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A Preliminary Analysis of Phylogenetic Relationships in *Viburnum* (Caprifoliaceae s.l.)

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ABSTRACT. In order to establish a working hypothesis of phylogenetic relationships within *Viburnum*, 23 presumably monophyletic "cladistic units" were scored for 34 characters, the polarity of the states of these characters was assessed (in most cases) by out-group comparison, and the data were analyzed using the WAGNER '78 computer program. Character state transitions were traced on the resulting cladogram; this helped pinpoint characters about which there was uncertainty concerning independence, homology, scoring, and/or polarity. The data were re-evaluated and a second cladogram was generated, which again prompted a re-evaluation of the characters. This process was continued until four cladograms were obtained. In interpreting these cladograms attention was focused on the clades that were best supported by apomorphies and hence remained "stable." Resolving the cladistic relationships of the "labile" clades requires additional data. The most important conclusions of this analysis are that the New World sect. *Lentago* and the subsect. *Punctata* of the Old World sect. *Megalotinus* are sister groups, and sects. *Odontotinus* and *Opulus* form a clade within which *Odontotinus* is paraphyletic.

Viburnum contains about 120 species of shrubs and trees. It is widespread in the northern hemisphere and extends into the southern hemisphere in the mountains of Malesia and of South America. The region of greatest diversity is in eastern Asia but eastern North America and the mountains of Mexico and Central and South America are also areas of high species diversity. Only five species are native to Europe and adjacent regions.

Plants of all species of *Viburnum* have opposite (or rarely whorled) leaves and produce inflorescences, flowers, and fruits that are strikingly uniform in overall construction. Because of these similarities the genus has long been considered a "natural" group. Evidence for the monophyly (sensu Hennig 1966) of the genus is provided by the unique construction and development of the ovary (Wilkinson 1948, 1949).

Although relatively uniform in many respects, there is considerable variation within the genus, especially in growth pattern (Donoghue 1981, 1982) and in aspects of leaf and fruit morphology. Some polymorphic characters are conspicuous and are widely known among botanists, e.g., the presence, in some species, of naked buds, of sterile marginal flowers in the inflorescences, of extrafloral nectaries, and of "stipules."

Owing to variation in these and other characters subdivisions of *Viburnum* have long been

recognized. Oersted's (1861) division of the genus into five separate genera has never since been taken up, but it does reflect the occurrence of very distinct groups of species. Rehder's (1908, 1940) studies of *Viburnum* (especially of the Asian species) culminated in his recognition of nine sections. Although these sections are widely accepted, it is clear that several of them, e.g., *Thyrsoma*, are quite heterogeneous (Donoghue 1982) and are composed of more or less discrete "species complexes." In a few cases, Rehder's sections have been formally subdivided (e.g., Kern 1951).

There has been little critical discussion of phylogenetic relationships within *Viburnum*, although there have been attempts to assess the relationships, and the "relative advancement," of selected species on the basis of floral anatomy (Wilkinson 1948), wood anatomy (DeVos 1951), intraspecific hybridization (Egolf 1956), chromosome number (Egolf 1962a), serology (Hillebrand and Fairbrothers 1969), and iridoid compounds (Norn 1978). These studies have concerned only single characters or suites of characters, and, by themselves, these are not sufficient to assess cladistic relationships within the genus. In addition, previous studies have been very incomplete in taxonomic coverage. In general, only the commonly cultivated species of temperate regions have been examined. With the exception of Norn (1978), who examined material of several Mexican species,

the Latin American viburnums have not been considered in any of these analyses. Recently, I surveyed the entire genus for additional, taxonomically underutilized characters, i.e., pollen morphology (Donoghue 1982) and growth pattern (Donoghue 1981, 1982), and a survey of endocarp morphology is in progress.

In the present study I have endeavored to construct a working hypothesis of phylogenetic (cladistic) relationships within *Viburnum*, based on a wide variety of characters. An understanding of such relationships is necessary in order to assess character state polarities and determine cladistic relationships among species *within* the sections and species complexes. Cladistic analysis will also provide the necessary basis (cf. Platnick and Nelson 1978; Rosen 1978) for discussion of the biogeographic history of the genus (Donoghue MS in prep.), and it is the only way to assess the extent of homoplastic evolution.

The cladograms generated in the present study were published earlier in a very different context (Coombs et al. 1981), where they were used solely to demonstrate that cladograms can sometimes be "unstable" and to urge caution in cladogram interpretation. In this paper I present the data upon which the cladograms are based and discuss in detail how I think they should be interpreted and what they tell us about the evolutionary history and classification of *Viburnum*.

METHOD OF ANALYSIS

A logic for assessing phylogenetic relationships was developed by Hennig (1966), who recognized that only shared derived character states (synapomorphies) can provide evidence of common ancestry, and hence of monophyly (i.e., all and only the descendants of a particular ancestor), and that shared ancestral states (symplesiomorphies) cannot. This logic, which has been labeled cladistics, is not without theoretical and practical limitations (Hull 1979; Bremer and Wanntorp 1979) but is at present the only rigorous approach to phylogeny reconstruction in groups of organisms in which certain basic assumptions can be made (Arnold 1981; Coombs et al. 1981). Some zoological systematists have consistently employed cladistic methods and have actively extended and modified the theory outlined by Hennig (cf.

Eldredge and Cracraft 1980; Nelson and Platnick 1981; Wiley 1981). In contrast, botanists have only recently taken an interest in this form of analysis (Bremer and Wanntorp 1977; Funk and Stuessy 1978).

Unfortunately, most botanical applications of cladistics (e.g., Estabrook and Anderson 1978; Gardner and La Duke 1978; Duncan 1980; Meacham 1980) 1) have tended to use only computer approaches, especially character compatibility analysis (see Funk and Stuessy 1978 and Meacham 1980 for an explanation of this method, and Farris and Kluge 1979 for a critique) and 2) have not paid sufficient attention to the problem of assessing the polarity of character states. This second deficiency, in particular, reliance on the in-group ("common is primitive") method, may have resulted from a confusion of the in-group and out-group methods (cf. Crisci and Stuessy 1980; but see Stevens 1980, 1981; Watrous and Wheeler 1981; and Wheeler 1981, for clarification and explanations of the out-group method). It may also be due to uncertainty concerning the appropriate out-groups in particular cases (but see Watrous and Wheeler 1981; Coombs et al. 1981; Donoghue 1982, in press; for possible solutions to this undoubtedly common problem).

In this study I have employed a 1978 version (WAGNER '78) of a computer program developed by Farris (1970), which has received wide application in zoology. Parsimony is the basic principle underlying this method. The program allows character state changes from the plesiomorphic (ancestral) to the apomorphic (derived) state, equally allows reversals to the plesiomorphic state, and attempts to construct a cladogram with the minimum total number of state transitions. For each character, I have listed the criterion(a) by which the polarity of the character states was determined. I tried in every case to use only the out-group comparison method, however, as discussed in more detail below, in some cases there was uncertainty in this procedure and in a few instances another criterion was employed.

CLADISTIC UNITS

For purposes of this study *Viburnum* was divided into the 23 cladistic units (CUs) listed in table 1. In order to root the network computed by the Farris program, a hypothetical CU

TABLE 1. Cladistic units (CUs) in *Viburnum*. Each CU is named after a single species. The number of species examined is given in parentheses; ' = incomplete, i.e., not all species in the CU were examined. CUs assigned to taxonomic section according to Rehder (1908, 1940); N.P. = not placed by Rehder.

Cladistic unit	Code	Section	Geographic range
opulus (2)	O	<i>Opulus</i> DC.	Circumboreal
edule (1)	E	<i>Opulus</i>	North America
kansuense (1)	K	<i>Opulus</i>	Asia
betulifolium (3')	B	<i>Odontotinus</i> Rehder	Asia
dilatatum (2')	I	<i>Odontotinus</i>	Asia
foetidum (2')	J	<i>Odontotinus</i>	Asia
acerifolium (2)	W	<i>Odontotinus</i>	North America and Europe
rafinosquianum (3)	R	<i>Odontotinus</i>	North America
dentatum (6)	D	<i>Odontotinus</i> and N.P.	North America and Mexico
acutifolium (7')	A	N.P.	Latin America
hartwegii (3')	H	N.P.	Latin America
farreri (1)	G	<i>Thyrsoma</i> (Raf.) Rehder	Asia
erubescens (1)	Q	<i>Thyrsoma</i>	Asia
sieboldii (4')	S	<i>Thyrsoma</i>	Asia
plicatum (1)	P	<i>Pseudopulus</i> Dippel	Asia
tinus (5')	T	<i>Tinus</i> Maxim.	Asia and Europe
cylindricum (1)	Y	<i>Megalotinus</i> Maxim.	Asia
lepidotulum (2)	M	<i>Megalotinus</i>	Asia
lentago (7)	L	<i>Lentago</i> DC.	North America and Mexico
lantana (9')	N	<i>Lantana</i> Spach	Asia
urceolatum (1)	U	<i>Lantana</i>	Asia
cordifolium (1)	C	<i>Pseudotinus</i> Clarke	Asia
furcatum (2)	F	<i>Pseudotinus</i>	Asia

with all plesiomorphic states was also entered in each analysis. CUs are single species or, more often, two or more morphologically very similar species (i.e., "species complexes"). The CUs were delimited by examining in detail the species placed by Rehder (1908, 1940) into the nine sections that he recognized, as well as the Latin American viburnums, which he did not place in his system. Some of these sections were retained as CUs (i.e., sects. *Pseudopulus*, *Tinus*, and *Lentago*); others were subdivided into a variable number of CUs if they contained species, or groups of species, whose relationships to others appeared problematical or that were intermediate in morphology between other CUs.

Each CU is thought to be monophyletic owing to the possession of one or more derived character states. Although it is possible that one or more of the CUs is not monophyletic, there is no reason to suppose that this is true at present. Of course, in subsequent analyses of *Viburnum* the monophyly of the CUs should be critically evaluated and not assumed.

It is evident in table 1 that I have not examined in detail every species in every one of the CUs. The problem in the instances of incomplete coverage is that the species level taxonomy within these groups is as yet not satisfactorily resolved, and, hence, I am not certain of the total number of species involved. However, in my survey of each CU, I tried to capture the total range of variation. Further sampling is obviously desirable (and is underway) but it is not likely to alter substantially the results obtained.

CHARACTERS

The 23 CUs were surveyed and scored for the 34 characters in table 2. These data are based largely upon my studies of the extensive collection of *Viburnum* specimens in A and GH and on the living collections at the Arnold Arboretum in Jamaica Plain, Massachusetts, especially characters 1-7 (Donoghue 1981, 1982), character 23 (Donoghue 1982; also see Böhne-Gütlein and Weberling 1981), and

TABLE 2. Characters, character states (e.g., A, B, C, etc.), binary codings of states (e.g., 0, 01, 101, etc.), polarity criteria, and transformation series used in a cladistic analysis of *Viburnum*. Criteria in brackets have been used in ordering the derived states of multi-state characters (see Stevens 1980 and text for discussion of criteria). (?) indicates uncertainty concerning the interpretation of the character in the out-group.

1. Number of pairs of bud scales: A. 1-2 = 000. B. 2(+) = 100. C. 1(0) = 010. D. 0 = 011. Out-group (?) [divergent correlation]. A → B; A → C → D. 2. Arrangement of outer envelope of buds: A. Valvate-imbricate = 0000. B. Valvate = 1000. C. In-rolled = 1100. D. Imbricate = 0010. E. Fused = 0011. Out-group (?) [divergent correlation]. A → B → C; A → D → E. 3. Terminal bud: A. Produced regularly = 0. B. Not or very rarely produced = 1. Out-group. A → B. 4. Shoot orientation: A. Orthotropic only = 00. B. Orthotropic and monopodial plagiotropic = 10. C. Orthotropic and sympodial plagiotropic = 01. Out-group [divergent correlation]. A → B; A → C. 5. Shoot polymorphism: A. All equivalent = 0000. B. Ephemeral reproductive shoots = 1000. C. Type I short shoots = 0100. D. Type II short shoots = 0010. E. Type III short shoots = 0001. Out-group [divergent correlation]. A → B; A → C; A → D; A → E. 6. Inflorescence development: A. Preformed, not exposed = 00. B. Neoformed, not exposed = 10. C. Neoformed, exposed = 11. Out-group [ontogeny]. A → B → C. 7. Branch development: A. Not preformed = 0. B. Preformed in bud = 1. Out-group. A → B. 8. Leaf retention: A. Deciduous = 0. B. Evergreen = 1. Out-group. A → B. 9. Large petiole glands: A. Absent = 0. B. Present = 1. Out-group. A → B. 10. Stipules: A. Absent = 0. B. Present = 1. Out-group (?). A → B. 11. Leaf lobing: A. Not lobed = 0. B. Tri-lobed = 1. Correlation. A → B. 12. Secondary veins: A. Pinnate = 00. B. 3-nerved from base into lobes or teeth = 10. C. 3-nerved, curving and not ending in margins = 01. Correlation [divergent correlation]. A → B; A → C. 13. Secondary veins: A. Approaching but not ending directly in teeth = 00. B. Parallel, straight, ending in teeth = 10. C. Curving and anastomosing = 01. Correlation [character sequence, divergent correlation]. A → B; A → C. 14. Leaf margins: A. Curved dentate-serrate = 000. B. Strongly and regularly dentate = 100. C. Sparsely and irregularly dentate = 010. D. Entire = 001. Correlation [character sequence, divergent correlation]. A → B; A → C; A → D. 15. Hairs on lower leaf surface: A. Glabrous or simple and/or fascicled = 00. B. Large, stalked, stellate = 10. C. Small, sessile, stellate = 01. Out-group [divergent correlation]. A → B; A → C. 16. Peduncle: A. Present, long = 0. B. Absent (sessile) or very short = 1. Out-group. A → B. 17. Inflorescence: A. Umbel-

TABLE 2. Continued.

like = 0. B. Panicle-like = 1. Out-group (?). A → B. 18. Inflorescence primary rays: A. 5-7 = 0. B. 4 = 1. Out-group. A → B. 19. Enlarged, sterile flowers: A. Absent = 0. B. Present = 1. Out-group. A → B. 20. Corolla shape in relation to stamens: A. Small, rotate, stamens exserted = 000. B. Large, rotate, stamens short = 100. C. short-tubular, lobes upright, stamens exserted = 010. D. Long-tubular, lobes spreading, stamens included = 001. Out-group [divergent correlation]. A → B; A → C; A → D. 21. Style: A. Glabrous = 0. B. Pubescent = 1. Out-group. A → B. 22. Leaf shape: A. Elliptic = 00. B. Ovate = 10. C. Broadly oval = 01. Correlation [divergent correlation]. A → B; A → C. 23. Pollen exine: A. Regular reticulum, psilate muri = 000. B. Irregular reticulum, scabrate muri = 100. C. Intectate, scabrate pilae = 110. D. Intectate, psilate pilae = 101. Out-group [character sequence, general trend]. A → B → C; B → D. 24. Chromosome number: A. $2n = 16 = 000$. B. $2n = 16 + 18 = 100$. C. $2n = 18 = 110$. D. $2n = 36 = 111$. Correlation [character sequence, general trend]. A → B → C → D. 25. Fruit color: A. Red → purple-black = 0000. B. Red (scarlet) = 1000. C. Glaucous blue = 0100. D. Green → purple-black = 0010. E. Metallic blue = 0001. Out-group (?) [divergent correlation, ontogeny]. A → B; A → C; A → D; A → E. 26. Mesocarp texture and amount: A. Gritty or mealy, thin = 00. B. Juicy, thick = 10. C. Mealy, thick = 01. Out-group (?) [divergent correlation]. A → B; A → C. 27. Stone shape in cross-section: A. Moderately compressed = 00. B. Nearly round = 10. C. Very flat = 01. Out-group [character sequence, divergent correlation]. A → B; A → C. 28. Fruit size (length): A. Small (<10 mm long) = 0. B. Large (12-20 mm long) = 1. Out-group. A → B. 29. Stone grooving in cross-section: A. Large central intrusion = 00000. B. Moderate intrusion = 10000. C. Small intrusion = 11000. D. "Wavy," grooves dorsal and ventral = 00100. E. Slightly or not grooved, flat = 00110. F. Slightly or not grooved, round = 00001. Correlation [character sequence, divergent correlation]. A → B → C; A → D → E; A → F. 30. Endosperm: A. Not ruminate = 0. B. Ruminate = 1. Out-group. A → B. 31. Flowering time: A. With or after leaf expansion = 0. B. Before leaf expansion = 1. Out-group. A → B. 32. Petiole length: A. Long = 0. B. Short = 1. Out-group. A → B. 33. Glycosides: A. Present = 0. B. Absent = 1. Out-group. A → B. 34. Red glands on leaves and inflorescence: A. Upright, rounded apex = 0. B. Flattened, peltate "scales" = 1. Out-group. A → B.

character 31 (Donoghue 1980). Additional information was obtained from monographic and floristic treatments (Oersted 1861; Rehder 1908, 1940; Schneider 1912; Killip and Smith 1931; Morton 1933; Fernald 1950; Kern 1951; Kern and Van Steenis 1951; McAtee 1956) and from the horticultural literature (Egolf 1962b, c, 1963). For two characters information was obtained from other sources: chromosome number (char. 24; Egolf 1962a) and glycosides (char. 33; Norn 1978). Like the characters themselves, the character states (table 2) were selected after having examined actual patterns of variation in *Viburnum*.

ASSESSING POLARITIES AND ORDERING CHARACTER STATES

I have attempted to use the out-group comparison method to assess the plesiomorphic state of each character. *Sambucus* and *Adoxa*, together, appear to be the sister group of *Viburnum* (Donoghue 1982, in press) and can therefore be used as the out-group to assess the polarity of characters in *Viburnum*. There is no evidence that *Viburnum*, *Sambucus*, and *Adoxa* are directly related to any of the ten genera of the Caprifoliaceae s.str. (Donoghue 1982, in press). The newly described genera *Sinadoxa* (Wu et al. 1981) and *Tetradoxa* (Wu 1981), which may be close relatives of *Adoxa*, *Sambucus*, and *Viburnum*, could not be considered for lack of sufficient data. If both *Sambucus* and *Adoxa* share a character state with some members of *Viburnum*, then that state is considered the plesiomorphic condition within *Viburnum*. Character data for *Sambucus* were obtained primarily from Schwerin (1920) and Ferguson (1966) and those for *Adoxa* from Sturm (1910) and Sprague (1927).

For 21 of the characters it was possible unambiguously to determine the plesiomorphic condition in *Viburnum* by out-group comparison. For six characters (1, 2, 10, 17, 25, and 26) out-group assessment is problematical because of variation within *Sambucus* and/or *Adoxa*. In some of these instances there is also uncertainty concerning homology, e.g., it is not clear that "stipules" in *Sambucus* are homologous with "stipules" in *Viburnum* (char. 10). The polarity of these six characters cannot be determined with any more certainty until they are studied

in more detail and until cladistic relationships within *Sambucus* and *Adoxa* are established. For the remaining seven characters (11, 12, 13, 14, 22, 24, and 29) out-group comparison was not possible, principally because *Sambucus* and *Adoxa* have a state that does not occur in *Viburnum*. This is especially a problem with leaf characters 11, 12, 13, 14, and 22 because all members of *Viburnum* have simple leaves and all *Sambucus* and *Adoxa* have compound leaves. The leaves of *Viburnum* could be compared with the leaflets of *Sambucus* and *Adoxa* but it is not clear that this would be meaningful. Therefore, for these characters I have used the criterion of correlation (Stevens 1980) because no out-group comparison is required. As Stevens (1980) has pointed out this criterion is of questionable value and ideally should not be used. Although I agree with this view, leaf characters have played such an important role in all previous discussions of relationships in *Viburnum* that I considered it desirable to retain the characters. However, in later runs of the data three of these characters (13, 14, and 24) were eliminated.

In out-group analysis the plesiomorphic state of a character is "determined" and the remaining character states (one or more) are considered to be apomorphic. For multistate characters, there is often considerable uncertainty in ordering the derived states. A rigorous logic has not been developed for determining the structure of complex transformation series, and there has often been a reliance on "logical sequences" or "natural trends" (i.e., from largest to smallest or vice versa; Stevens 1980 and references therein).

In this study the problem of ordering multiple derived states of a character was encountered frequently. The criteria in brackets in table 2 were used to order the derived states. In most instances there was an evident trend (e.g., reduction in the central intrusion of the endocarp, char. 29) and states were ordered accordingly. This is referred to as "character sequence" in table 2. In many of these cases the "evident trend" is also a "general trend," i.e., it has been corroborated in other groups of angiosperms (e.g., char. 23). In some cases the two (or more) apomorphic states are found to be correlated with two (or more) different suites of apomorphic states of other characters (e.g., char. 27). In these instances I considered that the

apomorphic states arose independently from the plesiomorphic state. This method is called "divergent correlation" in table 2. In a few cases ontogenetic information helped in ordering the apomorphic states (e.g., char. 25). In my view none of these methods is completely satisfactory and hence I am not confident of these assessments. All of the multistate characters in this preliminary analysis should be studied in more detail. Ultimately it may be possible to decompose them into two-state characters.

In general, the greater the number of character states to be ordered, the greater is the number of possible errors in the transformation series, and hence the greater is the possibility of "mistakes" in the resultant cladogram (Coombs et al. 1981). Fortunately, in this study, eight of the 17 multistate characters are three-state characters, and another five are four-state characters. Uncertainty is greatest for the transformation series of characters 2, 5, 25, and 29 (table 2).

When two or more states occur within a CU, I scored the CU as having the least derived of the states, except when there was reason to believe that a reversal to a more ancestral state had occurred within the CU, as when an ancestral state occurs only in a species that, in all other respects, appears to be derived within the CU. For example, in CU A elliptic leaves (char. 22, state A) are found only in one, apparently derived, species; ovate leaves occur in all of the other species. In order to retain in the analysis those characters and CUs for which character states are unknown (marked "nk" in table 3), I scored all unknowns in character 24 as C (chromosome number $2n = 18$, the most common number in *Viburnum*, Egolf 1962a) and all unknowns in character 33 as A (glycosides present, the ancestral condition, Norn 1978).

As noted several times in this and preceding sections there is considerable uncertainty concerning several important operations in the present analysis. This is especially true of polarity assessment and the establishment of transformation series. In some instances I have chosen to make an educated guess rather than eliminate characters or CUs even though I am aware that this increases the chance of error in the resulting cladograms. It should be borne in mind that this is a preliminary analysis aimed at establishing an outline of cladistic relationships in the genus and focusing attention on

characters in need of study. Progress in systematics often (always?) demands that we proceed even though a complete foundation has not been laid. In my view this is acceptable so long as we are explicit about our doubts and actually return to the character data and try to rid them of uncertainties. In the meantime, given uncertainties in the data, it is not wise to lean too heavily on the results of the analysis. Hence, as discussed below, I have tried to be very cautious in interpreting the cladograms obtained.

CLADOGRAMS

Table 3 is the basic data matrix used in this study. When all 34 characters were coded as binary characters 65 columns were entered into the computer. As detailed below, in several analyses some data were omitted from the basic matrix. Although the order of data input can sometimes result in cladograms of different overall length (Coombs et al. 1981; Jensen 1981), I did not try entering the CUs in many different orders. This should be done in future analyses but, considering the cautious interpretation presented below, it is unlikely that finding any slightly more parsimonious cladograms would substantially alter my conclusions.

In the first analysis the entire matrix in table 3 was entered; the resultant cladogram is shown in figure 1A. Upon studying character state changes on this cladogram, it was apparent that in characters 13 and 14 there were many more parallelisms and reversals than in any other characters. For this reason these characters were reconsidered. It can be seen from table 2 that the out-group method was not used to assess character state polarity in these instances; only the correlation criterion was applied. In addition, an argument can be made that these two characters do not vary independently but instead are developmentally correlated; this was made evident by their simultaneous changes on the cladogram and also seems likely from a developmental standpoint (i.e., there is, in general, a strong correlation between toothed leaf margins and veins that end in the teeth, and between entire margins and curving veins). Third, in both characters there is considerable variation within CUs, in fact, nearly twice as many instances as in any other character (asterisks in table 3). This suggests that these characters have been subject to repeated evolution-

TABLE 3. *Viburnum* data matrix—23 CUs (cf. table 1) by 34 characters (cf. table 2). An asterisk (*) by a character state indicates that there is variation in that character within the CU; "nk" indicates that the state of the character is unknown for a particular CU.

CU	Characters																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34			
O	B	E	B	A	B	A	A	A	B	B	B	B	B	C	A	A	A	A	B	A	A	B	A	C	B	B	C	A	E	A	A	A	A	A	A		
E	B	E	A	A	B	A	A	A	A	A	B*	B	B	B	A	A	A	A	A	A	A	A	B	A	C	B	B	C	A	E	A	A	A	nk	A		
K	B	D	A	A	A	A	A	A	A	B	B	B	B	C	A	A	A	A	A	A	A	B	A	C	C	B	B	A	D	A	A	A	nk	A			
B	B	D	A	A	A	A	A	A	A	B	A	B*	B	B	A	A	A	A	A	A	A	B	A	C	C	B	B	A	D	A	A	B	A	A	A		
I	B	D	A	A	A	A	A	A	A	A	A	A	B	B*	A*	A	A	A	A	A	A	B	A	C	C	B	B	A	D	A	A	A	A	A	A		
J	B*	D	A	A	A	A	A	B*	A	A	A	A	A	B*	C	A	A	A	A	A	A	A	C	C	B	B	A	D	A	A	A	A*	nk	A	A		
W	B	D	A	A	A	A	A	A	A	B	B	B	B	B	A	A	A	A	A	A	A	B	A	C	A*	A	A	A	D	A	A	A	A	A	A	A	
R	B	D	A	A	A	A	A	A	A	B	A	B*	B	B	A	A	A	A	A	A	A	B	A	C*	A*	A	A	A*	D	A	A	B*	A	A	A	A	
D	B	D	A	A	A	A	A	A	A	A*	A	A	B	B	B*	A	A	A	A	A	B	B	A	D*	D	A	B	A	A	A	A	A	A	A	A	A	
A	B	D	A	A	A	A	A	A	A	A	A	A	B*	B*	B*	A	A	A	A	A	A	B*	A	D	D	D	A	B	A	B	A	A	A	A	A	A	
H	B*	D	A	A	A	A	A	B*	A	A	A	A	C	D	A	A	A	A	A	A	A	A	A	D	D	A	A	B	A	C	A	A	A	A	A	A	
G	B	D	A	A	A	A	A*	A	A	A	A	A	B	A*	A	B	A	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	
Q	C	B	A	A	A	A	A	A	A	A	A	A	B*	A*	A	A	B	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	nk	A	A	
S	A	A	A	A	A	A	A	A*	A	A	A	A	B*	A*	A	A	B	A	A	A	A*	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A
P	C	B	A	B	D	A	A	A	A	A	A	A	B	B	B*	A	A	A	B	A	A	A	A	B	A	A	A	A	A	D	A	A	A	A	A	A	A
T	C	B	A	A	A	A*	B	A	A	A	A	C	C	D	A	A	A	A	A	A	A	A	A	C	E	A	B	A	F	B	A	A	A	A	A	A	A
Y	A*	A	A	A	A	A	A	B	A	A	A	A	C	D	A	A	A	A	A	C	A	A	A	C	A	A	A	A	D	A	A*	A	A	A	B	A	B
M	C	B	A	A	A	A	B*	B	A	A	A	A	C	D	A	B*	A	A	A	A	A	A	B	nk	A	A	A	C*	B	E*	B*	A	A	A	nk	B	B
L	C	B	A	A	A	A	B	A	A	A	A	A	C	D	A	B*	A	B*	A	A	A	A	C	C	C	C*	C	B*	E	A	A	A	A	A	A	A	A
N	D	C	A	A	A	C	A	A*	A	A	A	A	B*	A*	C	A	A	A	A*	A*	A	A*	B*	C	C	A	A	A	D	A	A	A	A	A	A	A	A
U	D	C*	A	C*	A	B*	A	A	A	A	A	A	A	A	C	C	A	A	A	C	A	A	C	A*	A*	C	A*	C*	A	E*	A	A	A	A	nk	A	A
C	D	C	A	C	E	C	A	A	A	B	A	A	A*	A	C	B	A	A	A	A	B	A	C*	D	nk	A	A	A	A	D*	B	A	A	A	nk	A	A
F	D	C	A	C	E	C	A	A	A	B	A	A	A*	A	C	C	B	A	A	B	A	A	C	C	A	A	A	A	A	D*	B	A	A	A	A	A	A

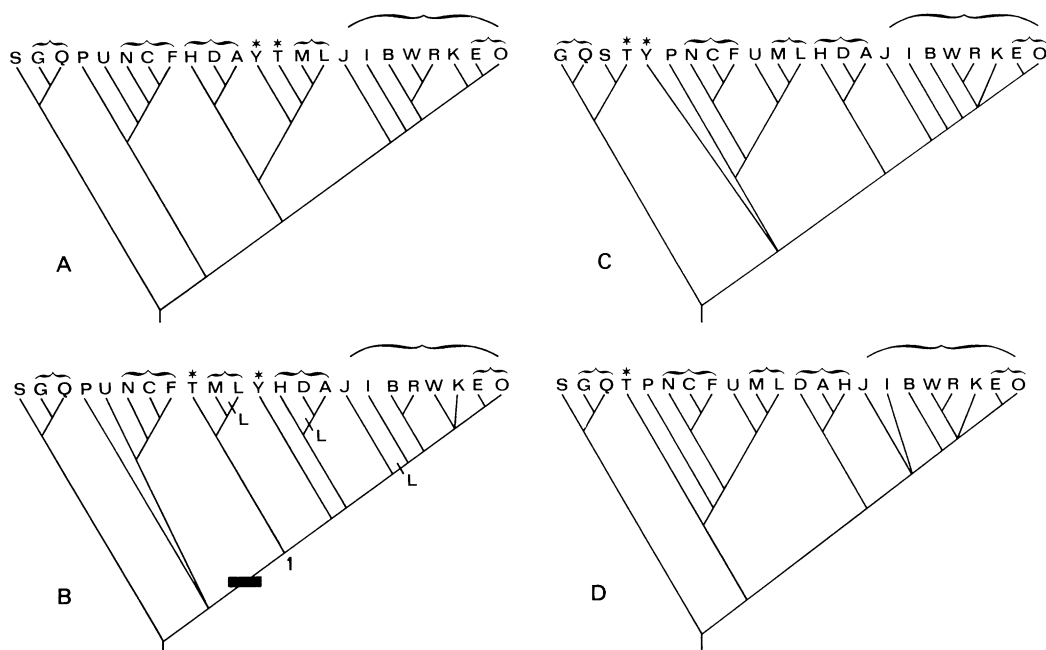


FIG. 1. Cladograms of *Viburnum*. Letters represent cladistic units (CUs; table 1); brackets indicate "stable" clades; asterisks (*) indicate "labile" CUs. A. Based on 23 CUs scored for 34 characters (table 3). B. Based on 23 CUs scored for 32 characters (chars. 13 and 14 eliminated from table 3). All CUs above node 1 are united only by the evergreen condition (char. 8); this was lost three times. L = lost. C. Based on 23 CUs scored for 28 characters (chars. 8, 13, 14, 15, 24, and 32 eliminated from table 3). D. Based on 22 CUs scored for 28 characters (CU Y and chars. 8, 13, 14, 15, 24, and 32 eliminated from table 3).

any change in all directions, and, from a practical standpoint, this variation greatly increases the probability of errors in scoring. Thus, characters 13 and 14 were eliminated in subsequent runs of the data.

When only characters 13 and 14 were eliminated from table 3 the cladogram in figure 1B was obtained. The overall homoplasy was considerably reduced over the initial run (a total homoplasy of 1018 and a deviation ratio of 0.26 in the second run, versus a total homoplasy of 1556 and a deviation ratio of 0.36 in the first run). Character state changes were mapped on this cladogram and again this prompted a reconsideration of some of the characters used in the analysis. Characters 8, 15, 24, and 32 were eliminated from the data matrix for the following reasons. Character 8 (leaf retention) exhibited more homoplasy than any other character (four changes), and the character state evergreen, alone, supported a clade consisting mostly of CUs that are actually deciduous (all CUs above node 1 in fig. 1B). In addition, there

were five cases of variation in character 8 within a CU, and in several of the CUs scored as evergreen (B), this condition may be only marginal and greatly affected by environmental conditions.

Character 15 (trichomes) was eliminated because of uncertainty concerning the scoring of the stellate hairs and because this character exhibited considerable variation within CUs (four asterisks in table 3).

Character 24 (chromosome number) was eliminated because of uncertainty concerning polarity. The polarity assessment adopted here (table 2) is based on Egolf's (1962a) very extensive survey of chromosome numbers and his analysis of trends in chromosome evolution in *Viburnum*. The out-group criterion is difficult to apply in this case because *Sambucus* and *Adoxa* both have $2n = 36$, a state that occurs in *Viburnum* but is highly unlikely to be the ancestral state based on our general understanding of chromosomal evolution (Stebbins 1971). It could be argued, however, that out-group com-

parison supports a hypothesis that $2n = 18$ is the ancestral condition and that $2n = 16$ was derived by the loss of a pair of chromosomes. The polymorphism in CU P (*V. plicatum*) is especially difficult to interpret (Egolf 1962a); on cladogram 2 there must have been a reversal to $2n = 16$ in some members of this species. It should also be noted that some members of CU D (i.e., within *V. dentatum*) have $2n = 18$, and on this cladogram this must be a reversal from the $2n = 36$ condition that characterizes the clade H,D,A.

Character 32 (petiole length) was eliminated because of variation within one of the two CUs characterized by the derived state and, hence, uncertainty concerning scoring.

The cladogram in figure 1C was obtained when characters 8, 13, 14, 15, 24, and 32 were all eliminated from the basic data matrix.

On each of the cladograms (figs. 1A, 1B, 1C) the position of CU Y (*V. cylindricum*) was quite different. In preliminary character compatibility (CLINCH) and phenetic (UPGMA) analyses it was also evident that the position of this taxon was highly variable. The taxonomic position of *V. cylindricum* has been disputed; although placed by Rehder (1908) in sect. *Megalotinus*, it is clearly unlike other members of that section (Kern 1951). Its unusual combination of character states, and the occurrence of considerable variation in several characters that are invariant within most CUs, suggests the possibility that *V. cylindricum* is of hybrid origin. For this reason (Wagner 1980), it was eliminated from the data matrix that was used to obtain figure 1C. The resulting cladogram is shown in figure 1D.

COMPARISON OF CLADOGRAMS

The basic data matrix (table 3) and the three modifications of it discussed above resulted in four cladograms (fig. 1). It is not surprising that no two of these cladograms are identical, because the data used to construct them differed in each case. It is clear from these analyses, however, that what appear to be minor changes in a data matrix (elimination of a character or a taxon) can result in significant differences in the resulting cladograms and, in turn, in one's interpretation of the evolutionary history of a group. The extent and nature of such cladogram changes appears to be a function of

the number of apomorphies that support individual linkages. If a clade is very well supported by apomorphies it is unlikely that its composition will be altered when small changes are made in the data, but if there is little support for a particular node in a cladogram, then the clade that it subtends is more likely to change. For this reason, entering slightly altered data sets can be helpful in establishing which clades are best supported and which, therefore, inspire the greatest confidence. The relationships of a CU, or a clade of CUs, the position of which is radically altered as a result of small changes in the character data, must be considered doubtful.

Extending this reasoning, it would be valuable to compare cladograms derived by methods (algorithms) that differ somewhat in their underlying assumptions. If the same clades emerge when the same data are analyzed by different methods, then these clades can be considered "robust," and our confidence that the clade is an evolutionary reality increases (see Levins 1968 for a discussion of robustness in an ecological-evolutionary context).

In this analysis the positions of CUs T and Y changed significantly from one run to the next, and other CUs (e.g., R) underwent minor shifts in position. In addition, the position of the clade including M and L shifted from figure 1A to 1B, i.e., when characters 13 and 14 are eliminated it is not linked to the clade H,D,A. Other minor differences (e.g., the appearance and disappearance of unresolved trichotomies) are evident in comparing the cladograms.

Six clades remained stable throughout the analyses (i.e., G,Q; N,C,F; M,L; H,D,A; E,O; J,I,B,W,R,K,E,O), although there were minor changes in the positions of particular CUs within some of these. The discussion below of phylogenetic relationships in *Viburnum* focuses on these groups.

Several conclusions of general interest emerge from the comparison of cladograms. First, analyzing the "behavior" of characters on a cladogram motivates a reconsideration of the character data, and this may result in the elimination of characters that are the most homoplastic and/or about which there is uncertainty concerning homology, scoring, and/or polarity. While this is one of the great benefits of cladistic analysis, it can be misused so as to

reinforce preconceived ideas of relationships (Coombs et al. 1981). The proper relationship between cladogram construction and the reanalysis and recoding of data has not been clearly set forth and should be considered in greater detail.

Second, there is a tendency to use as much data as possible in cladistic analysis. But if the addition of even a single character about which there is uncertainty can alter the structure of the resulting cladogram, it may be better to work with a smaller number of very thoroughly studied characters, the states of which can be confidently polarized by the out-group method.

Finally, the computer program is designed to yield a cladogram regardless of the level of homoplasy; it constructs the most parsimonious arrangement of all of the data. As a result, in some cases clades may be produced that are united by a single derived character state that is, in fact, lacking in most CUs in the clade. For example, as noted previously (above and in Coombs et al. 1981), in figure 1B the taxa above node 1 are united only by the derived state evergreen (char. 8). But only five of these 15 CUs are actually evergreen (T, M, Y, H, and J), the evergreen condition having been lost three times (losses marked by "L"). It is essential to trace character state changes on a cladogram in order fully to be aware of situations of this kind.

PHYLOGENETIC RELATIONSHIPS IN *VIBURNUM*

The cladistic analyses presented here provide a basis for discussing the phylogeny of *Viburnum*. Each cladogram in figure 1 can be considered an hypothesis of phylogenetic relationships. In this discussion I concentrate on the intersection of these hypotheses (i.e., the "stable" clades), what these indicate about monophyletic groups within *Viburnum*, and the correspondence of these groups with the previously recognized sections of the genus.

Section *Thyrsoma* was divided into three CUs (G, Q, and S). In figures 1A, 1B, and 1D these formed a monophyletic group but were united only by their possession of paniculate inflorescences (char. 17). This condition is considered apomorphic in this analysis based on out-group comparison, but this assessment is uncertain because the plesiomorphic state within *Sambu-*

cus and *Adoxa* is not entirely clear. In all previous work on *Viburnum* the paniculate inflorescence has been considered the ancestral condition, apparently based on its correlation with presumably primitive states (Wilkinson 1948; DeVos 1951; Egolf 1962a). If it is, in fact, the plesiomorphic state, then there is no synapomorphy that unites these CUs. It is worth noting that in all other respects sect. *Thyrsoma* is extremely heterogeneous (Donoghue 1982).

In figure 1C, S (of sect. *Thyrsoma*) and T (sect. *Tinus*) are sister groups; this arrangement is concordant with growth pattern and pollen similarities between the CUs (Donoghue 1982). CUs G and Q (both of sect. *Thyrsoma*) are always united by their possession of elongate corolla tubes. However, this condition appears to have evolved several times in *Viburnum* (see char. 20 in table 3).

Section *Pseudotinus* was divided into two CUs in this analysis (C and F); these differ in pollen exine (char. 23), corolla shape (char. 20), and presence or absence of sterile flowers in the inflorescences (char. 19). In each analysis, however, C and F are sister groups supported by apomorphic growth pattern character states (chars. 4–5) and presence of stipules (char. 10), sessile inflorescences (char. 16), broadly oval leaves (char. 22), and ruminant endosperm (char. 30).

Section *Lantana* was divided into two CUs, CU N consisting of all of the species except *V. urceolatum* (CU U). In every analysis, N is the sister group of C and F. These three CUs are united by their naked buds (char. 1), stellate hairs (char. 15), and neoformed, exposed inflorescences (char. 6). The relationships of U are unclear. In figures 1A and 1B, U is the sister group of the clade N,C,F, but in figures 1C and 1D it is the sister group of the clade M,L. In either case, the linkage is not well supported. In figures 1C and 1D it is the result of corolla shape (char. 20) and stone shape and grooving (chars. 27 and 29); the former must have evolved independently in *Viburnum* several times and, according to this hypothesis, must have been lost in M and L. The two stone characters may be developmentally correlated. In any case these cladograms suggest that a taxon that included only N and U (sect. *Lantana* sensu Rehder) would not be monophyletic.

Section *Megalotinus* is represented by two CUs in this study, i.e., *V. cylindricum* (CU Y), and

the species complex that Kern (1951) segregated as subsect. *Punctata* (CU M). As discussed above, the position in the cladogram of *V. cylindricum* changed so much in the first three runs that it was eliminated in the fourth run because of its possible hybrid origin. The CUs Y and M were not united as sister groups in any of the analyses. Instead, M is directly united to L (sect. *Lentago*) on every cladogram. A close relationship between the New World sect. *Lentago* and some species of the Old World sect. *Megalotinus* has not been suggested previously but is supported by synapomorphies in characters 1 (bud scale number), 2 (bud scale arrangement), 7 (branch development), 16 (inflorescence structure), 23 (pollen exine), and 34 (red gland type). The two groups differ principally in their fruits (chars. 25, 26, and 28) and seeds (char. 30).

In figures 1C and 1D the clade M,L,U is the sister group of the clade N,C,F. The monophyly of this entire group of CUs is supported in these analyses by synapomorphies in the number and arrangement of bud scales (chars. 1-2), inflorescence development (char. 6), and pollen exine (char. 23). A direct relationship between sects. *Lantana*, *Pseudotinus*, *Megalotinus*, and *Lentago* has never before been proposed.

Rehder's sect. *Opulus* (represented by three CUs: E, O, and K), his sect. *Odontotinus* (represented by six CUs: J, I, B, W, R, and D), and the Latin American CUs (A and H) together form a monophyletic unit in figures 1B, 1C, and 1D. This is based on the number of bud scales (char. 1) and their arrangement (char. 2) and on leaf shape (char. 22). In figure 1A the CUs Y, T, M, and L are inserted (as a group) into the *Opulus*-*Odontotinus* clade, as the sister group of H,D,A. This linkage is supported only by characters 13 (leaf venation) and 14 (leaf margins), and according to this hypothesis the apomorphic states of these characters must have been lost in D and A. For the reasons discussed above characters 13 and 14 were eliminated after the first run.

Within the *Opulus*-*Odontotinus* clade, sects. *Odontotinus* and *Opulus* are not sister groups. Instead, sect. *Odontotinus* (sensu Rehder) is paraphyletic, i.e., no apomorphy unites only the CUs of sect. *Odontotinus*, and the CUs of sect. *Opulus* "arise within" sect. *Odontotinus*.

Section *Opulus* (sensu Rehder) may or may not be monophyletic. This depends entirely on

the relationships of *V. kansuense* (CU K), which are at present uncertain; in figures 1B, 1C, and 1D there is an unresolved trichotomy involving the CUs A and R, K, and E and O. That E and O together form a monophyletic group seems well established. Even though plants of *V. edule* (CU E) produce terminal buds (char. 3) and lack large petiolar glands (char. 9) and sterile flowers (char. 19), the hypothesis that E and O are sister taxa is supported by bud scale arrangement (char. 2), shoot type (char. 5), and endocarp shape (char. 27) and grooving (char. 29).

Within the *Opulus*-*Odontotinus* clade (in figs. 1B, 1C, and 1D) there are two primary clades that differ from one another in fruit characters. The clade H,D,A is characterized by fruits with purple-black flesh (char. 25) that are mealy or gritty in texture (char. 26) and have a rounded stone (char. 27), while, according to figures 1B, 1C, and 1D, the CUs, J, I, B, W, R, K, E, and O are united by red fruits with juicy flesh and flattened stones. However, in each of the cladograms there must have been at least one independent derivation of purple-black, mealy fruits in CUs W and R. Curiously, if these hypotheses are correct, the independent derivation of these character states occurred in such a way that all the New World members of sect. *Odontotinus* have purple-black, mealy fruits and all of the Old World CUs have red, juicy fruits. This would mean that the New World species of sect. *Odontotinus* are not a monophyletic group, a result that was not anticipated. The parallel evolution of purple-black fruits, if it did, in fact, occur, could be attributed to an historical accident, but because of the geographical correlation an adaptive explanation may be called for.

The clade H,D,A remained stable throughout the analyses, being supported by the fruit characters discussed above. This is of great interest because it suggests that the Latin American CUs A and H, along with CU D, form a monophyletic group. CU D, which is composed of North American and eastern Mexican species, is considered a monophyletic group on the basis of style pubescence (char. 21), but it is also characterized by presumably derived fruit, leaf, and trichome character states.

The exact cladistic relationships of H, D, and A to one another are uncertain. In figures 1A, 1B, and 1C, CUs D and A are sister groups

and H is the out-group. In figure 1A, D and A are united by apomorphies of characters 8, 15, and 22 and by reversals in characters 13 and 14. In figure 1B they are united only by characters 8, 15, and 22, and in figure 1C only by character 22, which exhibits some homoplasy on all cladograms. However, in figure 1D, A and H are sister groups united by the reduction of the central intrusion of the stone (char. 29), and D is the out-group. It is necessary to resolve further the cladistic relationships of these groups before proceeding with cladistic analysis of the Latin American species complexes.

CONCLUSIONS

This study is a first step towards an understanding of the evolutionary history of *Viburnum*. There were uncertainties in the initial data used in this analysis concerning 1) homology of character states, 2) independence of characters, 3) scoring of CUs (due to sample size and variation within CUs), and 4) polarity assessment. The "behavior" of characters, and of CUs, on each of the cladograms was studied, and this information was used to re-evaluate the data and to eliminate successively some of these uncertainties. Uncertainty was also minimized by focusing attention only on those clades that were most strongly supported by apomorphies and hence were "stable" throughout the analyses. Labile CUs or clades pinpoint poorly supported areas on the cladograms. Additional data must be sought to resolve more confidently the relationships of these groups.

The following conclusions are reached concerning phylogenetic relationships in *Viburnum*. (1) The hypothesis that sect. *Thyrsoma* is monophyletic hinges on whether the paniculate inflorescence is considered plesiomorphic or apomorphic; however, in any case, *V. erubescens* (Q) and *V. farreri* (G) appear to constitute a monophyletic group. (2) Section *Pseudotinus* appears to be monophyletic and is the sister group of sect. *Lantana* (excepting *V. urceolatum*, the relationships of which remain unclear). (3) The New World sect. *Lentago* and the Old World sect. *Megalotinus* subsect. *Punctata* are probably sister groups, and hence, sect. *Megalotinus* (sensu Rehder) is not monophyletic. (4) The relationships of *V. cylindricum*

and of sect. *Tinus* are unresolved. (5) Sections *Opulus* and *Odontotinus*, together, form a monophyletic group, within which sect. *Opulus* (sensu Rehder) may or may not be monophyletic (depending on the relationships of *V. kansuense*), and sect. *Odontotinus* (sensu Rehder) is probably paraphyletic. (6) Within the *Opulus*-*Odontotinus* clade the primary division is between a group of CUs that are predominantly of the Old World and have red, juicy fruits (with the exception of CUs W and R), and a New World group with purple-black, mealy-fleshed fruits. (7) Although the Latin American species are most closely related to eastern North American species (the *V. dentatum* complex), the exact cladistic relationships between the *V. acutifolium*, *V. hartwegii*, and *V. dentatum* complexes remain uncertain.

The results presented here are preliminary and are not sufficient to begin a subgeneric reclassification of *Viburnum*. This analysis does, nevertheless, clarify phylogenetic relationships within the genus by revealing clades that are well supported by shared derived character states and by pinpointing clades whose relationships require further study. It also focuses attention on the character data themselves and helps identify those characters most in need of more detailed study.

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