions of monophyly the relationships of *Viburnum* are equivocal. Until evidence is accumulated to the contrary, *Viburnum* is best considered to be phylogenetically most closely related to *Sambucus* and *Adoxa* as illustrated in Figure 10.11.

The derived *Adoxa*-type embryo sac (and, depending on the outgroup(s), many other character states) support the sister-group relationship of *Sambucus* and *Adoxa*. *Adoxa* possesses many derived features (e.g., divided stamens and a 3-merous calyx), and these account for its placement, by most systematists, in a separate family. However, according to this analysis any family which includes *Sambucus* along with other genera and does not also include *Adoxa* would be paraphyletic.

There are several acceptable ways in which the relationship of *Sambucus* with *Adoxa*, and of *Viburnum* to these two genera, could be reflected in their classification. (1) All three genera could be placed in a subfamily (Sambucoideae) of the Caprifoliaceae. Within this subfamily *Viburnum* could constitute one tribe (Viburneae) and *Sambucus* and *Adoxa* a second tribe (Sambuceae). (2) All three genera could be removed from the Caprifoliaceae and placed together in the family Adoxaceae,⁵ within which two subfamilies could be recognized. (3) All three could be dissociated from the Caprifoliaceae and placed in two families, the Adoxaceae (*Sambucus* and *Adoxa*) and the Viburnaceae (*Viburnum*). In this case the relationship between the two families should be recognized at a higher level (i.e., superfamily or order).

The relationship of the clade *Viburnum*, *Sambucus*, and *Adoxa* to other groups is uncertain. As shown above, the monophyly of the Caprifoliaceae s.l. is questionable. It may be paraphyletic, and *Viburnum*, *Sambucus*, and *Adoxa* basal within a monophyletic Dipsacales; however, the monophyly of the Dipsacales is also questionable. It has been noted that some members of *Viburnum* share type V carboxylic iridoid compounds ("Valeriana compounds") with some Valerianaceae, and that this might reflect a close relationship between these groups (Dahlgren et al., 1981; Norn, 1978). If this is the case, and if *Viburnum* is related to *Sambucus* and *Adoxa* as suggested here, then it might be argued that the Dipsacales is monophyletic. However, all other members of the Dipsacales lack type V iridoids, and these compounds are also known to occur in the

⁵The family name Adoxaceae is conserved and hence must be applied to this family unless a proposal is made to accept the name Sambucaceae on the basis of its increasingly common usage for a family including *Sambucus* and, sometimes, *Viburnum*.

Hydrangeaceae and Scrophulariaceae. Considering the analyses presented here, it is more parsimonious to assume either that type V iridoids arose independently in *Viburnum* and the Valerianaceae or that they are the ancestral condition for a more inclusive group and have been lost independently several times.

The Caprifoliaceae and Dipsacales may be polyphyletic and the clade *Viburnum*, *Sambucus*, and *Adoxa* more directly related to the Cornaceae and/or the Araliaceae. This would be consistent with, for example, the similarities between the pollen grains of some Cornaceae, *Viburnum*, *Sambucus*, and *Adoxa* (Chao, 1954; Donoghue, 1982; Ferguson, 1977), and possibly with the finding that *Sambucus* and *Viburnum* are serologically as "close" to *Cornus* as to members of the Caprifoliaceae s.s. (Hillebrand and Fairbrothers, 1970). However, it is clear that the phylogenetic interpretation of these data is dependent on the distributions of other characters and on initial assumptions of monophyly and of outgroups.

"PHENETIC GROPING" AND PHYLOGENETIC ANALYSIS

The approach I have taken in this study focuses attention on the importance of synapomorphy for establishing cladistic relationships. It demonstrates, and hopefully clarifies, the outgroup method of assessing character-state polarity, and its foundation on the principle of parsimony. For a three-taxon statement only certain distributions of character states allow us to hypothesize ancestral and derived states. No character state distribution is informative about the polarity of a state possessed by a basal group in a three-taxon cladogram. For a taxon in this position other, cladistically basal, outgroups are necessary. The more outgroups are available, and the more certain we are about their relationships to the study group, the greater our confidence becomes in any polarity assessment.

To employ the outgroup method a hypothesis of the broader cladistic relationships of one's study organisms is required. In botany there is often so much uncertainty about the overall structure of relationships that cladistic analysis might seem impossible. However, as I have demonstrated, it is possible to proceed by hypothesizing outgroups, beginning first with the assumption that plant phylogenists have correctly narrowed down (or have at least suggested) the relatives of one's study organisms, but then proceeding to question this framework and to consider other possibilities (i.e., the non-monophyly of established taxa and other plausible outgroups). This general approach can be made rigorous by systematically considering all possible outgroups in all possible combinations, performing cladistic analysis on the study group in each case, and then finding robust hypotheses of relationships within the group. These robust groups could provisionally be accepted as monophyletic taxa in more detailed cladistic analyses at other levels, either within or outside of the group.

In the present study, this rigorous approach has not been possible, because my knowledge of the character states and their distributions in all of the possible outgroups is insufficient. Instead, I have considered only the most plausible (most often suggested) outgroups and, in most cases, have performed only a partial cladistic analysis searching for evidence (in the form of synapomorphies) to support particular suspected relationships. Unfortunately, this is basically a "verificationist" approach (Brown, 1977). However, it may be justified as a first step, in the absence of more complete knowledge, because it forces a consideration of alternative hypotheses and helps clarify the conditions under which particular hypotheses of relationship are supported by particular character data. It also specifies what conditions must be met, and what data gathered, in order to "falsify" such hypotheses. If we are conscientious, this compels us to reexamine the character data at hand and to search out new characters for use in subsequent analyses.

In any case, Hennigian cladistic analysis (at least in practice) presupposes a "phenetic groping" phase during which the overall relationships of a group are roughed out enough that meaningful polarity assessments can be made. This requires a degree of reliance on the research and judgments of previous generations of systematists (see Eldredge, 1979, quoted above) and a faith that overall similarity reflects (at least in a very general way) phylogenetic relationships. Working in this broader framework, cladistic analysis allows us to refine rigorously our hypotheses of descent and modification.

Acknowledgments

My initial interest in this topic was encouraged by J. H. Beaman at Michigan State University. This interest waned for several years because I could see no way to formulate testable hypotheses of evolutionary history; the placement of *Viburnum* seemed solely a matter of personal preference. At Harvard University I was introduced to phylogenetic systematics (*sensu* Hennig) by S. Fink and W. Fink. My understanding of cladistics developed in discussions with them and with P. Stevens, whose clear thinking about the outgroup method and the relationships between cladistics and phenetics influenced me greatly. Conversations with P. Cantino, E. Coombs, W. Maddison, and B. Mishler were also important in the development of my thoughts. Correspondence with R. Thorne stimulated this particular formulation of my ideas.