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## Phylogenetic Relationships of *Sambucus* and *Adoxa* (Adoxoideae, Adoxaceae) Based on Nuclear Ribosomal ITS Sequences and Preliminary Morphological Data

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**ABSTRACT.** We inferred the phylogeny of *Sambucus* and *Adoxa* (Adoxoideae, Adoxaceae) based on nucleotide sequences of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA, preliminary morphology, and a combination of the two data sets. Our morphological analysis implies that *Adoxa* is nested within *Sambucus*, based primarily on herbaceous habit and aspects of flower morphology. However, there is strong support for the monophyly of *Sambucus* based on ITS sequences and in the combined analysis, implying that morphological similarities shared by *Adoxa* and the two Australian species of *Sambucus* may have evolved independently. The relatively small variation in ITS sequences within *Sambucus* makes the sequences easy to align, but results in some ambiguity due to a limited number of informative characters. Nevertheless, there are several well-supported clades within *Sambucus*. Species with paniculate inflorescences (sect. *Botryosambucus*) form a well-supported clade, within which the red-fruited species are monophyletic. These results support the view that paniculate inflorescences and red fruits evolved independently in *Sambucus* and *Viburnum*. In all analyses *S. ebulus* and its relatives (sections *Ebulus* and *Scyphidanthé*) form a clade supported by valvate corolla lobes. Based on the combined analysis the first Adoxoideae may have been characterized by flowers with an equal number of carpels and perianth parts, and more-or-less separated style branches/stigma lobes. If so, reduction in the number of carpels and fusion of styles occurred within *Sambucus*.

Previous phylogenetic analyses have established that *Sambucus* and *Adoxa* are directly related (Donoghue 1983a; Donoghue et al. 1992; Chase et al. 1993; Olmstead et al. 1993; Judd et al. 1994). The name Adoxoideae has been applied by Thorne (1992) to this clade, which is characterized by such morphological features as compound leaves, extrorse anthers (at least at maturity), and the *Adoxa*-type embryo sac. The *Sambucus*-*Adoxa* clade appears to be related to *Viburnum* (references above, also see Benko-Iseppon 1993; Erbar 1994; Backlund and Donoghue 1996) and the clade stemming from the common ancestor of these three groups has been called Adoxaceae by several authors (Donoghue 1983b; Thorne 1992; Judd et al. 1994; Donoghue 1995). Phylogenetic relationships within *Viburnum* have received some attention (Donoghue 1983b, 1985; Donoghue and Baldwin 1993; Donoghue and Sytsma 1993), but little work has been done on the phylogeny of Adoxoideae.

The aim of the present paper is to clarify relationships within the *Sambucus*-*Adoxa* clade through phylogenetic analyses of molecular and morphological evidence. Of special interest is the possibility that *Adoxa* is nested within *Sambucus*; that is, that *Sambucus* is paraphyletic, with some

*Sambucus* species being more closely related to *Adoxa*. This remains a distinct possibility for a number of reasons. First, in previous studies it has simply been assumed that *Sambucus* is monophyletic—it has been scored as a single terminal taxon in morphological studies, and only a single accession has been used in molecular studies. Second, morphological apomorphies of *Sambucus* have not been identified (see below), and several characters suggest that it may be paraphyletic. In particular, *Sambucus* includes a number of herbaceous species, some of which also show reduction in the number of perianth parts, fruits that are greenish in color, and a tendency toward split stamens and style branches. It is possible that these characters unite several *Sambucus* species with *Adoxa* and its relatives. In other words, as suggested by Hallier (1912, p. 224), *Adoxa* may be nothing but a reduced *Sambucus* (also see Eichler 1875; Takhtajan 1980).

In order to establish whether *Sambucus* is monophyletic or paraphyletic, and to evaluate previous classifications of *Sambucus* itself, we assembled and analyzed nucleotide sequences of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA as well as a preliminary data set of morphological characters. ITS sequences

TABLE 1. Comparison between three classifications of *Sambucus* species. The species listed are the ones used in our analyses; assignment to sections is listed for each author. Note that Schwerin (1920) used the invalid name “*Eusambucus*” (Greuter et al. 1994, article 21.3) for the sect. *Sambucus*. Since the classifications of Weberling and Hara focused on local floras, some of the species (marked by \*) were not considered by them. Notes: 1. Weberling mentioned only *S. glauca* Nutt.; 2. These species were mentioned in passing by Hara who seemed to agree with Weberling; 3. Hara mentioned *S. mexicana* C. Presl. ex DC., which, according to Bolli (1994), has often been used erroneously for *S. caerulea*.

	Schwerin (1920)	Weberling (1966)	Hara (1983)
<i>S. adnata</i> DC.	Scyphidanthè	Sambucus	Ebulus
<i>S. javanica</i> Blume	Scyphidanthè	Sambucus	Ebulus
<i>S. africana</i> Standl.	Ebulus	*	*
<i>S. ebulus</i> L.	Ebulus	Ebulus	Ebulus
<i>S. wightiana</i> Wall. ex Wight & Arn.	Ebulus	Ebulus	Ebulus
<i>S. callicarpa</i> Greene	Botryosambucus	Botryosambucus	*
<i>S. pubens</i> Michaux	Botryosambucus	Botryosambucus	*
<i>S. racemosa</i> L.	Botryosambucus	Botryosambucus	Botryosambucus
<i>S. sieboldiana</i> Blume ex Miq.	Botryosambucus	Botryosambucus	Botryosambucus
<i>S. melanocarpa</i> A. Gray	Botryosambucus	Botryosambucus	Botryosambucus
<i>S. canadensis</i> L.	Sambucus	Sambucus	Sambucus
<i>S. peruviana</i> H. B. K.	Sambucus	Sambucus	*
<i>S. maderensis</i> Lowe	Sambucus	*	*
<i>S. nigra</i> L.	Sambucus	Sambucus	Sambucus
<i>S. australasica</i> (Lindl.) Fritsch	Tripetalus	Sambucus	2
<i>S. gaudichaudiana</i> DC.	Tetrapetalus	Sambucus	2
<i>S. australis</i> Cham. & Schltdl.	Sambucus	Sambucus	2
<i>S. caerulea</i> Rafinesque	Sambucus	Sambucus <sup>1</sup>	Sambucus <sup>3</sup>

were chosen for this purpose based on the evident success of previous phylogenetic analyses within and among closely related angiosperm genera (Baldwin et al. 1995), including *Viburnum* (Donoghue and Baldwin 1993). We also analyzed a combined morphological and molecular data set.

*Sambucus* is a widespread genus with centers of diversity in eastern Asia and North America. Several species are noteworthy for their wide geographic ranges, such as the circumboreal *Sambucus racemosa* (s.l.). The genus was revised by Schwerin in 1909 and again in 1920, by which time at least 115 species and a large number of subspecific taxa had been described. In 1920 Schwerin provisionally recognized 28 species, and since that time some 15 more species have been named. In a recent revision by Bolli (1994), only nine species were recognized, with most previously recognized species being synonymized or reduced to subspecific rank.

The genus was subdivided by Schwerin (1909, 1920) into sections that closely matched those recognized earlier by, for example, De Candolle (1830) and Fritsch (1891b). These sections (Table 1) were arranged in 1909 into three informal subgenera corresponding to the major branches in his diagram of relationships (Fig. 1a). This subdivision was based solely on the number of perianth lobes.

*Sambucus gaudichaudiana* (sect. *Tetrapetalus*), with four corolla lobes, and *Sambucus australasica* (sect. *Tripetalus*) with three, were considered primitive by Schwerin because they occurred in Australia, which he presumed to be an ancient floristic province. In Schwerin’s 1920 treatment, the position of the root shifted, based mainly on the belief that a smaller number of perianth lobes was likely to be derived (Fig. 1b). Much the same reasoning was maintained by Bolli (1994). With the exception of the largest sect. *Sambucus* (“*Eusambucus*”), Schwerin noted one or more unusual features of each section: dimorphic flowers in sect. *Heteranthè*; flowers modified into urn-shaped nectaries in sect. *Scyphidanthè*; herbaceousness, valvate buds, acute perianth lobes, and rhizomes in sect. *Ebulus*; and paniculate inflorescences, thick winter buds, brownish pith, and punctate endocarps in sect. *Botryosambucus*.

Several other subgeneric classifications of *Sambucus* have been proposed (Table 1). Rehder (1912) argued that Schwerin’s sections *Ebulus* and *Scyphidanthè* should be combined because valvate buds and herbaceousness occurred in both groups. Weberling (1966b) lumped all sections, except *Ebulus* and *Botryosambucus*, into an expanded sect. *Sambucus*. A similar arrangement was adopted by Hara (1983) but he followed Rehder’s suggestion and joined *Scyphidanthè* with *Ebulus*. Fukuoka

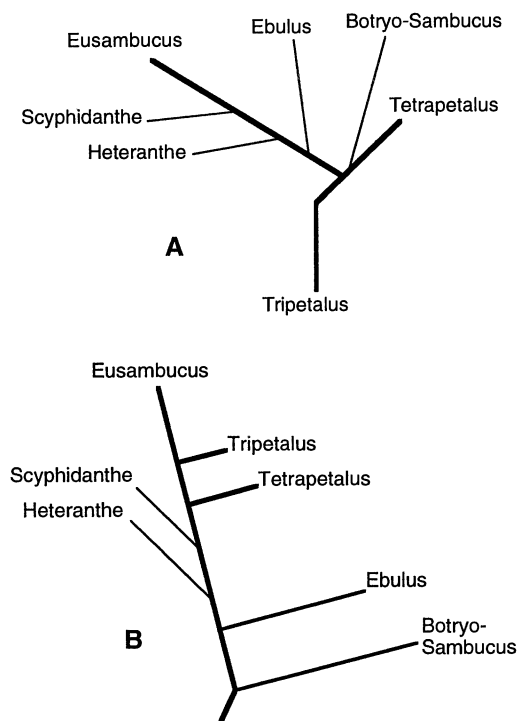


FIG. 1. Phylogenies of *Sambucus* presented by Schwerin: "A" (1909 p. 11); "B" (1920 p. 203). The names are the sections accepted by Schwerin ("Eusambucus" is sect. *Sambucus*; see Table 1). For comparison tree A was interpreted as being rooted along the branch leading to *Tripetalus*.

(1987) returned to a scheme similar to Schwerin's; however, he joined sections *Tripetalus* and *Tetrapetalus* based on evident variability in the number of corolla lobes. It is noteworthy that these treatments differ in the interpretation of characters that may have a direct bearing on the placement of *Adoxa*, including herbaceousness and the number of perianth lobes. Bolli (1994) concluded that all previously recognized subgenera and sections were unnecessary, and he refrained from offering an alternative classification.

*Adoxa moschatellina* L. is a small herb found in temperate and boreal regions around the Northern Hemisphere. The morphology of these plants has resisted standard interpretation (Lagerberg 1909; Sturm 1910; Sprague 1927; Weberling 1966a; Fukuoka 1974; Li and Ning 1987; Erbar 1994). For example, whereas the cauline leaves are opposite, those along the rhizome are alternately arranged. And, whereas the terminal flowers in the compact, head-like, inflorescences are four-merous, the lat-

eral flowers are five-merous (but with three calyx lobes). The perianth parts themselves have been interpreted as calyx and corolla, calyx and subtending bracts, or as corolla and bracts (Jussieu 1791; Wydler 1850; Eichler 1875; Drude 1879, 1884; Martinovsky' 1931; Fukuoka 1974). Also noteworthy are the stamens, being divided into two separate segments, each with a single anther sac, and the semi-inferior ovary terminating in several distinct style branches.

These characteristics of *Adoxa* have suggested a wide variety of possible relationships, including with Araliaceae, Caprifoliaceae, Saxifragaceae, and even Fumariaceae and Ranunculaceae (e.g. Adanson 1763; De Candolle 1830; Hooker 1873; Sprague 1927; Warming and Möbius 1929; Hutchinson 1973). Fritsch (1891a) concluded that "there is no genus in the plant kingdom with which *Adoxa* is without doubt closely related," and he therefore placed it in a monotypic Adoxaceae. This strategy has been taken up in most recent taxonomic systems (e.g., Takhtajan 1980; Cronquist 1981; Dahlgren et al. 1981; but see Thorne 1992) with Adoxaceae then usually allied with Caprifoliaceae within Dipsacales. As noted above, all recent phylogenetic studies have supported the view that *Sambucus* and *Adoxa* are directly related, and this clade has been formally recognized by Thorne (1992) as Adoxoideae.

Until recently only a single species of *Adoxa* was known (*A. moschatellina*) and no close relatives except for *Sambucus*. However, in 1981, two new species were described from China, both presumably related to *Adoxa*: *Tetradoxa omeiensis* (H. Hara) C. Y. Wu (Hara 1981; Wu 1981) from the vicinity of Mt. Omei in Sechuan Province, and *Sinadoxia corydalis* C. Y. Wu, Z. L. Wu & R. F. Huang (Wu et al. 1981) from southern Qinghai Province. These species are both exceedingly rare, and have only recently been recollected. Subsequently, *Adoxa orientalis* Nepomn. was described from the Amur region of Russia by Nepomnyashchaya (1984). Owing to the lack of material of these new species when the present study was conducted, we were unable to include them in our analysis. *Sinadoxia* and *Tetradoxa* were included in a morphological analysis by Backlund and Donoghue (1996), which indicated that they were linked to *Adoxa*.

#### MATERIALS AND METHODS

**Choice of Taxa.** We considered all *Sambucus* species recognized by Bolli (1994), along with nine

TABLE 2. Specimens used for the ITS analysis, with data on source, geographic origin, voucher specimens, and GenBank accession numbers. When ITS spacers were submitted separately, the first GenBank accession number refers to ITS1 and the second one to ITS2. Abbreviations for source are: Fresh leaves; Fresh/frozen leaves; Herbarium material; Silica gel dried leaves.

Species	Source	Origin	Voucher (herbarium abbrev.)	GenBank Accession
<i>A. moschatellina</i>	H	Japan	Togashi MT7005 (A)	U88194
<i>S. adnata</i>	H	China	Sino-Amer. Exped. 38 (A)	U88209, U88210
<i>S. africana</i>	F	Kenya	Knox 2539 (GH)	U88195
<i>S. australasica</i>	H	Australia (NSW)	Schodde 5172 (A)	U41381
<i>S. australis</i>	H	Argentina	Vanni, Daviña & Pietrarelli 584 (A)	U88196
<i>S. caerulea</i>	F	USA (AZ)	Donoghue s.n. (A)	U88197
<i>S. callicarpa</i>	F	USA (CA)	Voucher not known; cult. Rancho Santa Ana Bot. Gard., acc. # 14770	U88198
<i>S. canadensis</i>	F/fr	Eastern USA	No voucher; cult. Arnold Arboretum (area 16B)	U88199
<i>S. javanica</i>	H	Japan	Takahashi 1783 (A)	U88201
<i>S. ebulus</i>	S	Greece	Sundin s.n. (GH)	U88200
<i>S. gaudichaudiana</i>	S	Australia (ACT)	Crisp & Telford 8540 (CBG)	U41382
<i>S. maderensis</i>	S	Madeira	No voucher allowed; cult. Bot. Gard. Madeira	U88202
<i>S. melanocarpa</i>	H	USA (Idaho)	Collotzi & Davidse 698 (GH)	U88203
<i>S. nigra</i>	F	Sweden	Eriksson s.n. (S)	U88204
<i>S. peruviana</i>	H	Argentina	Bolli A91 (Z)	U88205
<i>S. pubens</i>	F	USA (NH)	Donoghue s.n. (GH)	U88206
<i>S. racemosa</i>	F	Sweden	Eriksson s.n. (S)	U88207
<i>S. sieboldiana</i>	F	Japan	Donoghue s.n., 25 May 87 (A); cult. Arnold Arbor., acc. # 1887-77-G	U88558, U88559
<i>S. wightiana</i>	H	India (Punjab)	Stewart 5814 (A)	U88208
<i>V. dentatum</i>	F	Eastern USA	Elsik et al. 1311 (A); cult. Arnold Arbor., acc. # 5070-1	U88552, U88553
<i>V. lentago</i>	F	Eastern USA	Elsik et al. 823 (A); cult. Arnold Arbor., acc. # 18021-A	U88554, U88555
<i>V. sieboldii</i>	F	Japan	Elsik et al. 2640 (A); cult. Arnold Arbor., acc. # 616-6-B	U88556, U88557

additional species accepted by Schwerin (1909, 1920). This allowed us to test the circumscription of three species in Bolli’s revision, *S. nigra*, *S. racemosa* and *S. ebulus*, into which he lumped a number of taxa accepted as separate species by Schwerin. One specimen of *Adoxa moschatellina* was included in the sequence study, and three species of *Viburnum*, representing three major evolutionary lines (Donoghue 1983b; Donoghue and Baldwin 1993; Donoghue and Sytsma 1993), were included in the analysis for rooting purposes (Farris 1982; Maddison et al. 1984). Additional information on the 22 taxa used in our analyses is given in Table 2, including data on specimens from which DNA’s were obtained (see below).

**Morphological Data.** Data for the preliminary morphological analysis were compiled primarily from published sources, including the monographs by Schwerin (1909, 1920), and especially Bolli’s (1994) recent revision. In scoring *Adoxa* we relied on

Sturm (1910), Fukuoka (1974), Hara (1983), and Erbar (1994), and for *Viburnum* on Donoghue (1983b). We also studied herbarium specimens in the Harvard University Herbaria (A, GH) to confirm the distribution of character states and to help delimit several characters. The morphological characters and states used in our analysis are given in Table 3, and the morphological data set is shown in Table 4. The amount of missing data was 5.8%, and polymorphism 3.3%. The morphological matrix was submitted to TreeBASE (<http://phylogeny.harvard.edu/treebase/>); accession number M172c6x25x97c14c22c13.

**Molecular Methods.** DNA’s were extracted from fresh material, silica-gel dried specimens, or from herbarium specimens in A and GH (Table 2). Sequences of *Sambucus sieboldiana*, and the three *Viburnum* species were obtained from a previous study (Donoghue and Baldwin 1993). Extractions were carried out using either the CTAB extraction

TABLE 3. Morphological characters used in phylogenetic analyses (see Table 4).

1. <b>Habit:</b> shrub or tree (0); herbaceous perennial (1). <i>S. javanica</i> appears to be polymorphic (Bolli 1994); the subspecies we sampled is herbaceous (Hara 1983).
2. <b>Rhizome:</b> absent (0); present (1). <i>S. nigra</i> is scored polymorphic based on Bolli (1994). Information is missing for some species.
3. <b>Pith color:</b> white (0); yellowish brown (1). <i>Adoxa</i> lacks a well developed pith and is scored as unknown.
4. <b>Upper lateral leaflets:</b> not decurrent (0); decurrent (1). Bolli (1994) reports decurrent upper leaflets in five species. However, two species appear to be polymorphic (e.g., Bolli's fig. 33 of <i>S. gaudichaudiana</i> ). <i>Viburnum</i> has simple leaves and is scored as unknown.
5. <b>Winter buds:</b> without pre-formed inflorescences (0); with inflorescences (1). Herbaceous species are scored as unknown for this character.
6. <b>Stipules:</b> absent (0); wart- or stalk-like (1); foliaceous (2). Bolli (1994) reported variation in stipule organization in two species, which are coded polymorphic. The stalk-like stipules are nectariferous in many cases (Bolli 1994).
7. <b>Glands on rachis:</b> absent (0); present (1). These are short appendages with glands at the apex situated on the rachis in between the leaflets in some species. <i>S. javanica</i> is coded polymorphic in this character based on herbarium specimens lacking glands. <i>Viburnum</i> is scored as unknown since it has simple leaves.
8. <b>Inflorescence form:</b> flat topped (0); ovoidal (1); glomeruloid (2). <i>S. callicarpa</i> and <i>S. melanocarpa</i> have inflorescences which are sometimes intermediate, varying between flat and ovoidal (Schwerin 1909, 1920).
9. <b>Aestivation of buds:</b> imbricate (0); valvate (1). Our scoring follows Hara (1983).
10. <b>Number of corolla lobes:</b> five (0); less than five (1). We have scored all taxa in which at least some flowers regularly have less than five corolla lobes as state 1. Lateral flowers of <i>Adoxa moschatellina</i> have four lobes and the apical flower has five.
11. <b>Anther dehiscence:</b> extrorse (0); introrse (1). Scored as uncertain in some cases due to problems in delimitations of the states; e.g., Bolli (1994) indicated that <i>S. javanica</i> has latrorse anthers.
12. <b>Fruit exocarp (surface) color when ripe:</b> black or blue (0); red (1); yellow to green translucent (2). In several species with red or black fruits, uncommon light colored variants have been reported; these have been disregarded in coding characters 12 and 13. Bolli's (1994) description of <i>S. canadensis</i> suggests polymorphism.
13. <b>Fruit mesocarp (pulp) color when ripe:</b> purple (0); yellow to orange (1); white to green (2). Information is lacking for three species which are coded as unknown.
14. <b>Number of style branches:</b> equal to number of corolla lobes (0); fewer (1). Bolli (1994) noted that two species are variable; these are scored here as polymorphic; <i>S. peruviana</i> may be a hybrid between <i>S. canadensis</i> (scored 1) and <i>S. australis</i> (scored 0).
15. <b>Base chromosome number:</b> $X = 9$ (0); $X = 18$ (1).
16. <b>Style branches:</b> narrow, separate (0); wide, fused (1). The style branches of <i>S. australis</i> are intermediate and it is scored as unknown.
17. <b>Corolla lobe direction:</b> erect or flat (0); reflexed (1).
18. <b>Corolla lobe apex:</b> obtuse (0); acute (1). We have not seen flowering material of <i>S. wightiana</i> and published accounts are unclear.

method described by Doyle and Doyle (1990) with 1% PVP (polyvinylpyrrolidone) added to the extraction buffer or, in the case of dried material, a version of this extraction procedure scaled down to microfuge tubes (R. Jansen, pers comm.). In the case of the "mini-preps" ca. 15–40 mg of leaf tissue was rehydrated in water for ca. 15–30 minutes prior to grinding in either liquid nitrogen or in CTAB buffer. The ITS region was amplified using a Perkin-Elmer 9600 thermal cycler. The primers used for

amplification were "ITS4" and "ITS5" (White et al. 1990). In most cases we used a Perkin-Elmer GeneAmp kit with AmpliTaq DNA polymerase, but in a few cases a Gibco BRL PCR reagent kit was used. PCR reaction setup followed Baldwin (1992) and PCR conditions followed Eriksson et al. (1997). Amplified DNA samples were purified using GeneClean II (Bio 101) and sequenced using standard cycle sequencing 10 µl reactions following the manufacturer recommendations (Applied Bio-

TABLE 4. Morphological data set. All characters treated as unordered; unknown and inapplicable data are coded with question-marks; slashes separate character states in polymorphic species. See Table 3 for a list of characters and character states.

	1			5			10			15			18					
<i>V. dentatum</i>	0	0	0	?	1	?	?	0	0	0	1	0	0	1	0	1	0	0
<i>V. lentago</i>	0	0	0	?	1	0	?	0	0	0	1	0	0	1	0	1	0	0
<i>V. sieboldii</i>	0	0	0	?	1	0	?	1	0	0	1	0	0	1	0	1	0	0
<i>A. moschatellina</i>	1	1	?	0	?	0	0	2	0	1	0	2	2	0	1	0	0	0
<i>S. adnata</i>	1	1	0	1	0	2	1	0	1	0	1	1	?	1	1	1	0	0
<i>S. africana</i>	1	1	0	1	?	2	1	0	1	0	0	0	0	1	1	1	0	1
<i>S. australasica</i>	0	?	0	0	0	1/2	0	0	0	1	0	2	1	0	1	0	0	0
<i>S. australis</i>	0	1	0	0	0	2	0	0	0	0	0	0	2	0	1	?	0	1
<i>S. caerulea</i>	0	?	0	0	0	0	0	0	0	0	0	0	2	1	1	1	0	0
<i>S. callicarpa</i>	0	0	1	0	1	1	0	0/1	0	0	0	1	1	1	1	1	1	0
<i>S. canadensis</i>	0	1	0	0	0	1	0	0	0	0	0	0/1	0	1	1	1	0	0
<i>S. ebulus</i>	1	1	0	1	?	2	1	0	1	0	0	0	0	1	1	1	0	1
<i>S. gaudichaudiana</i>	1	1	0	0/1	?	2	0	0	0	1	0	2	2	0/1	?	0	0	0
<i>S. javanica</i>	1	1	0	0/1	0	1/2	0/1	0	1	0	1	1	?	1	1	1	1	0
<i>S. maderensis</i>	0	0/1	0	0	0	1	0	0	0	0	0	0	0	1	?	1	0	0
<i>S. melanocarpa</i>	0	0	1	0	1	1	0	0/1	0	0	0	0	1	1	1	1	0	0
<i>S. nigra</i>	0	0/1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0
<i>S. peruviana</i>	0	?	0	0	0	1	0	0	0	0	0	0	0	0/1	1	1	0	0
<i>S. pubens</i>	0	0	1	0	1	1	0	1	0	0	0	1	1	1	1	1	1	0
<i>S. racemosa</i>	0	0	1	0	1	1	0	1	0	0	0	1	1	1	1	1	1	0
<i>S. sieboldiana</i>	0	0	1	0	1	1	0	1	0	0	0	1	1	1	1	1	1	0
<i>S. wightiana</i>	1	1	0	1	?	2	1	0	1	0	0	0	?	1	1	1	0	?

systems). Primers used for sequencing were “ITS2”, “ITS4”, and “ITS5” (White et al. 1990), and “ITS3B” (Baum et al. 1994). Both nucleotide strands were sequenced in all species except *S. africana*; in this case the “ITS2” primer failed and a portion of the sequence is based on only one strand. In the case of *S. adnata* it was not possible to read the middle portion of the 5.8S gene. Sequences were obtained using an Applied Biosystems 370A automated fluorescent DNA sequencer. For data collection, base calling, proofreading and editing we used Apple Macintosh computers with Applied Biosystems software (Data Collection 1.1.1, Analysis 1.1.1., SeqEd 1.0.3).

Sequences were submitted to Clustal W 1.5 (Higgins et al. 1992; Thompson et al. 1994) in “Pearson/FASTA” format and a multiple alignment performed. Clustal was run on a Macintosh Quadra computer using the default parameters, and several minor adjustments were made following inspection. The ITS data set is presented in Appendix 1. There are 623 ITS nucleotide positions in this data set, of which 135 are parsimony informative [sensu PAUP (Swofford 1993)] and 303 characters are constant. With the addition of 11 binary indel characters (chars. 624–634; see below) a total of 634 characters were included in our ITS analyses. The amount of uncertainty in the data set is 5.1% if gaps and unsequenced parts of 5.8S

are considered. The amount of other uncertainty is 0.7%. Sequence divergences within *Sambucus* (calculated using PAUP) range from 0.16–5%, whereas they range from 12–13% between *Sambucus* and *Adoxa*, from 15–18% between *Sambucus* and *Viburnum* species, and 19–20% between *Adoxa* and *Viburnum* species. The molecular matrix was submitted to TreeBASE; accession number M173c6x25x97c14c24c06.

**Phylogenetic Analyses.** Parsimony analyses were conducted using PAUP 3.1.1 (Swofford 1993). All characters were unordered and weighted equally, in the separate as well as in the combined analyses of all 652 characters. In the morphological data set, polymorphisms were coded with all applicable states and uncertain or unknown states were coded as question-marks and treated as missing in the analyses; autapomorphies were not included. In the ITS data set gaps were coded with hyphens (-) and treated as missing in the PAUP analyses. Potentially informative gaps were scored as present (1) or absent (0), yielding 11 additional binary characters. In proofreading the ITS sequences several ambiguous base-callings were encountered and these were coded using IUPAC ambiguity codes.

Heuristic searches were conducted with MUL-PARS and TBR branch swapping. Starting trees were constructed using 1,000 replicates of random

addition sequence. Consensus trees were computed using the strict consensus option. In order to assess node support, bootstrap analyses (Felsenstein 1985; Hillis and Bull 1993) were performed, as well as decay analyses (Bremer 1988; Donoghue et al. 1992) using the reverse constraint option in PAUP and the AutoDecay program of T. Eriksson (a freeware program designed to obtain decay indices for all nodes in a tree using PAUP). In the bootstrap runs PAUP was set to run 5,000 bootstrap replicates with TBR branch swapping, saving one tree in each replicate. In the reverse constraint runs for the decay analyses PAUP was set to run 100 random addition sequences (in some cases saving a maximum of five minimal length trees in each replicate).

Alternative phylogenetic arrangements were tested using constraints in PAUP and using MacClade 3.05 (Maddison and Maddison 1992). MacClade was also used to explore implications for the evolution of particular morphological characters, and to explore alternative rootings of ingroup networks (cf. Lundberg rooting; Lundberg 1972). Consistency and retention index values were obtained from PAUP.

## RESULTS

The morphological data set yielded 931 trees of 32 steps (CI = 0.69, RI = 0.87). A strict consensus of these trees is shown in Fig. 2, along with decay indices and bootstrap values. We stress that this morphological analysis is preliminary, being based principally on those characters recorded by previous workers. While this helps us understand what these characters imply about relationships when subjected to parsimony analysis, a more detailed analysis of morphological characters might yield different (and better) results.

As expected, many clades are not well supported in the morphological analysis. Ten clades appear in the strict consensus of the shortest trees, and only a few of these have decay indices greater than one. Nevertheless, several of these results are noteworthy. Most importantly, *Adoxa* is nested within *Sambucus*, united with the two Australian species, *S. gaudichaudiana* and *S. australasica*, on the basis of reduction in the numbers of perianth parts, fruit color, and narrow style branches. Forcing *Adoxa* to be sister group to a monophyletic *Sambucus* adds three steps with this data set.

Those *Sambucus* species with paniculate inflorescences, reddish-brown pith color, and buds with preformed inflorescences appear as a clade in the

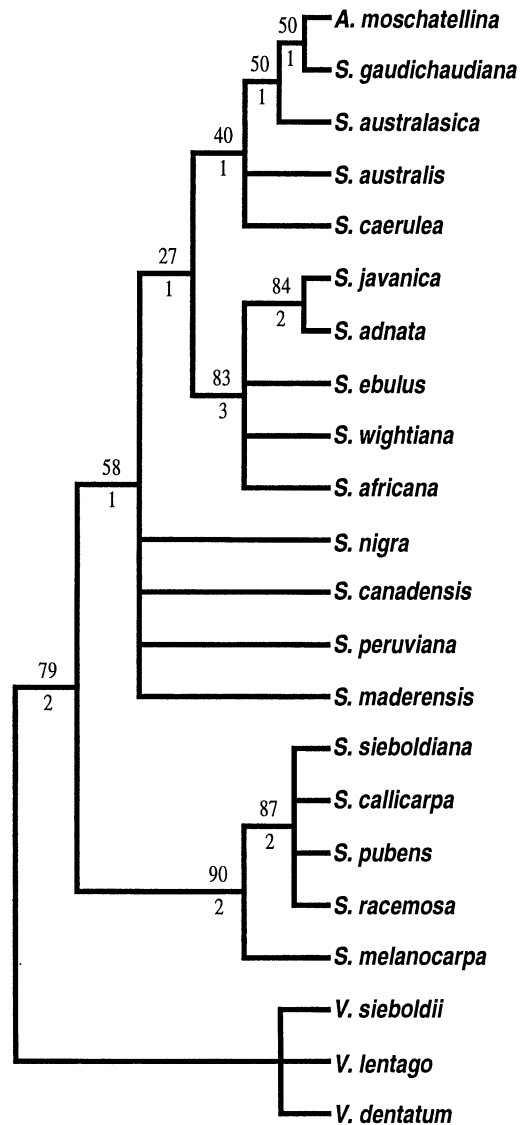


FIG. 2. Strict consensus tree from the 931 most parsimonious trees (32 steps) obtained in the analysis of the morphological data alone. Bootstrap values (above branches) and decay indices (below branches) are indicated for each node.

morphological trees. In these species the inflorescences are also borne on short lateral shoots (Troll and Weberling 1966; Bolli 1994). This group corresponds to the sect. *Botryosambucus* of Schwerin (1909, 1920), and to Bolli's species *S. racemosa* (Bolli 1994). Within this group there are evidently several phylogenetically separate lines. In particular, the several red-fruited species (*S. sieboldiana*, *S. race-*



*mosa*, *S. pubens*, *S. callicarpa*) form a clade related to the black-fruited *S. melanocarpa*. The relationship between sections *Ebulus* and *Scyphidanth* suggested by Rehder (1912) and Hara (1983) is supported, *Scyphidanth* being a monophyletic group nested within *Ebulus*. These species—*S. javanica*, *S. adnata*, *S. ebulus*, *S. africana* and *S. wightiana*—are united by valvate corolla lobes. One additional section with more than one species, *Sambucus* ("*Eusambucus*"), was recognized by Schweinin, but no explicit character support was given by him. It is not supported as monophyletic in our analysis. Relationships among Bolli's subspecies of *S. nigra* and those of *S. ebulus* are unresolved in our strict consensus tree, but among the shortest trees are those in which his subspecific taxa are seen to form monophyletic groups.

The sequence of the ITS1 spacer was found to vary in length between 220 and 224 bases and 17 of the 22 sequences were 222 bases long. In aligned form it comprised 227 characters of which 103 were variable. The ITS2 spacer sequence varied in length between 220 and 227 bases. It was 231 characters when aligned of which 127 were variable.

Analysis of the ITS sequence data set (including the 11 gap characters) yielded 520 trees of 341 steps (CI = 0.70 excluding, and 0.76 including, uninformative characters; RI = 0.77). The strict consensus of these trees is shown in Fig. 3 (with bootstrap and decay values) and one randomly chosen minimal length tree is presented in Fig. 4 to show average branch lengths. The branches separating the three genera are exceptionally long, whereas those within *Sambucus* are relatively short. An analysis excluding the gap characters yields 2,184 trees of 324 steps. The strict consensus of these trees (not shown) is almost identical to the tree in Fig. 3 except that two clades (marked with an asterisk) are collapsed.

*Adoxa* is seen in the ITS analysis to be the sister group of *Sambucus*, which is strongly supported as being monophyletic. Forcing *Adoxa* within *Sambucus* results in trees that are at least eight steps longer, and connecting *Adoxa* to the Australian species adds two more steps. Directly linking *Adoxa* with *S. gaudichaudiana*, as in the morphological trees, adds a minimum of 17 steps. In agreement with the morphological tree, ITS sequences support the monophyly of the sect. *Botrysosambucus* clade, and the valvate corolla clade [sect. *Ebulus* sensu Rehder (1912) and Hara (1983)]. In addition, ITS characters support a clade that contains the subspecies of *S. nigra* [sensu Bolli (1994)], with the

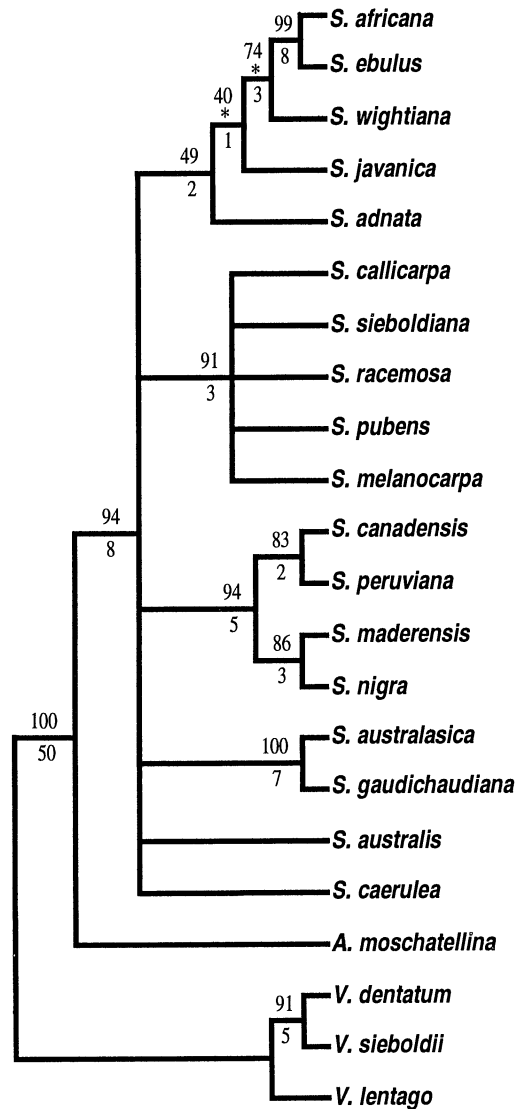


FIG. 3. Strict consensus tree from the 520 most parsimonious trees (341 steps) based on the ITS data alone (Appendix 1). Bootstrap values (above branches) and decay indices (below branches) are indicated for each node. The two nodes which collapsed in a strict consensus when the data was analysed without the 11 gap characters are indicated with asterisks.

exception of *S. caerulea*, whose position is here unresolved. Any tree in which all subspecies of *S. nigra* sensu Bolli are united requires at least three additional steps.

Analysis of the combined data set resulted in three trees of 378 steps (CI = 0.69 excluding, and 0.75 including, uninformative characters; RI =

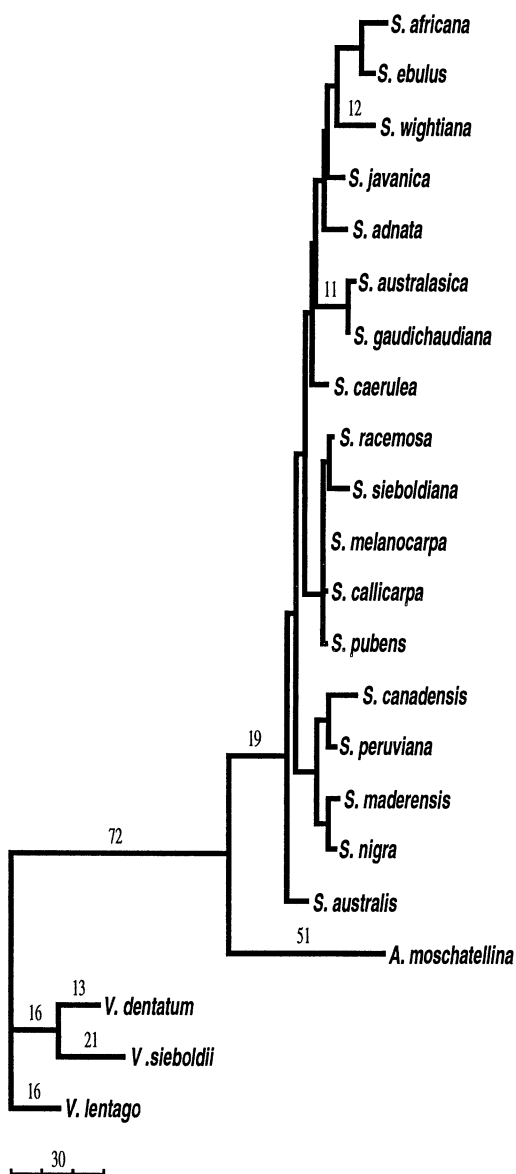


FIG. 4. A randomly selected tree from the set of most parsimonious trees for the ITS data, with branch lengths proportional to the number of changes (ACCTRAN optimization in PAUP). Branch lengths indicated above branches with ten or more changes; scale bar corresponds to 30 character changes.

0.78). The strict consensus tree is shown in Fig. 5, along with bootstrap and decay values. This tree is almost completely consistent with the ITS tree but more resolved owing to the addition of morphological characters. Only one clade (*S. adnata* with *S. javanica* in the combined tree) differs.

Bootstrap and decay values are generally higher in the combined analysis, implying that morphological characters strengthen the support for several clades. Thus, the decay index for the *Botryosambucus* clade increases from three in the ITS trees to seven in the combined trees. The decay value for the valvate clade (sect. *Ebulus*) increases from two to five. The cost of joining *S. caerulea* [*S. nigra* subsp. *caerulea* (Raf.) R. Bolli] to the *S. nigra* clade increases from three steps in the ITS tree to four in the combined analysis. Decay values decrease in the combined analysis in a few cases; for example, in the *S. nigra* clade (which includes *S. nigra*, *S. maderensis*, *S. peruviana*, and *S. canadensis*) the decay index decreases from five to four. There is no morphological character support for any of the clades in which the decay index decreases. If *Adoxa* is forced to be nested within *Sambucus* nine steps are added, and this number is also obtained when *Adoxa* is directly linked with the Australian species. Linking *Adoxa* with *S. gaudichaudiana*, as in the morphological trees, adds a minimum of 15 steps, indicating that the ITS data provide strong support for the monophyly of the Australian species. Bolli's (1994) view that *S. gaudichaudiana* is related to the herbaceous species with valvate corollas (with a reversal to imbricate lobes accompanying the reduction in lobes) is clearly not supported by these analyses.

Imposing the structure of the phylogenetic trees suggested by Schwerin (1909, 1920; Fig. 1) on our combined data yields trees that are at least 23 steps longer. This is true for both of his trees and whether or not *Viburnum* and *Adoxa* are included in the analyses.

Bolli (1994) presents his views on the phylogeny of *Sambucus* in a general discussion of character evolution and trends rather than in tree form. We tried nevertheless to interpret his views on relationships and used a constraint tree with our combined data set. This yielded trees 25 steps longer than our shortest trees if *Viburnum* and *Adoxa* were removed from consideration. Bolli suggested that *S. ebulus* has retained the largest number of ancestral features in the genus. To explore the impact of this suggestion we moved *Viburnum* and *Adoxa* to the *S. ebulus* branch in our shortest trees, which increased the tree length by eight steps.

#### DISCUSSION

The primary difference in these analyses concerns the placement of *Adoxa* in relation to

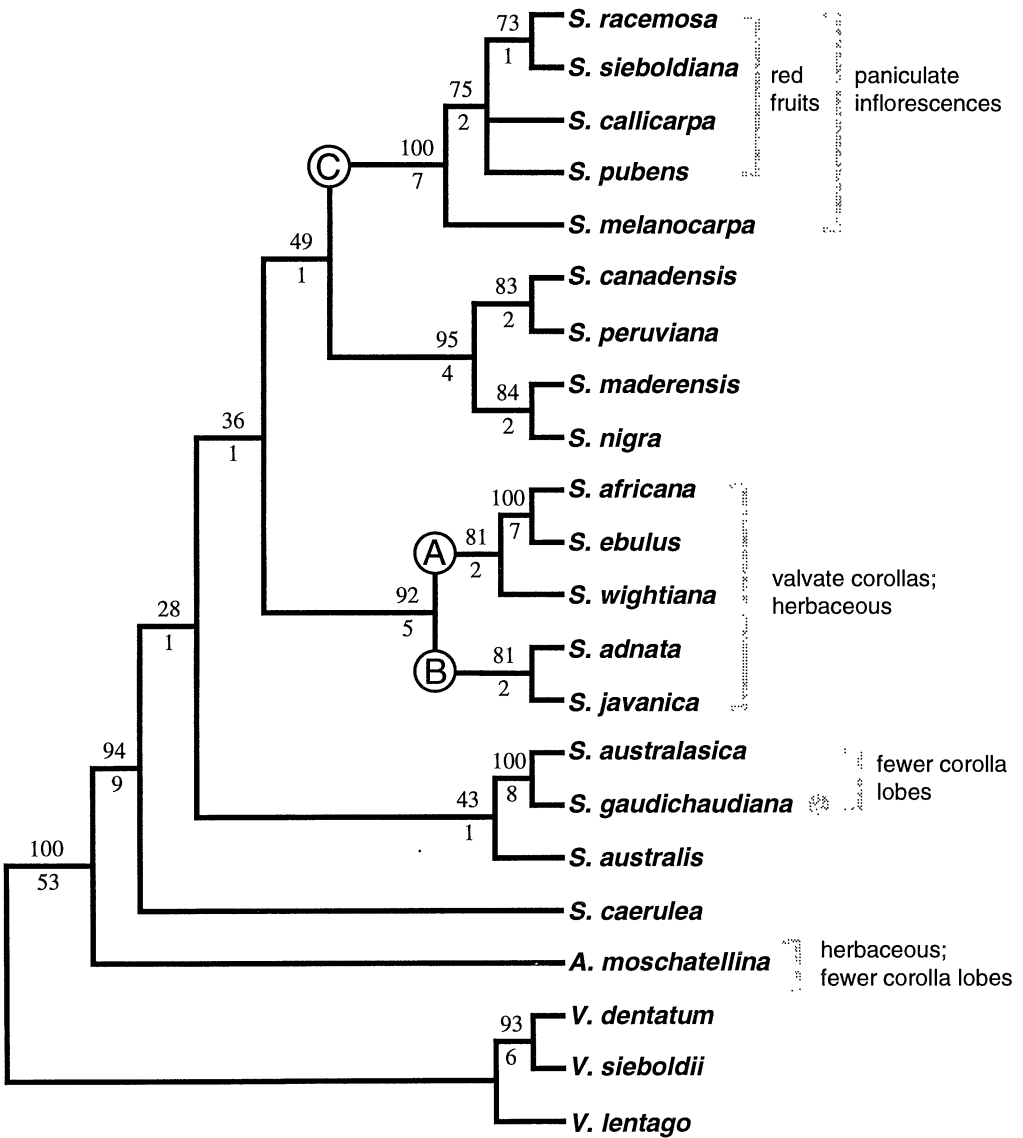


FIG. 5. Strict consensus tree from the three most parsimonious trees (378 steps) based on the combined data set. Bootstrap values (above branches) and decay indices (below branches) are indicated for each node. The distribution within *Sambucus* and *Adoxa* of several characters discussed in the text is indicated with brackets; *S. gaudichaudiana*, indicated with a dot, is also herbaceous. Nodes labeled with letters A-C indicate sections recognized by Schwerin (1909, 1920) that are monophyletic in our analysis: A. *Ebulus*; B. *Scyphidanthæ*; C. *Botryosambucus*.

*Sambucus*. In the morphological analysis *Adoxa* appears within *Sambucus*, linked with the Australian species, while in the ITS and combined analyses *Adoxa* is the sister group of a monophyletic *Sambucus*. Whereas this is clearly an important topological difference, with potentially many consequences for our understanding of character evolution (see below), the conflict between the two data

sets does not appear to be strong. The main reason for this is that the results of the morphological analysis are rather weakly supported (e.g., with only one node having a decay value greater than two). Consequently, the morphological data are not in strong conflict with the ITS results, which are much more strongly supported. In the combined analysis the strongly supported ITS results deter-

mine the basic structure of relationships, including the conclusion that *Sambucus* is monophyletic. However, the morphological characters still have an important impact on the strength of support for the major branches of the tree and on our understanding of relationships within these major clades.

One may wonder whether in the morphological analyses we simply failed to include characters that might support the monophyly of *Sambucus*. In fact, at the outset we were unable to identify any such characters, which seems surprising in view of the apparently great differentiation of *Sambucus* based on ITS sequences. Although Bolli (1994) mentioned that *Sambucus* has unique features these were not clearly specified. For example, wood anatomy was cited as being unique in several but unspecified respects (Bolli 1994 p. 17, 21). However, the wood anatomy of critical species has not yet been examined, and a number of species are herbaceous. One character said to be "typical for the genus" is crystal sand in parenchymatous cortical cells and phloem cells of the roots (Bolli 1994, p. 17). The distribution of this character is still unclear, as several *Sambucus* species have not been examined.

Erbar (1994, Fig. 44) indicated two characters as evolving along the *Sambucus* branch, but both are potential artifacts of taxon sampling, especially the use of *Viburnum farreri* Stearn in studies of nectary structure and corolla/stamen development. Loss of nectaries is shown as a character of *Sambucus*, but this may well be a retained ancestral feature in the *Viburnum-Sambucus-Adoxa* clade. *Viburnum* is assumed by Erbar (1994) to be characterized by the presence of nectaries, specifically the "ovary roof nectary." This is based on her examination of *Viburnum farreri* and *Viburnum carlesii* Hemsl. and the earlier study of *V. farreri* by Wagenitz and Laing (1984). However, *V. farreri* and *V. carlesii* are exceptional within *Viburnum* in having distinct ring-like nectaries, and phylogenies of *Viburnum* based on morphological and molecular data (Donoghue 1983b; Donoghue and Baldwin 1993; Donoghue and Sytsma 1993) indicate that these species are nested within the genus. It appears, in other words, that nectaries of this type evolved (probably several times) within *Viburnum*, and that the ancestral condition may be the absence of nectaries.

Much the same reasoning applies to the loss of the stamen-corolla tube as a character of *Sambucus* (Erbar 1994). This conclusion is based on the view that *Adoxa* and *Viburnum* are characterized by the lack of a distinct border between the corolla tube s. str. and the stamen corolla tube. However, it is

based on a study of *Viburnum farreri* (Reidt and Leins 1994), and again we stress that this species is unusual within *Viburnum* for its elongate corolla tube as well as the nature of stamen attachment within the tube (Erbar 1994, p. 275). Phylogenetic studies of *Viburnum* imply that these features of *V. farreri* are derived within the genus. Moreover, Erbar's interpretation of the difference in flower ontogeny between *Adoxa* and *Sambucus* is challenged by Roels and Smets (1994), who state that "there is no fundamental difference between the initiation of the stamen corolla tube in *A. moschatellina* and *S. ebulus*." Until *Viburnum* and *Sambucus* are better sampled for this character, paying closer attention to existing phylogenetic information, we are doubtful that the loss of the stamen-corolla tube is an apomorphy of *Sambucus*.

There are, however, unverified candidate synapomorphies for *Sambucus*. For example, the small opening in the apical part of the endocarp is a morphological character present in all species. Other possible characters may be found among chemical constituents, for example the production of sambunigrin (Stroh et al. 1962; references in Bolli 1994).

In view of the apparent lack of strong conflict between the two data sets, simultaneous analysis of all of the evidence seems warranted and should yield the best inference of phylogenetic relationships (see de Queiroz et al. 1995, for a review of the theoretical issues underlying this conclusion). Based on the combined trees (Fig. 6) we conclude that the herbaceous habit (char. 1) and the reduction in the number of perianth parts (char. 10) probably evolved in parallel in *Adoxa* and within *Sambucus*. The same is true of a number of other characters such as the fruit surface color (char. 12., but not necessarily the pulp color), the separation of style branches (char. 16), and possibly also the tendency toward separation of the anther sacs and splitting of the filaments seen in several species. In contrast, the morphological trees imply that these features are homologous in *Adoxa* and the Australian species of *Sambucus* (with the exception of *S. australasica* for char. 1). Bolli (1994) favors a third option, which is not among the minimal length solutions in any of our analyses, but only requires two or three extra steps in the combined analysis. That is, the view that the herbaceous habit is ancestral in *Sambucus* (and by extension in the Adoxoideae), and that woody species evolved secondarily. In support of this idea he cites the presence of rhizomes and adventitious roots in

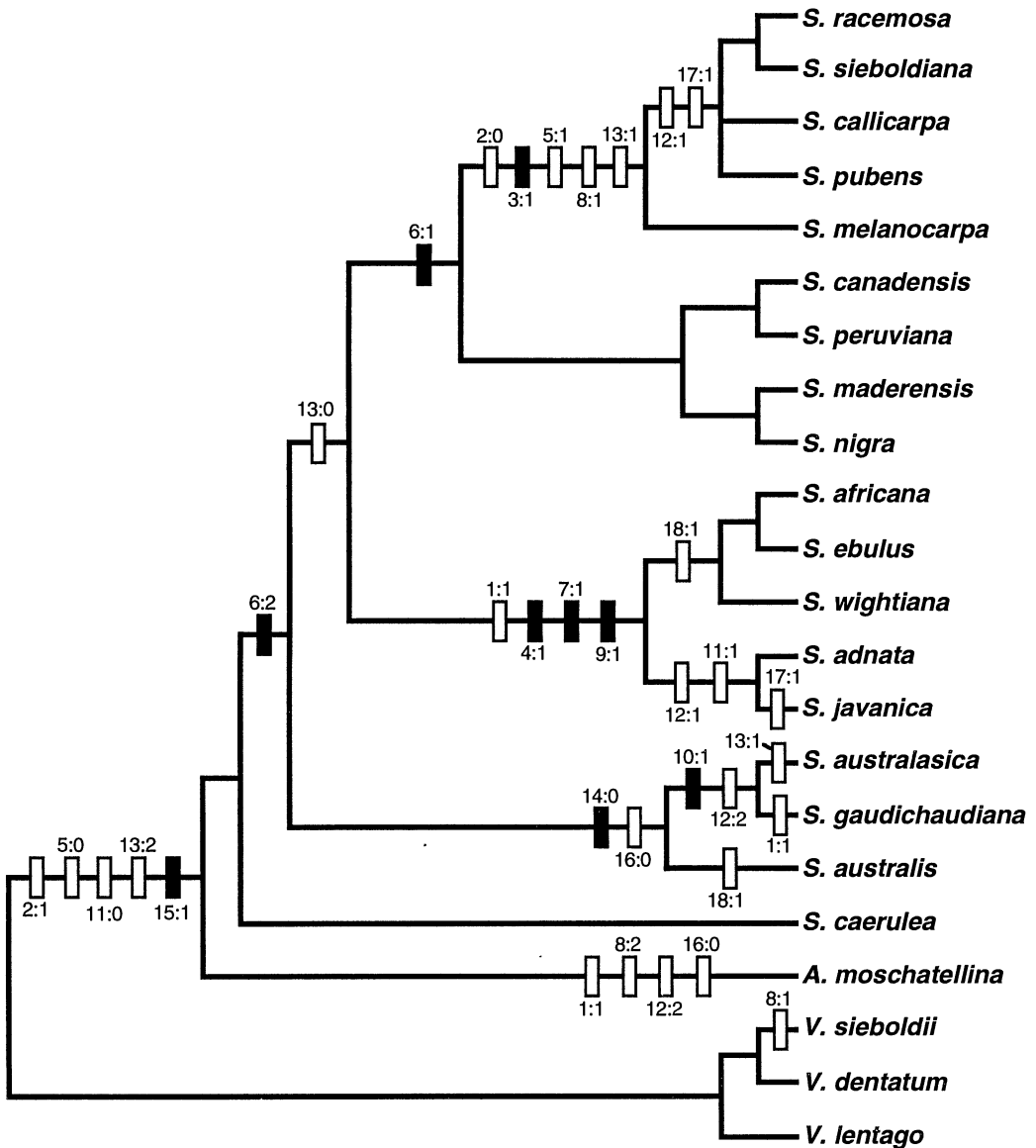


FIG. 6. One of the three most parsimonious trees from the combined analysis showing the ACCTRAN character optimization of morphological characters. Characters (number before colon) and character states (number after colon) are given in Table 3; characters without homoplasy are black. The morphological data require 35 steps on this tree, i.e., three more than on the shortest morphological trees.

some of the woody species, as well as their generally short life spans.

The morphological trees suggest a transition from fewer carpels than corolla lobes and more-or-less fused style branches to having the same number of carpels as lobes and more or less separate style branches (i.e., an increase in the number of carpels/style branches, and a separation

of parts). The combined trees are instead generally compatible with the view expressed by Bolli (1994), namely that the ancestor of *Sambucus* had five petals and three carpels, and that there were trends in two directions: towards an increase in carpel number (yielding species such as *S. australis*), and a decrease in petal number giving rise to species such as *S. gaudichaudiana* and *S. australasica*. However, in

our analysis both trends occur in the same clade, which may not be what Bolli envisioned. Interestingly, if more carpels and separate styles are interpreted as ancestral in the *Sambucus-Adoxa* clade only one step is added to the shortest trees for the combined analysis. That is, these states might be retained similarities in *Adoxa* and the Australian species of *Sambucus*, with a subsequent reduction in the number of carpels and the fusion of style branches taking place later in the evolution of *Sambucus*.

Considering all of these flower features at once and the low support of clades at the root of *Sambucus*, it may be that the South American species *S. australis* has retained the ancestral suite of characteristics; that is, flowers that are five-merous throughout, and in which the style branches are somewhat separate from one another. Its style arrangement may be intermediate between the more separate condition seen in *Adoxa* and the Australian species and the greater fusion and reduction seen in other species of *Sambucus*. This is in contrast to Bolli's (1994) contention, based in part on karyological characteristics, that *S. australis* is advanced in these respects. Detailed studies of flower development in *S. australis* and the Australian species are clearly needed to further evaluate such hypotheses.

All of our analyses imply that red fruits and paniculate inflorescences evolved within *Sambucus* (Figs. 5, 6). As regards the inflorescence, this finding contrasts with the view of Troll and Weberling who supposed that panicles were ancestral in the group (Troll and Weberling 1966; Weberling 1966b, 1981; but see Bolli 1994). Our result is especially significant in view of variation in these characters within *Viburnum* and ambiguities concerning the ancestral condition in that clade and in the Adoxaceae as a whole. These analyses, together with those in *Viburnum* (Donoghue 1983b; Donoghue 1988), support the view that red fruits and paniculate inflorescences evolved independently in *Viburnum* and in *Sambucus*.

Our combined analysis supports, although weakly, a connection between the *Botryosambucus* clade and the *S. nigra* clade. This arrangement is not seen in the consensus trees from either the morphological or molecular analyses. It is noteworthy that Bolli (1994) suggested a relationship between these groups based on similarities in flavonoid chemistry and karyology, and these characters clearly warrant additional attention.

Based on the combination of ITS and morphologi-

cal characters we conclude that *Sambucus* is monophyletic, and that *Sambucus* is the sister group of *Adoxa* (presumably along with *Tetradoxa* and *Sinadoxa*; Backlund and Donoghue 1996). This result contradicts our preliminary analysis based on morphology alone, and implies that several similarities shared by *Adoxa* and the Australian species of *Sambucus* have evolved independently or are symplesiomorphies.

It is possible that ITS sequences are misleading in this case, owing to the phenomenon of "long branch attraction" (Felsenstein 1978); that is, the placement of the root along the *Adoxa* branch may be a spurious consequence of the great divergence of this line and the great distance of the *Viburnum* sequences (Fig. 4). Sequencing of less variable genes (perhaps the chloroplast genes *matK* and/or *ndhF*) will be useful in evaluating this possibility. Likewise, the addition of *Tetradoxa* and *Sinadoxa* to the ITS data set might serve to "shorten" the branch leading to *Adoxa*. Several morphological characters of *Tetradoxa*, in particular, suggest that its addition to the analysis might have this effect (e.g. stamens split only partly to the base; open, elongate inflorescences).

Within *Sambucus*, the monophyly of several groups is well supported by ITS and morphological characters. In particular, sect. *Botryosambucus*, characterized primarily by paniculate inflorescences, is strongly supported. Within this clade the red-fruited species appear to form a clade. Section *Ebulus* is also well supported and can be diagnosed by valvate corolla lobes and generally herbaceous habit. Our results support Fukuoka's (1987) treatment of the Australian species, with the reduced number of perianth parts, as being directly related to one another. Our accessions of *Sambucus nigra* sensu Bolli (1994) form a clade with the exception of *S. caerulea*, which we conclude should be treated as a separate species.

It is clear that additional characters are needed to establish relationships among the major lines within *Sambucus*. More work on the morphology and secondary chemistry will undoubtedly prove useful, as will additional molecular evidence. Eventually it may be possible to incorporate information on fossils, although *Sambucus* species are mostly known only as endocarps. Our results will also permit studies of character evolution in the Adoxaceae as a whole. Of special interest are those characters that vary both within *Viburnum* and in the *Sambucus-Adoxa* clade, such as fruit color, extrafloral nectaries, and inflorescence architecture.

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APPENDIX 1. ITS data set. ITS1 corresponds to positions 1–227; the 5.8S gene to positions 228–392 (in bold face); and ITS2 to positions 393–623. The last 11 characters correspond to presence (1) or absence (0) of indels as implied by the alignment; the indels start at positions 90, 109, 365, 408, 409, 416, 434, 435, 503, 566, and 575. Unsequenced portions of the 5.8S gene and ITS2 are scored as question marks.

	10	20	30	40	50	60	70	80
V. dentatum	TCGAAACCTG	CTCAGCAGAA	CGACCCGCGA	ACACGTTTAA	CTA-CTAGGG	TGCATCGGTC	GGGGTGCGTC	AGCCC-CTGG
V. lentago	TCGAAACCTG	CCCAGCAGAA	CGACCCGCGA	ACACGTTCAA	CAA-CTGGGG	TGCNCCGGTC	GGGGTGCGTC	AGCCC-TCGG
V. sieboldii	TCGAAATCC-	--TAGCAGAA	CGACCCGCGA	ACATNTTCAA	TTA-CTAGGG	TGCATTCGGT	GGGGTGCGTC	AGCCC-CTGG
A. moschatellina	TCGAAACCTG	CATAGCAGAA	TGACCCGTGA	ACTTGTTTTT	TNTCTCGTGG	CTCGTCGGAC	TAGGCATGCA	AGTGCCTCGA
S. adnata	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGCGC-TCGG
S. africana	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTCTC	ATA-TCGGGG	CTCGTCGGCC	TAGGCGCGCG	AGCGC-TCGG
S. australasica	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGCGCGCA	AGCGC-TCGG
S. australis	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TARGTGCGCA	AGCGC-TCGA
S. caerulea	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGTGC-TCGG
S. callicarpa	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGTGC-TTGG
S. canadensis	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TYGGGG	CTCGTCGGYC	TAGGTGCGCA	AGTGC-TCAG
S. ebulus	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TCGGGG	CTCGTCGGCC	TRGGTGCGCA	AGCGC-TCGG
S. gaudichaudiana	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGCGCGCA	AGCGC-TCGG
S. javanica	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGKCC	TAGGTGCGCA	AGCGC-TTGG
S. maderensis	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGCGC-TCGG
S. melanocarpa	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGTGC-TTGG
S. nigra	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGCGC-TCGG
S. peruviana	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGCGC-TCAG
S. pubens	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGTGC-TTGG
S. racemosa	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTAC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGTGC-TTGG
S. sieboldiana	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTAC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGTGC-TTGG
S. wightiana	TCGAAACCTG	CACAGCAGAA	TGACCCGCGA	ACTCGTTTTC	ATA-TTGGGG	CTCGTCGGCC	TAGGTGCGCA	AGCGC-TCGG
	90	100	110	120	130	140	150	160
V. dentatum	CCGGTGCCCC	CTCGGTCCGG	GCGCTCTTCG	AGCGACCCGG	CCCAACAACG	AACCCCGGCG	CGATCTGCGC	CAAGGAAATT
V. lentago	TCGGTGCCCC	CCCGGTCCGG	ACGCTNTTCG	AGCGNCNTGG	CC-AACAACG	AACCCCGGCG	CGATCTGCGC	CAAGGAAATT
V. sieboldii	CCGATGCCCC	CTCGGTCCGG	ACGCTCTTCG	AGCGGCACGG	CCCAACAACG	AACCCCGGCG	CGATCTGCGC	CAAGGAAATT
A. moschatellina	TCGACAAGC-	TTCGGTCCAG	GCGCCATC--	GGTGTCATGA	CCAAACAACG	AACCCCGGSA	CGGTCTGTGC	CAAGGAAATT
S. adnata	TCGGYGGAC-	TTCGNTCAGG	GCGCCCTC--	GGTGACTGA	CCAAACAACG	AACCCCGGCG	CGATCTGCGC	CAAGGAAATT
S. africana	CCGCGCGAC-	TTCGGTCCAG	GCGCCCTC--	GGCGCGCTGA	CCAAACAACG	AACCCCGGCG	CGATCTGCGC	CAAGGAAATT
S. australasica	TCGCGGAGC-	TTCGGTCCAG	GCGCCCTC--	GGGTGTGCTGA	CCAAACAACG	AACCCCGGCG	CGATCTGCGC	CAAGGAAATT
S. australis	TCGACGTAC-	CTCGGTCCAG	GCGCCCTC--	GGGTGTGCTGA	CCAAACAACG	AACCCCGGCG	CGATCTGCGC	CAAGGAAATT
S. caerulea	TCGCGGAGC-	TTCGGTCCAG	GCAACCCTC--	GGGTGTGCTGA	CCAAACAACG	AACCCCGGCG	CGATCTGCGC	CAAGGAAATT
S. callicarpa	CCGCGCAAC-	TTCGGTCCAG	GCGCCCTC--	GGGTGTGCTGA	CCAAACAATG	AACCCCGGCG	CGAATCTGCGC	CAAGGAAATT

APPENDIX 1. Continued.

	90	100	110	120	130	140	150	160
S. canadensis	YCGRCGAAC-	TTCGGTACAG	GCGCCMTC--	GGTGCCTGA	CCAAACAACG	AACCCCGGCG	CGAAGTGC	CAAGGAATTT
S. ebulus	CCGGCGGAC-	TTCGGTACAG	GCGCCCTC--	GGCGTGCTGA	CCAAACAACG	AACCCCGGCG	CGATCTGC	CAAGGAATTT
S. gaudichaudiana	TCGGCGGAC-	TTCGGTACAG	GCGCCCTC--	GGTGTGCTGA	CCAAACAACG	AACCCCGGCG	CGATCCGC	CAAGGAATTT
S. javanica	CCGGCGGAC-	TTCGGTACAG	GCGCCCTC--	GGTGTACTGA	CCAAACAACG	AACCCCGGCG	CGATCTGC	CAAGGAATTT
S. maderensis	CCGGCGAAC-	TTCGGTACAG	GCGCCCTC--	GGTGTGCTGA	CCAAACAACG	AACCCCGGCG	CGAAGTGC	CAAGGAATTT
S. melanocarpa	CCGCCGAAC-	TTCGGTACAG	GCGCCCTC--	GGTGTGCTGA	CCAAACAATG	AACCCCGGCG	CGAAGTGC	CAAGGAATTT
S. nigra	CCGGCGAAC-	TTCGGTACAG	GCGCCCTC--	GGTGTGCTGA	CCAAACAACG	AACCCCGGCG	CGAAGTGC	CAAGGAATTT
S. peruviana	TCGACGAAC-	TTCGGTACAG	GCGCCCTC--	GGTGCCTGA	CCAAACAACG	AACCCCGGCG	CGAAGTGC	CAAGGAATTT
S. pubens	CCGGCGAAC-	TTCGGTACAG	GCGCCCTC--	GGTGTGCTGA	CCAAAYAAATG	AACCCCGGCG	CGAAGTGC	CAAGGAATTT
S. racemosa	CCGGCGAAC-	TTCGGTACAG	GACCCCTC--	GGTGTGCTGA	CCAAACAATG	AACCCCGGCG	CGAAGTGC	CAAGGAATTT
S. sieboldiana	CCGGCGAACC	TTCGGTACAG	GCGCCCTC--	GGTGTGCTGA	CCAAACAATG	AACCCCGGCG	CGAAGTGC	CAAGGAATTT
S. wightiana	CCGRCGGAC-	TTCGGTACAG	GACCCCTT--	GGTGTACTGA	CCAAACAACG	AACCCCGGCG	CGATCTGC	CAAGGAATTT
	170	180	190	200	210	220	230	240
V. dentatum	TAAGTGAAGA	GCATGCCCC	TGCTGCCCCG	TTGCGGGTGC	GCGCGGTTGG	CTTGCGCTTT	CGAATCAC??	??????????
V. lentago	TAAGTGAAGA	GCATGCCCC	CGTCGCCCCG	TTGCGGGTGT	GCGCGGTTGG	CTGTGCTTT	CGAATCAC??	??????????
V. sieboldii	TAAGTGAAGA	GCATGCCCC	CATTGCCCCG	TTGCGGGTGT	GCACGGTTGG	CTTG?GCTTT	TGAATCAC??	??????????
A. moschatellina	TATATAAAGA	GCGTGTCTAT	TGTTGCCCCG	TTGCGGGTGT	GCACGGTAGG	CATGCGCCTT	TGAACACATA	AACGACTCTC
S. adnata	TTACTAAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	RCACGGTAGA	CATGCGCCTT	TGAACAC-A	RNCGACTCTC
S. africana	TTACTAAAGA	GCTTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CCCGCGCCTT	TGAACAC-A	AACGACTCTC
S. australasica	TTACCGAAGA	GCGTGTCTTC	CGTTGBCCCG	TTGCGGGTGT	GCACGGTAGG	CCCGCGCCTT	TGAACAC-A	AACGACTCTC
S. australis	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CATGCGCCTT	TGAACAC-A	AACGACTCTC
S. caerulea	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CHTGCGCCTT	TGAACAC-A	AACGACTCTC
S. callicarpa	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
S. canadensis	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
S. ebulus	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
S. gaudichaudiana	TTACTGAAGA	GCGTGTCTGC	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CCCGCGCCTT	TGAACAC-A	AACGACTCTC
S. javanica	TTACTAAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
S. maderensis	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
S. melanocarpa	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
S. nigra	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTTGCGCCTY	TGAACAC-A	AACGACTCTC
S. peruviana	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	TCACGGTAGG	CTTGCGCCTT	TGAACAC-A	AACGACTCTC
S. pubens	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
S. racemosa	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
S. sieboldiana	TTACTGAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC??	??????????
S. wightiana	TTACTAAAGA	GCGTGTCTAT	CGTGTGCCCG	TTGCGGGTGT	GCACGGTAGG	CTGCGCCTT	TGAACAC-A	AACGACTCTC
	250	260	270	280	290	300	310	320
V. dentatum	??????????	??????????	??????????	??????????	??????????	??????????	??????????	????CCGTGA
V. lentago	??????????	??????????	??????????	??????????	??????????	??????????	????TTGCAG	AATCCCGTGA
V. sieboldii	??????????	??????????	??????????	??????????	??????????	??????????	?????????AG	AATCCCGTGA
A. moschatellina	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. adnata	G?????????	??????????	??????????	??????????	??????????	ATACTYGGTG	TGAATTGCAG	AATCCCGTGA
S. africana	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. australasica	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. caerulea	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. callicarpa	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GMGAAATGCG	ATACTTGGTG	TGAATAGMAG	AATCCCGTGA
S. canadensis	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. ebulus	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. gaudichaudiana	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. javanica	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. maderensis	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. melanocarpa	GGCAANGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. nigra	GGCAACGGAT	ATCTCGGTTT	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. peruviana	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. pubens	GGCAACGGAT	ATCTCGGCTC	TCGGATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA

APPENDIX 1. Continued.

	250	260	270	280	290	300	310	320
S. racemosa	GGCAACGGAT	ATCTCGGCTC	TCGCATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTTGGTG	TGAATTGCAG	AATCCCGTGA
S. sieboldiana	??????????	??????????	??????????	??????????	??????????	??????????	????TTCGAG	AATCCCGTGA
S. wightiana	GGCAACGGAT	ATCTCGGYTC	TCGNATCGAT	GAAGAACGTA	GCGAAATGCG	ATACTNGGTG	TGA-TAGCAG	AATCCCGTGA
	330	340	350	360	370	380	390	400
V. dentatum	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CAAAGCCATT	AGNC--GAGG	NACGTCTGCC	TGGGCGTCAC	GCATT---GT
V. lentago	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	CACGTCTGCC	TGGGCGTCAC	GCATTGC-GT
V. sieboldii	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CAAGCCATT	AGGC--GAGG	-ACGTCTGCC	TGGGCGTCAC	GCATTGC-GT
A. moschatellina	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCAAGGG	CACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. adnata	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. africana	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. australasica	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	CACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. australis	ACCATCGAGT	TTTKGANCGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. caerulea	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. callicarpa	ACCATCAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCTGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. canadensis	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. ebulus	ACCATCGAGT	TTTKGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	CACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. gaudichaudiana	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. javanica	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	CACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. maderensis	ACCATCGAGT	TTTKGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. melanocarpa	ACCATCGAGT	TTTKGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCTGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGTG
S. nigra	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. peruviana	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	CACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. pubens	ACCATCGAGT	TTTKGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCTGAGGG	MACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. racemosa	ACCATCGAGT	TTTKGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGYTGAGGG	AACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. sieboldiana	ACCATCGAGT	TTTTGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGTCAAGG-	--CGTCTGCC	TGGGCGTCAC	ACATTGCCGT
S. wightiana	ACCATCGAGT	TTTKGAACGC	AAGTTGCGCC	CGAAGCCATT	AGGCCGAGGG	AACGTCTGCC	TGGGCGTCAC	ACATTGCCGT
	410	420	430	440	450	460	470	480
V. dentatum	CGCCCC-AC	ACCCT---GT	GTCCCCAAAA	GAGGCATATT	GGGCGAGGGG	GCGGATATTG	GCCTCCCGTG	CTTTCGGGTG
V. lentago	CGCCCC-AC	ACCCT---GT	GTCCCCAAAA	GGG---CACC	GGGCGCGGGG	-CGGATATTG	GCCTCCCGTG	CTCTAGGGCG
V. sieboldii	CGCCCC-AC	ACCTT---GT	GTCCCTAAAG	GGG---CATT	GGGCGAGGGG	-CGGATATTG	GCCTCCCGTG	CTTTTCGGCG
A. moschatellina	CGCCCC-AT	TCCAA---CT	CCCTTTGYTT	GGGA-GT-JT	GTTGTAGGGG	-CGGAAATTG	GCCTCCCGTG	CCTCTGGTG
S. adnata	CGCCCC--T	TCCAA---GT	TCCCATTCCT	GGGK-ACGTT	GGWAGTCCGN	-CGGATATTG	GTCTCCCGTG	CTTTCGAGTG
S. africana	CGCCCC--T	TCCAA---TT	TCCCATTCCT	TGGGAACGCT	GGCAGTCGGG	-CGGATATTG	GCCTCCCGTG	CTCCCCAGCG
S. australasica	CGCCCC--T	TCCAA---TT	TCCCATTCCT	GGTG-ACGTT	GGTGGTCGGG	-CGGATATTG	GCCTCCCGTG	CTCTCGAGCG
S. australis	CGCCCC-NT	TCCAA---TT	TCCCATTCCT	GGGG-ACGTT	GGTAGTCGGG	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. caerulea	TGCCCC--T	TCCAA---WT	TCCCATTCCT	GGGG-ACATT	GGTAGTCGGG	-CGAATATTG	GTCTCCCGTG	CTCTCGAGCG
S. callicarpa	CGCCCC--T	TCCAA---TT	TCCCATTCCT	GGGG-ACGTT	GGTAGTCGGG	-CGGATAWTG	GTCTCCCGTG	CTCTCGAGCG
S. canadensis	CGCCCCCTCT	TCCAAATTCT	TCCATTCCT	GGGG-ACGTT	GGTGGTCGGA	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. ebulus	CGCCCC--T	TCCAA---TT	CCCCATTCCT	TGGGAACGCT	GGTAGTCGGG	-CGGATACTG	GCCTCCCGTG	CTCCCCAGCG
S. gaudichaudiana	CGCCCC--T	TCCAA---TT	TCCCATTCCT	GGTG-ACGTT	GGTNGTCGGG	-CGGATATTG	GCCTCCCGTG	CTCTCGAGCG
S. javanica	CGCCCC--T	TCCAA---TT	TCCCATTCCT	GGGG-ACGTT	AGTAGTCGGG	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. maderensis	CGCCCC-CK	TCCAAATTCT	TCCCATTCCT	GGGG-RCGTT	GGTAGTCGGG	-NGGRTWTTK	GTCTCCCGTG	CTCTCGAGCG
S. melanocarpa	CGCCCC--T	YCCAA---TT	TCCCATTCCT	GGGG-ACGTT	GGTAGTCGGG	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. nigra	CGCCCC-CY	TCCAAATTCT	TCCCATTCCT	GGGG-ACGTT	GGTAGYCGGG	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. peruviana	CGCCCCCTCT	ACTAATTTTT	TCCCATTCCT	GGGG-ACGTT	GGTAGTCGGG	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. pubens	CGCCCC--T	TCCAA---TT	TCCCATTCCT	GGGG-ACGTT	GGTAGTCGGG	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. racemosa	CGCCCC--T	TCCAA---TT	TCCCATTCCT	GGGG-AYGTT	GGTAGYCGGS	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. sieboldiana	CGCCCC--T	TCCAA---TT	TCCCATTCCT	GGGG-ACGTT	GGTAGTCGGG	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
S. wightiana	CGCCCC--T	TCCAA---TT	TCCCATTCCT	TGGGGACGTT	GGTAGTCGGG	-CGGATATTG	GTCTCCCGTG	CTCTCGAGCG
	490	500	510	520	530	540	550	560
V. dentatum	CGGTTGGCCC	AAAACGAGT	CCCCGGCAAC	G-ACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCGG
V. lentago	CGGTTGGCCC	AAAAGCGAGT	CCCCGGCAAC	GGACGTCACG	ACGAGCGGTG	GTTNAAAAGC	CTTCTTATCC	TGTCGTGCGG
V. sieboldii	CGGTTGGCCT	AAAAGCGAGT	CCTCGGCAAT	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCGG

APPENDIX 1. Continued.

	490	500	510	520	530	540	550	560
A. moschatellina	CGGTTGGCCC	AAATGAGAGT	ACCCGACAAC	GTACGTCACA	ACAAGTGGTG	GTTGAAAAGC	CGTAT-ATCA	TGTTGTGCAC
S. adnata	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTAATCC	TGTCGTGCAC
S. africana	CGGTTGGCCC	AAAAGCGAGT	CC-CGACAGC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTAATCC	TGTCGTGCAC
S. australasica	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. australis	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGATGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. caerulea	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. callicarpa	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCATG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. canadensis	CGGTTGGCCC	AAAAGAGAGT	CCTCGACAGC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. ebulus	CGGTTGGCCC	AAAAGCGAGT	CC-CGACAAC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTAATCC	TGTCGTGCAC
S. gaudichaudiana	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. javanica	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTAATCC	TGTCGTGCAC
S. maderensis	GGGTTGGCCC	AAAAGCGAGT	CCTCGSCARV	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. melanocarpa	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCATG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. nigra	GGGTTGGCCC	AAAAGCGAGT	CCTCGCAAC	GGACGTCACG	AMAAGTGGKG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. peruviana	CGGTTGGCCC	AAAAGCGAGT	CCTCGACAAC	GGACGTCAG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. pubens	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCATG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. racemosa	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAS	GGACGTCATG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. sieboldiana	CGGTTGGCCC	AAAAGCGAGT	CCCCGACAAC	GGACGTCATG	ACAAGTGGTG	GTTGAAAAGC	CTTCTTATCC	TGTCGTGCAC
S. wightiana	CGGTTGGCCC	AAAAGCGAGT	CC-CGACAAC	GGACGTCACG	ACAAGTGGTG	GTTGAAAAGC	CTTCTAATCC	TGTCGTGCAC
	570	580	590	600	610	620		
V. dentatum	TCCTC-CGTT	GCCATCGGGC	ACTCTCTTGA	CCCTGATGCG	CCGTTCCCTGA	CGGCGCTTCCG	A??	10110100010
V. lentago	TCCTC-CGTT	GCCACCGGGC	ACTCCCTTGA	CCCTGATGCG	TCGTTCCCTGA	CGGCGCTTCCG	A??	0001011?010
V. sieboldii	TCCTC-CGTT	GTCATCGGGC	ACTCCCTTGA	CCCTGATGCG	CCGTTCCCTGA	CGGCACTTCCG	A??	1011011?010
A. moschatellina	CAGTC-CGTT	GTCA-CGGGC	ACTGACTTGA	CCCTAAAGCG	TCGTCTTGA	TGTCGCTCCG	ACT	11010101011
S. adnata	CAATT-CGTT	GTCA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCCTNTGA	CGTCGCTCCG	ATT	11011101011
S. africana	CAATT-CGTT	GTCG-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCG	ATC	11011100111
S. australasica	CAATT-CATT	GTCC-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCG	ATC	11011101011
IS. australis	CAATT-TGTT	GTTA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCTGA	CGTCGCTCCG	ATC	1101?0101011
S. caerulea	TAATT-CGTT	GTCA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCCTNCGA	CGTCGCTCCG	ATC	11011101011
S. callicarpa	CAATT-CGTT	GTCA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCG	ATC	11011101011
S. canadensis	CAATT-CGTT	GTCA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCTGA	CGTCGCTTCCG	ATC	11000001011
S. ebulus	CAATT-CGTC	GTCG-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCG	ATC	11011100111
S. gaudichaudiana	CAATT-CATT	GTCC-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	C-TCGCTCCG	ATC	11011101011
S. javanica	CAATT-CGTT	GTCA-GGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCG	ATC	11011101011
S. maderensis	CAATTACGTT	GTCG-CGGGC	ATCGAGTTGA	CCYTACGCG	TCGTCTCTGA	CGTCGCTTCCG	ATC	11010001001
S. melanocarpa	CAATT-CGTT	GTCA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCG	ATC	11011101011
S. nigra	CAATT-CGTT	GTCG-SGGGM	ATCGAGTTGA	CCCTGACGCG	TCGTCTCTGA	CGTCGCTTCCG	ATC	11001001011
S. peruviana	CAATT-CGTT	GTCA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCTGA	CGTCGCTTCCG	ATC	11000001011
S. pubens	CAATT-CGTT	GTCA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCG	ATY	11011101011
S. racemosa	CAATT-CGTT	GTCA-CGGNC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCG	ATC	11011101011
S. sieboldiana	CAATT-CGTT	GTCA-CGGGC	A--GAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCGCTCCA	A??	01011101011
S. wightiana	CAATTACGTT	GTCA-CGGGC	ATCGAGTTGA	CCCTGACGCG	TCGTCTCCGA	CGTCCGCTCG	ATC	11011100101