

## Multiple Geographic Origins of Antillean *Styrax*

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**ABSTRACT.** The phylogenetic relationships within *Styrax* series *Valvatae* were estimated with DNA sequence data from the internal transcribed spacer region of nuclear ribosomal DNA to test hypotheses bearing on the historical biogeography of the Antilles. The results provide evidence for three dispersal events within *Styrax* to the Antilles, one from southern North America, the other two from South America. The data do not support a strict Greater Antillean vicariance scenario for *Styrax*. Vicariance between the Greater Antilles and southern North America without immediate prior dispersal would require a more basal position of *Styrax ochraceus* than that recovered, although low branch support values in the relevant portion of the tree do not preclude this possibility. Dispersal of *Styrax* from South America to the Greater Antilles could have proceeded across oceanic barriers, or more likely through GAARlandia. *Styrax obtusifolius* in Cuba and Hispaniola and the strictly South American Foveolaria clade have evolved small flowers and the gynodioecious condition independently. The predominance of microscopic pollinators in the Cuban fauna may have impelled the evolution of small flowers in *Styrax obtusifolius*. The data suggest that the Antilles have played little if any role in the intercontinental dispersal of *Styrax*.

The debate concerning the geographical origin and spread of the biota of the Antilles has a long history that continues today (Williams 1989; Crother and Guyer 1996a; Woods and Sergile 2001). A strict vicariance model for the evolution of the Antillean biota postulates a proto-Antillean Cretaceous landmass situated between North America and South America that subsequently fragmented and dispersed eastward in the early Cenozoic (Rosen 1975, 1985; Savage 1982; Guyer and Savage 1986; Crother and Guyer 1996a, b). This contrasts with over-water long-distance dispersal scenarios to the Antilles from mainland sources (Darlington 1938; Simpson 1956; Briggs 1984; Hedges 1996a, 1996b, 1996c, 1996d; Hedges et al. 1992, 1994). A model that combines elements of both dispersal and vicariance postulates a landspan between South America and much of the Greater Antilles through the Aves Ridge (GAARlandia; GAAR = Greater Antilles-Aves Ridge) during the latest Eocene and Early Oligocene (33–35 million years ago [Mya]; Iturralde-Vinent and MacPhee 1999).

Recent paleogeographic studies of the Caribbean have suggested that the Greater Antilles, as subaerial entities, are no older than Middle Eocene (Iturralde-Vinent and MacPhee 1999). If so, strict vicariance of the land biota did not take place between the Antilles and continental regions. Supplemental evidence against vicariance comes from the near certainty of the catastrophic impact of a large extraterrestrial object at the Cretaceous-Tertiary boundary (Alvarez et al. 1990; Hildebrand and Boynton 1990; Izett et al. 1991). The reduction or outright elimination of the land biota of the Antilles resulting from this event would mean that pre-Tertiary geohistorical events relating to tectonic history or paleogeography per se would have little direct bearing on the historical biogeography of the current Antillean biota. Nonetheless, persistent uncertain-

ties about the accuracy of paleogeographic reconstructions of the Caribbean Basin, and the paucity of fossils from the region (Perfit and Williams 1989; Graham et al. 2000; Graham 2003) impel the search for evidence bearing on Antillean biogeography that is independent from geological data.

The vicariance/dispersal debate has implications beyond the immediate evolution of the Antilles themselves. The history of the biota of North America and South America could have been dramatically affected by intercontinental migration across the Antillean region, because these two continents have been separated from each other by ocean throughout most of the Tertiary. Any connections between them, however brief, could potentially alter the biotic composition of both continents rapidly, as is known to have occurred after the formation of the Isthmus of Panama 3.1 Mya (Stehli and Webb 1985). The Antilles could have served as a filter bridge for the intercontinental exchange of some organisms during either the Cretaceous or early Tertiary via a proto-Antillean volcanic arc between North America and South America (Rage 1978, 1986; Pindell et al. 1988; Marshall and Sempere 1993) or after their postulated Eocene emergence or re-emergence (Iturralde-Vinent and MacPhee 1999). The latter scenario is especially likely to apply during the time of GAARlandia, when the western portion of the Antilles was separated from Mesoamerica only by two narrow straits (Iturralde-Vinent and MacPhee 1999).

A reasonable source of data complementary to geological evidence for testing hypotheses on Antillean historical biogeography comes from phylogenetic estimation of organisms with appropriate distributions and life history parameters (e.g., Liebherr 1988; Woods 1989; Hedges 1996b; Negrón-Ortiz and Hickey 1996; McDowell and Bremer 1998; Fontenla 2000; Judd 2001; Lavin et al. 2001; Schneider et al. 2001; Woods and Ser-

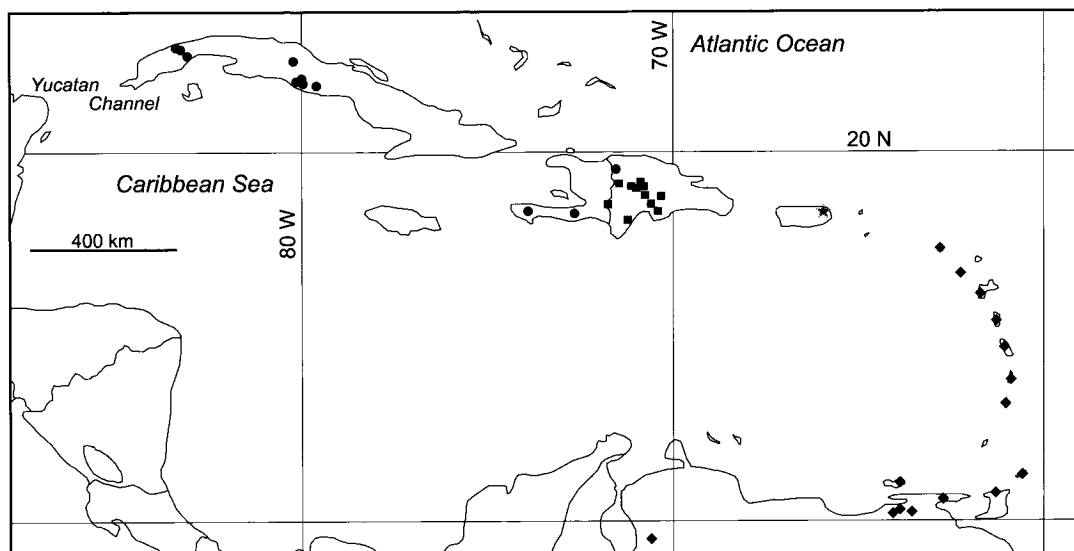


FIG. 1. Distribution of the four species of Antillean *Styrax*. Circles = *S. obtusifolius*; squares = *S. ochraceus*; star = *S. portoricensis*; diamonds = *S. glaber*. *Styrax glaber* also extends farther south in northern South America.

gile 2001; Negrón-Ortiz and Watson 2002). In this capacity, the four Antillean species of *Styrax* L. (Styracaceae) have excellent potential (Fig. 1). These species belong to *Styrax* series *Valvatae* Perkins, a monophyletic group of about 77 species distributed throughout the Neotropics (southern Mexico through northern Argentina; Fritsch 1999, 2001). This series is easily delimited from the rest of *Styrax* through the combination of evergreen leaves and fleshy mesocarp (Fritsch 1999). *Styrax obtusifolius* Griseb. is a Cuban and Hispaniolan endemic with a putatively (i.e., based on morphology) gynodioecious breeding system and relatively small flowers. It occurs in the uplands of Cuba and central-western Hispaniola. *Styrax ochraceus* Urb., the only yellow-flowered species of *Styrax*, is endemic to central and south-central Hispaniola. *Styrax portoricensis* Krug & Urb., one of the rarest endemic trees of Puerto Rico, occurs in the Sierra de Luquillo and vicinity. *Styrax glaber* Sw. ranges from the Lesser Antilles through northern South America. All species inhabit humid upland forests and together range in elevation from 250 to 2100 m.

Most species of section *Valvatae* possess fleshy drupes that turn dark purple upon maturation, in accordance with a syndrome of dispersal by birds. In *S. obtusifolius* and *S. ochraceus*, however, the mesocarp is thin and mealy, and in *S. ochraceus* the exocarp is yellowish green at maturity, so it is not clear whether bird dispersal can be assumed for either of these species. The fossil seed record of *Styrax* extends back to the Upper Eocene (Europe; Chandler 1925–1926; Kirchheimer 1957; Mai 1995), but, as is true for most plant groups (Graham et al. 2000), fossils of *Styrax* are not known from the Antilles.

From a study of pollen, seed, and leaf morphology of the Antillean species of *Styrax*, Mai (1988) concluded that *S. obtusifolius* and *S. ochraceus* were closest relatives. No cladistic analysis was conducted in that study to support this conclusion. A detailed phylogenetic analysis of *Styrax* based on 34 morphological characters (Fritsch 1999) suggested that none of the four Antillean species of *Styrax* can be considered as the closest relative of any of the others. In that analysis, *S. obtusifolius* was placed as the first-diverging member of a "gynodioecious clade" comprising all putatively gynodioecious species of the genus. Except for *S. obtusifolius*, the ten species comprising this clade are endemic to either the Andes or southeastern Brazil (Fritsch 1999, in review). As for the other Antillean species, *S. ochraceus* was placed as sister to a clade of seven species from southern North America, near the base of series *Valvatae*; *S. glaber* grouped within a large clade of mainly South American species; and *S. portoricensis* grouped in the same clade as *S. glaber* but was more highly nested.

Biogeographical analyses based on the morphological phylogenetic estimate of *Styrax* suggested that the current distribution of Antillean *Styrax* is the consequence of several dispersal events to the Antilles from the mainland, with or without subsequent vicariance, and not a result of strict vicariance itself (Fritsch 1999). *Styrax obtusifolius*, *S. portoricensis*, and *S. glaber* were inferred to have attained their distributions through dispersal from South America, whereas *S. ochraceus* was inferred to have attained its distribution through dispersal from southern North America. The evidence against land connections among the islands of the Lesser Antilles makes dispersal a reasonable postulate

TABLE 1. Collection and voucher information, and GenBank accession numbers of ITS sequences for samples of *Styrax* used in this study. Samples labeled with an asterisk are from Fritsch (2001). Species names in parentheses are the morphological OTU under which the sampled taxon is listed in Fritsch (1999). Herbaria for vouchers or sources of material are indicated in parentheses, with acronyms according to Holmgren et al. (1990). Boldface acronyms indicate that the leaf material was from the herbarium specimen indicated.

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***Styrax* series *Valvatae* Perkins.** *S. aureus* Mart. (*S. aureus*) - *Almeda et al.* 8382, Serra da Moeda, Minas Gerais, Brazil (CAS), AY143577; *S. camporum* Pohl (*S. ambiguus*)\* - *Schinini* 21491, Amambay, Paraguay (F), AF327504; *S. ferrugineus* Nees & Mart. (*S. ambiguus*)\* - *Almeda* 7868, Serra dos Pirineus, Goiás, Brazil (CAS), AF327503; *S. foxeolaria* Perkins (*S. foxeolaria*) - *Klitgaard* 390, Dept. Loja, Ecuador (CAS), AY143579; *S. gentryi* P. W. Fritsch (*S. ramirezii*)\* - *León de la Luz* 8414, Sierra La Laguna, Baja California Sur, Mexico (F), AF327502; *S. glaber* Sw. (Accession 1; *S. ambiguus*) - *Steyermark et al.* 131020, Isla de Margarita, Nueva Esparta, Venezuela (MO), AY143582; *S. glaber* Sw. (Accession 2; *S. ambiguus*) - *Rollet* 1668, Martinique, Lesser Antilles (A), AY143583; *S. lanceolatus* P. W. Fritsch (*S. lanceolatus*)\* - *Fairey* T26M-79p-101490, Rancho El Cielo, Veracruz, Mexico (RSA), AF327501; *S. latifolius* Pohl (*S. acuminatus*) - *Almeda et al.* 8379, Serra de São Jose, Minas Gerais, Brazil (CAS), AY143585; *S. leprosus* Hook. & Arn. (*S. acuminatus*) - *Pedersen* 16242, Dept. Rivera, Uruguay (F), AY143586; *S. maninul* B. Walln. (*S. aureus*) - *Almeda et al.* 8454, Near Diamantina, Minas Gerais, Brazil (CAS), AY143576; *S. martii* Seub. (*S. martii*) - *Almeda et al.* 8417, Serra da Piedade, Minas Gerais, Brazil (CAS), AY143584; *S. nunezii* (*S. cordatus*)\* - *Núñez* 23320, Dept. Cuzco, Peru (CAS), AF327509; *S. obtusifolius* Griseb. (*S. obtusifolius*) - *Fritsch* 1706, Cumanayagua, Prov. Cienfuegos, Cuba (CAS), AY143589; *S. ochraceus* Urb. & Arn. (*S. ochraceus*) - *Fritsch* 1778, Loma Golondrina, Prov. La Vega, Dominican Republic (CAS), AY143580; *S. pavonii* (Ruiz & Pav.) A. DC. (*S. cordatus*)\* - *Gentry et al.* 44158, Dept. Cuzco, Peru (F), AF327506; *S. pedicellatus* (Perkins) B. Walln. (*S. aureus*) - *Almeda et al.* 8502, Near Diamantina, Minas Gerais, Brazil (CAS), AY143578; *S. pentlandianus* J. Rémy (*S. pentlandianus*)\* - *Núñez et al.* 23488, Dept. Cuzco, Peru (CAS), AF327507; *S. pohlii* A. DC. (*S. ambiguus*) - *Almeda et al.* 8444, Near Diamantina, Minas Gerais, Brazil, AY143581; *S. portoricensis* Krug & Urb. (*S. acuminatus*)\* - *Axelrod & Ward* 10006, Caribbean National Forest, Luquillo, Puerto Rico (CAS), AF327505; *S. radians* P. W. Fritsch (Accession 1; *S. radians*)\* - *Calzada* 17840, Camichín de Jauja, Nayarit, Mexico (RSA), AF327498; *S. radians* P. W. Fritsch (Accession 2; *S. radians*)\* - *Fritsch* 1473, Near Puerto Vallarta, Mexico (RSA), AF327497; *S. ramirezii* Greenm. (*S. ramirezii*)\* - *Miller & Myers* 2608, State of México, Mexico (MO), AF327499; *S. rotundatus* Seub. (*S. martii*)\* - *Almeda* 8277, Bahia, Brazil (CAS), AF327508; *S. sieberi* Perkins (Accession 1; *S. acuminatus*) - *Nee* 50462, Dept. Santa Cruz, Bolivia (CAS), AY143587; *S. sieberi* Perkins (Accession 2; *S. acuminatus*) - *Nee & Saldias* 36881, Dept. Santa Cruz, Bolivia (MO), AY143588; *S. tomentosus* Humb. & Bonpl. (*S. tomentosus*) - *Jiggins & Losano* 124, Dept. Loja, Ecuador (LOJA), AY143590; *S. vilcabambae* (D. R. Simpson) B. Walln. (*S. aureus*)\* - *Núñez et al.* 23501, Dept. Cuzco, Peru (CAS), AF327496; *S. warszewiczii* Perkins (*S. ramirezii*)\* - *Haber* 7526, Prov. Puntarenas, Costa Rica (MO), AF327500

***Styrax* series *Benzoin* P. W. Fritsch.** *S. benzoin* Dryand. (*S. benzoin*)\* - *Stern* 363-365, Malaysia (unvouchered), AF327494; *S. chinensis* Hu & S. Y. Liang (*S. benzoin*)\* - *Fritsch* 1365, Cultivated, Los Angeles County Arboretum, California, USA (RSA), AF327492; *S. suberifolius* Hook. & Arn. (*S. benzoin*)\* - *Fritsch* 1484, Cultivated, Univ. California Botanical Garden, USA (UCB 81.0024) (CAS), AF327493

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for *S. glaber* (Fritsch 1999). Ancillary evidence for dispersal versus vicariance was considered to be lacking for the other species except *S. portoricensis*, thought to be a close relative of a widespread, presumably easily dispersed species (*S. glabratus* Schott).

The phylogenetic analysis of *Styrax* series *Valvatae* based on morphological data is here compared and combined with DNA sequence data from the intergenic transcribed spacer (ITS) region of nuclear ribosomal DNA to provide a more robust estimate of the phylogeny of the group. The historical biogeography of series *Valvatae* is then inferred by using analytical biogeographical methods to address the following questions: (1) does the molecular phylogeny support the dispersal scenarios inferred from the morphological analysis to explain the geographic distribution of Antillean *Styrax*? (2) was the Antilles a major corridor for the intercontinental migration between North America and South America of *Styrax* in the Tertiary? (3) could GAARlandia have been involved in any biogeographical events inferred from the analyses? (4) is the single origin of gynodioecy among Antillean and South American species that was inferred from morphology supported by the molecular data?

## MATERIALS AND METHODS

Thirty-two samples were used in the analysis (Table 1), representing 26 species of *Styrax* series *Valvatae* and three outgroup species of *Styrax* series *Benzoin* P. W. Fritsch. The sample comprises 34% of the total number of species in series *Valvatae*, and the combined distribution of the species sampled covers the geographic range of the series except for the Guayana Highland, which harbors several endemic species. The sample includes all four species known from the Antilles. Outgroup choice is based on the results of Fritsch (1999, 2001), in which series *Benzoin* is sister to series *Valvatae* in the morphological and combined ITS + morphological analyses (although the relative placement of these groups is unresolved with ITS alone).

DNA extraction was carried out with DNeasy plant extraction kits (Qiagen Inc.). All tissue was fresh or desiccant-dried except that from herbarium specimens (see Table 1). Thirteen ITS region sequences (including the 5.8S subunit) were newly generated for this study by following previously described direct sequencing methods (Fritsch et al. 2001). Boundaries of the ITS region and optimal sequence alignment were determined as previously described (Fritsch et al. 2001). Gaps introduced into the alignment were treated as missing data, but to exploit the utility of gapped positions, all parsimony-informative gaps were scored with the program Gap Recoder written by R. Ree (available at the web page [http://maen.huh.harvard.edu:8080/services/gap\\_recoder](http://maen.huh.harvard.edu:8080/services/gap_recoder)) that implements the simple indel coding method of Simmons and Ochoterena (2000; see also Fritsch et al. 2001).

Phylogenetic analyses employed maximum parsimony via the heuristic search option in PAUP\* 4.0b10 (Swofford 1998). The

search strategy for finding shortest trees followed that of Fritsch et al. (2001), except that steepest descent was deselected. Relative support for individual clades was estimated with the bootstrap method (Felsenstein 1985) under the conditions described in Fritsch et al. (2001), except that branches were collapsed if their maximum length was zero.

To provide a phylogenetic estimate based on all available data, the ITS data set was combined with a previously described 34-character morphological data set that included all *Styrax* species (Fritsch 1999; see Table 1), as modified to include only the species sampled for ITS data and parsimony-informative characters. Data set congruence was determined with incongruence length difference (ILD) tests (Farris et al. 1994, 1995; implemented in PAUP\* as the partition-homogeneity test) by using 200 randomizations and ten random-taxon-addition heuristic searches per randomization, saving no more than 2000 trees per search, and excluding uninformative characters. Because the placement of *Styrax obtusifolius* was found to differ dramatically between the morphological and ITS topologies, an ILD test was run with this species excluded; results were then compared to those from the test with *S. obtusifolius* included.

The historical biogeography of Antillean *Styrax* was inferred with standard Fitch parsimony optimization (FPO; Maddison et al. 1992) and dispersal-vicariance analysis (DIVA; Ronquist 1996, 1997) as previously described (Fritsch 1999, 2001; Fritsch et al. 2001). FPO incorporates dispersals only, whereas DIVA can incorporate both vicariance and dispersal. The DIVA method imparts no cost to vicariance, whereas dispersal is optimized, with each dispersal costing a single step. The input tree was derived from the strict consensus of the ITS analysis (Fig. 2), with the sole polytomy arbitrarily resolved (the use of the two alternative resolutions resulted in essentially the same general biogeographic patterns as the one employed). This analysis maximizes the combined number of taxa and characters. Because the topologies from the ITS and the combined data sets are identical, the results from either analysis are appropriate for use in the biogeographical analyses. If the combined analysis is preferred on the basis of total evidence (Kluge 1989, 1998; Barrett et al. 1991), then *S. obtusifolius* must be placed as sister to *S. portoricensis* a posteriori (on the basis of its position in the ITS analysis) because of the problem of data incongruence when *S. obtusifolius* is included.

The four areas circumscribed for both FPO and DIVA were eastern Asia, southern North America (comprising southern Mexico through Central America), South America, and the Antilles. Southern North America harbors 18 species of series *Valvatae* (Fritsch 1997), the Antilles four, and South America the remainder (~55). In addition to the three species of series *Benzoin* sampled for ITS, two outgroups (*Huodendron* Rehder and *Styrax* section *Styrax*) were added to the topology. The placement of these clades was based on previous work that showed unequivocally that the most recent common ancestor (MRCA) of section *Valvatae* arose in eastern Asia (Fritsch 2001; Fritsch et al. 2001). Two DIVA optimizations were conducted, one with an unrestricted maximum number of areas assigned to each node, the other with this number restricted to two; the latter follows the reasoning that no species of series *Valvatae* occurs presently in more than two areas (see Donoghue et al. 2001).

## RESULTS

Multiple sequence alignment resulted in a data matrix of 688 characters. After the exclusion of positions 131–144 in ITS1 because of alignment ambiguity, the data matrix contained 182 variable and 121 (18.0%) parsimony-informative characters. The inclusion of 43 binary characters for the presence or absence of gaps (21 of which were parsimony-informative) resulted in

a final data matrix (available through TreeBASE at the web site <http://www.herbaria.harvard.edu/treebase>) of 225 variable characters and 142 parsimony-informative characters. The data matrix contained 3.0% cells with missing values.

Parsimony analysis with uninformative characters excluded recovered three equally most parsimonious trees of 354 steps (CI = 0.49, RI = 0.72; Fig. 2). A small-flowered, strictly South American clade of gynodioecious species (64% bootstrap support) comprising *Styrax maninul* B. Walln. through *S. foveolaria* Perkins in Fig. 2 (henceforth referred to as the Foveolaria clade) is sister to a clade (70%) comprising the rest of series *Valvatae*. Within the Foveolaria clade, the species from southeastern Brazil [*S. aureus* Mart., *S. maninul*, and *S. pedicellatus* (Perkins) B. Walln.] form a clade (100%) that is sister to a clade (66%) comprising the Andean species *S. foveolaria* and *S. vilcabambae* D. R. Simpson. A paraphyletic group from southern North America plus the Greater Antillean species *S. ochraceus* is basal to a clade (89%) comprising the remaining species from South America and the Antilles. Within this clade, the two other species from the Greater Antilles (*S. obtusifolius* and *S. portoricensis*) form a clade (100%) that is highly nested within a series of extra-Andean lineages (*S. ferrugineus* Nees & Mart. through *S. leprosus* Hook. f. & Arn. in Fig. 2). The Andean species (*S. nunezii* P. W. Fritsch, *S. paxonii* A. DC., *S. pentlandianus* J. Rémy, and *S. tomentosus* Bonpl.) form a clade (88%). *Styrax ochraceus* groups as sister to the southern Mexican species *S. radians* P. W. Fritsch (52%), and the two samples of *S. glaber* of the Lesser Antilles and northern South America form a group (100%) that is sister to the widespread South American species *S. pohlii* (71%).

The modified morphological data set included 19 parsimony-informative characters. With all species included in an ILD test of combinability, the morphological and ITS data sets are significantly incongruent ( $P = 0.02$ ). With *Styrax obtusifolius* excluded from the analysis, the morphological and ITS data sets are not significantly incongruent ( $P = 0.23$ ). On this basis, the data sets were combined after *S. obtusifolius* was excluded from the combined matrix. The combined analysis with uninformative characters excluded (19 morphological characters, 139 ITS characters, 2.7% cells with missing values) recovered the same three equally most parsimonious trees as those from the ITS analysis (length = 377; CI = 0.50; RI = 0.73; Fig. 2). The bootstrap support values of several clades were substantially different than those estimated from the ITS analysis (Fig. 2). Most notably, the Foveolaria clade was much more highly supported (98% versus 64%), and the clade comprising *S. foveolaria* and *S. vilcabambae* was much less highly supported (<50% versus 66%).

Biogeographic analysis with FPO resulted in three equally most parsimonious optimizations of six steps

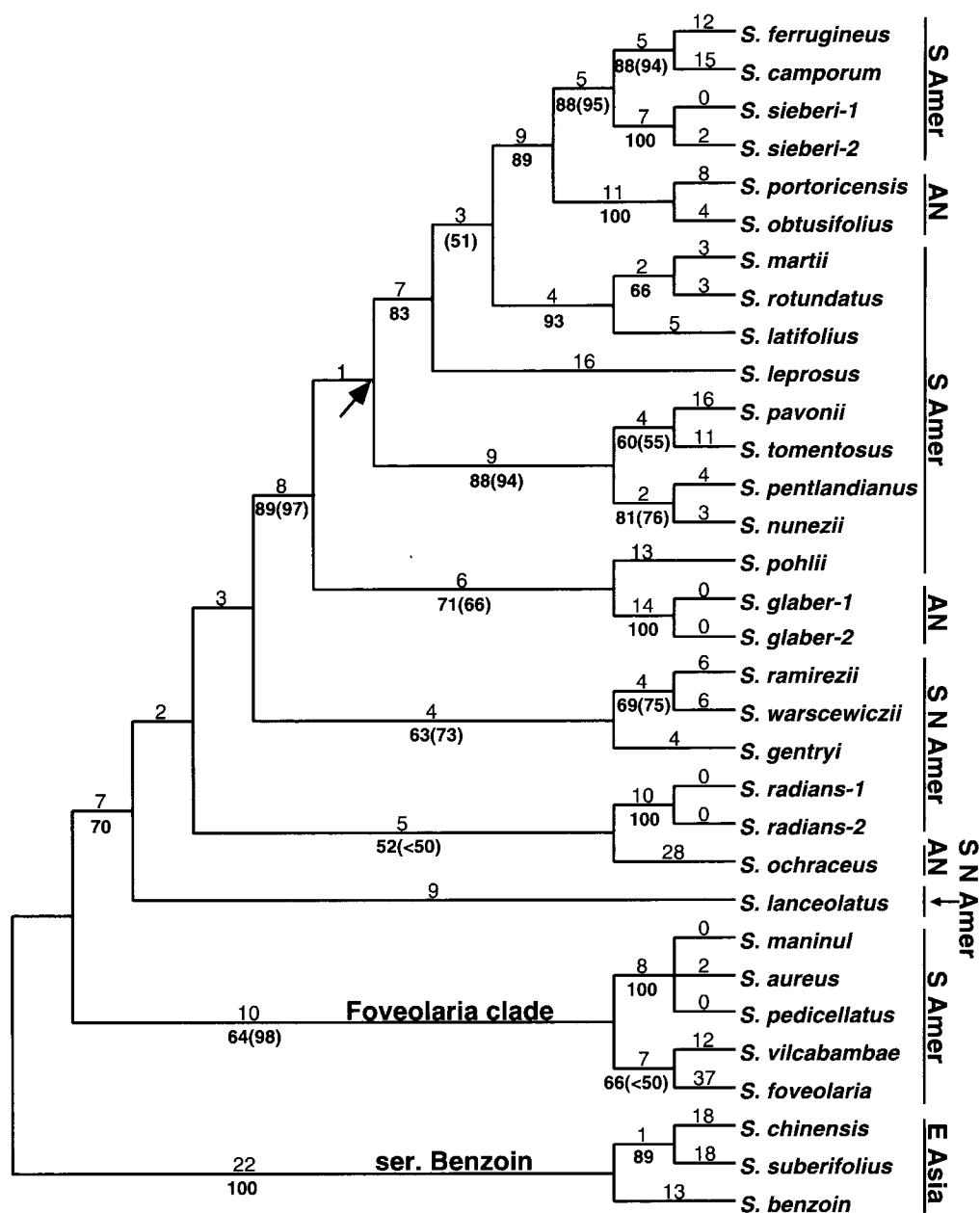


FIG. 2. One of three equally most parsimonious trees from analysis of ITS region DNA sequences of *Styrax* series *Valvatae* (length = 441, CI = 0.59, RI = 0.72). Numerals above each branch are ACCTRAN branch lengths (all variable characters are included to show the lengths of the terminal branches). Numerals below each branch are bootstrap values. Numerals in parentheses are bootstrap values based on an analysis from a combined morphological + ITS data set; values are shown only if they differ by  $\geq 5\%$  from the corresponding values from the ITS analysis. Arrow denotes the node not present in the strict consensus of the three equally most parsimonious trees. E Asia = eastern Asia; AN = Antilles; S Amer = South America; S N Amer = southern North America.

(Fig. 3). The only area of ambiguity was found along the branch subtending series *Valvatae*, which was assigned either eastern Asia, southern North America, or South America. Two dispersals into South America can be inferred from the tree, either once from eastern Asia and once from southern North America, or twice from southern North America. Three independent dispers-

als into the Antilles can be inferred, one from southern North America (*S. ochraceus*) and the other two from South America (the MRCA of *S. obtusifolius* + *S. portoricensis*, and an ancestor within the *S. glaber* lineage).

DIVA with the maximum number of areas assigned to each node restricted to two resulted in two equally optimal reconstructions of six dispersals (Fig. 3). DIVA

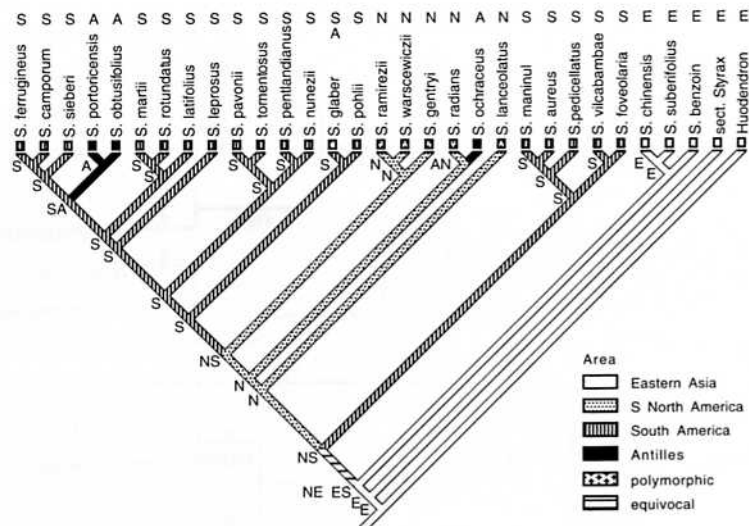


FIG. 3. Optimization of ancestral state area assignments with Fitch parsimony optimization (FPO) and dispersal-vicariance analysis (DIVA) over the tree in Fig. 2. FPO (three optimizations of six steps) is indicated by shading within branches; DIVA is indicated by letters. The two groups of letters at the third node from the base of the tree denote alternative ancestral state assignments in the two DIVA optimizations (of six dispersals). The results shown are based on a maximum number of two areas assigned to each node. E = Eastern Asia; N = southern North America; S = South America; A = Antilles.

with an unrestricted number of areas assigned to each node resulted in four equally optimal reconstructions of six dispersals (not shown), two of which were identical to those from two-area DIVA, and the other two of which differed only in the higher number of areas assigned to the most basal nodes (i.e., either E or ENS assigned to the MRCA of *S. ferrugineus* through *Huodendron* and *S. ferrugineus* through section *Styrox*, and ENS assigned to the MRCA of *S. ferrugineus* through *S. benzoin* Dryand. in Fig. 3). All optimal reconstructions required a dispersal from southern North America to South America along the branch subtending the MRCA of *S. ferrugineus* through *S. gentryi* P. W. Fritsch in Fig. 3, and three dispersals into the Antilles, one from South America along the branch subtending the MRCA of *S. ferrugineus* through *S. obtusifolius* in Fig. 3, one from southern North America along the branch subtending the MRCA of *S. radians* and *S. ochraceus* in Fig. 3, and one within the *S. glaber* lineage. A strict vicariance optimization between southern North America and the Antilles is recovered (six dispersals) only if *S. ochraceus* is placed as sister to all non-Foveolaria-clade species of series *Valvatae* (not shown).

#### DISCUSSION

**Phylogeny and Character Evolution.** The phylogenetic placement of three of the four Antillean species of *Styrox* based on ITS differs from that based on morphology (Fritsch 1999). Although *S. ochraceus* groups with species from southern North America in both analyses, in the ITS analysis it is sister to the Mexican species *S. radians*, whereas in the morphological anal-

ysis it is sister to a group of seven other southern North American species. *Styrox portoricensis* is sister to *S. obtusifolius* in the molecular analysis, and this clade is sister to a group of widespread South American species. In contrast, the morphological analysis separates these two species such that *S. portoricensis* forms a clade with many other South American species, and *S. obtusifolius* is sister to the Foveolaria clade. The hypothesis of a close relationship between *S. ochraceus* and *S. obtusifolius* (Mai 1988) is not supported by either analysis.

Of the four species of *Styrox* native to the Antilles, *S. obtusifolius* shows the most dramatic difference in phylogenetic position between morphological and molecular analyses, and this difference is reflected in the ILL test results. The placement of *S. obtusifolius* as sister to the Foveolaria clade in the morphological analysis was based on the following synapomorphies: (1) staminodia present (versus absent; unique change), (2) ventral distinct portion of the stamen filaments planar (versus concave; reversal), (3) anther connective 2–3.3 times as wide as the thecae in tangential view (versus <1.2 times as wide; unique change), and (4) style subulate (versus filiform; change arises more than once on the tree). A fifth character thought to support the morphologically based phylogenetic position of *S. obtusifolius* (although not scored in the analysis) was the number of ovules per carpel, because when mapped on the topology it followed the ordered series {multi-ovulate, 1–2-ovulate (*S. obtusifolius*), consistently 1-ovulate (Foveolaria clade)}. The reduced number of ovules per carpel in *S. obtusifolius* provided the basis for *Styrox*

section *Foveolaria* Perkins, which also included *S. foveolaria* (Perkins 1907; the rest of the *Foveolaria* clade was delimited by Perkins as the genus *Pamphilia* Mart. ex A. DC. on the basis of five-anthered flowers; see below).

Despite the partial consistency between Perkins (1907) and Fritsch (1999) as to the placement of *Styrax obtusifolius* based on morphology, the ITS data strongly suggest that convergent evolution has occurred between this species and the *Foveolaria* clade for the characters supporting this placement. Of the characters noted above, (1) and (3) are associated with breeding system [(3) because primarily staminodia were examined, with highly reduced anther sacs] and (2), (4), and (5) are associated with small flower size [(2) is a reversal that is probably contingent upon short filament length]. Gynodioecy and small flower size are undoubtedly derived character states within the genus, and appear to have evolved in concert. Female flowers are often smaller than those of hermaphrodites in gynodioecious species (Bell 1985; Gibson and Diggle 1997), and this is the case in the *Foveolaria* clade (Wallnöfer 1997; P. Fritsch, pers. obs.). This does not necessarily explain, however, the shift to small flower size of both sexual morphs. Much of the flora of the Antilles and especially Cuba consists of plants with "micranthia", small flowers that are pollinated by minute, endemic insects (Borhidi 1996). The predominance of these types of pollinators in the Antillean fauna may have spurred the evolution of reduced flower size in *S. obtusifolius*, although *S. portoricensis*, its sister species endemic to Puerto Rico, has shown no such reduction. Because of the concerted shift in these features and because gynodioecy appears to be of the relatively uncommon stable type in *Styrax* (Fritsch 2001), more intensive study of the reproductive biology of gynodioecious species of series *Valvatae* is likely to provide new insights into the evolution of gynodioecy in plants.

The six species of *Styracaceae* with five stamens per flower have been recognized at the generic level as *Pamphilia* (Candolle 1844; Seubert 1868; Perkins 1907) and as *Styrax* section *Pamphilia* (Wallnöfer 1997). In the morphological analysis of Fritsch (1999), they formed a clade that was sister to a clade comprising *S. foveolaria* and *S. nui* B. Walln., both of which possess the primitive number of ten stamens (occasionally more) per flower, and all the above species together formed a clade that was identical to the *Foveolaria* clade recovered from the ITS and combined analyses. The ITS analysis differs from the morphological analysis, however, in placing the five-anthered species *S. aureus*, *S. maninul*, and *S. pedicellatus* as the sister group of a clade comprising the five-anthered species *S. vilcabambae* and the ten-anthered species *S. foveolaria*. Thus, the ITS analysis suggests either that five-anthered flowers evolved twice in the *Foveolaria* clade, or that *S. foveo-*

*laria* reverted to the ten-anthered condition after the five-anthered condition evolved in the MRCA of the *Foveolaria* clade. In either case, the species of *Pamphilia* do not form a monophyletic group. Rather, the phylogeny of the *Foveolaria* clade reflects geographic proximity, such that the southeastern Brazilian endemics *S. aureus*, *S. maninul*, and *S. pedicellatus* form one clade and the Andean endemics *S. foveolaria* and *S. vilcabambae* another. No morphological synapomorphies are yet apparent as a basis for this topology.

**Antillean Biogeography.** The ITS results corroborate those based on morphology in providing evidence for multiple origins of Antillean *Styrax* from mainland progenitors. DIVA based on either the ITS or combined topology reconstructs three dispersals to the Antilles, one from southern North America and two from South America. The DIVA optimization based on ITS differs from that based on morphology alone (Fritsch 1999) only in the number of dispersals required to explain the data (three to the Antilles versus four). The difference is solely attributable to the disparate placement of *S. obtusifolius* among the topologies from the two data sets. The high bootstrap support (100%) for the placement of *S. obtusifolius* as sister to *S. portoricensis* in the ITS analysis strongly suggests that the biogeographical reconstruction based on ITS (or combined) data is more likely than that based on morphology alone.

The simplest vicariance model predicts that Antillean *Styrax* should at least form a clade, a prediction that is not supported by any of the phylogenetic studies of *Styrax*. This suggests that the Antillean species of *Styrax* did not respond to vicariance events associated with the breakup of a putative proto-Antillean landmass in the sense of Rosen (1975, 1985) and Savage (1982). Long-distance dispersal to the Greater Antilles from South America has been postulated to account for *S. portoricensis* in Puerto Rico (Fritsch 1999). As inferred from the present data, the ancestor involved in this event, if such occurred, would have been the same one that also gave rise to *S. obtusifolius* in Cuba and Hispaniola.

Although long-distance over-water dispersal remains a viable scenario for the dispersal event from South America to the Antilles as inferred from DIVA, the GAARlandia model (Iturralde-Vinent and MacPhee 1999) poses a viable alternative. The geographic distribution and biogeographic analysis of the clade containing *S. obtusifolius* and *S. portoricensis* are consistent with the GAARlandia model, because this clade extends from Puerto Rico through western Cuba, but apparently occurs neither in Mesoamerica nor the Lesser Antilles. The vicariance event between the Greater Antilles and South America inferred from DIVA after dispersal to the Greater Antilles would correspond to the disintegration of GAARlandia resulting from the Oligocene submergence of the Aves Ridge.

The notable lack of *Styrax* on Jamaica provides an-

cillary support favoring migration via GAARlandia versus long-distance over-water dispersal in *Styrax*. Jamaica was submerged during the middle Tertiary, re-emerging only in the Late Miocene (Buskirk 1985; Lewis and Draper 1990) and most or all of the island was likely never connected to the rest of the Greater Antilles subaerially (Iturralde-Vinent and MacPhee 1999). If *Styrax* migrated via long-distance over-water dispersal from northern South America to Cuba or Hispaniola, then it would seem reasonable to expect that it could also do so from northern South America or one of the Greater Antilles to Jamaica or other regions of the Caribbean. The absence of *Styrax* from Jamaica suggests that long-distance dispersal capacity is limited in this clade, and that the events that shaped the distribution patterns of Greater Antillean *Styrax* occurred prior to the Late Miocene.

One problem for the GAARlandia model as applied to *Styrax* is that *S. obtusifolius* and *S. portoricensis* are primarily montane species (250–1400 m and 250–900 m elevation, respectively; P. Fritsch, unpubl. data), whereas much of GAARlandia is proposed to have been continuous only through low elevations ( $\leq 200$  m; Iturralde-Vinent and MacPhee 1999). To accommodate this aspect of the GAARlandia model, one must postulate either that the MRCA of *S. obtusifolius* and *S. portoricensis* occurred at lower elevations than its descendants today, or that it was able to disperse directly from one upland area to another. *Styrax obtusifolius* must have had some capacity for direct dispersal in the past, because the montane regions of western and central Cuba where this species occurs today were separated from each other until the Late Miocene by a water gap and subsequently by low-elevation dry land (Graham 2003).

A DIVA optimization that infers a dispersal from southern North America to the Greater Antilles by the MRCA of *Styrax ochraceus* and *S. radians* supports the strong affinity proposed between the flora of the Antilles and that of Mesoamerica (Borhidi 1996). A strict vicariance scenario (i.e., the divergence of an ancestor common to the two areas without immediate prior dispersal) between the Antilles and southern North America would require a sister-group relationship between *S. ochraceus* and the rest of the non-Foveolaria members of series *Valvatae*, and paleogeographical evidence of a subaerial connection between the proto-Antilles and southern North America. As to the first requirement, the low support values for the relevant branches in the ITS topology do not preclude an alternative placement of *S. ochraceus* as basal to the rest of series *Valvatae*. As to the second, it is possible that Hispaniola and other islands of the proto-Antilles may have been in close proximity to the Chortis block in the Late Cretaceous, but there is no evidence that they were directly connected to it (Perfit and Williams

1989). Furthermore, this configuration is postulated to have occurred too early in the history of the Greater Antilles to have affected the composition of their current biota (Iturralde-Vinent and MacPhee 1999).

*Styrax glaber*, distributed in the Lesser Antilles and widely throughout northern South America (Colombia, Venezuela, the Guianas, and Brazil) and the only species of *Styrax* native to these islands, groups with the widespread South American endemic *S. pohlii* in the ITS analysis. This is consistent with its placement on the basis of morphology (Fritsch 1999). The islands of the Lesser Antilles began to form in the Oligocene, after the submergence of the Aves Ridge (Iturralde-Vinent and MacPhee 1999), and are likely never to have been directly connected to one another (Donnelly 1988). Thus, the presence of *S. glaber* on many of the islands of the Lesser Antilles appears to be the result of post-GAARlandia over-water dispersal from South America.

Why *Styrax glaber* has not extended its range from northern South America and the Lesser Antilles into the Greater Antilles despite its apparent ability for at least short-distance over-water dispersal is uncertain, but some insight may be gained from studying some aspects of its distribution. The islands of the Lesser Antilles fall into two distinct types: those with volcanic geological facies (Grenada north to Saba) and those with limestone facies (Marie Galante north to Sombro; Howard 1974). *Styrax glaber* occurs exclusively on the volcanic islands of the chain, i.e., St. Kitts, Montserrat, the Basse-Terre portion of Guadeloupe, Dominica, Martinique, St. Lucia, and St. Vincent (P. Fritsch, unpubl. data). This pattern holds even on Guadeloupe, where *S. glaber* occurs on the volcanic Basse-Terre portion, but not on the limestone Grande-Terre portion. None of the Greater Antilles have active volcanic regions currently, and when they did, the Lesser Antilles were not yet available for land colonization, suggesting that the restriction of *S. glaber* in the West Indies to the Lesser Antilles is a consequence of an ecological parameter associated with active vulcanism. Alternatively, because they are much older, the limestone islands of the Lesser Antilles might have been occupied by other *Styrax* species and therefore unavailable for colonization through niche saturation at the time that the southern, volcanic islands emerged. Nonetheless, there is no evidence fossil or otherwise that *Styrax* has ever occurred on any of these limestone islands. Neither of these scenarios explains the species' distribution in northern South America, where a different set of causal factors for its presence there must be sought.

From previous (Fritsch 1999, 2001) and the present biogeographical analyses of *Styrax*, it can be inferred that the MRCA of series *Valvatae* dispersed from the Northern Hemisphere (most likely southern North America) to South America, but the details of how this



proceeded are uncertain. Possibilities include via the Antilles in any of their configurations in the Cretaceous or more recently, the Isthmus of Panama, or long-distance (intercontinental) trans-oceanic dispersal that bypassed any intervening islands. If the inference of dispersal of the MRCA of *S. obtusifolius* and *S. portoricensis* from South America to the Greater Antilles through GAARlandia is correct, the role of the Isthmus of Panama for the original dispersal from North America to South America can be rejected, because *Styrax* would already have been in South America, long before the formation of the isthmus.

No matter what the likelihood of the other two possibilities, the present study strongly suggests that the Antilles (at least in their post-Cretaceous configurations) did not serve as an intercontinental corridor for *Styrax*; rather, they served as a repository for the few species that occur there. In the Greater Antilles, enough time has elapsed for distinct species to evolve from mainland progenitors. In the Lesser Antilles, individuals have dispersed through the volcanic island arc without concomitant speciation. The sum of the biogeographical data suggests that all three of the inferred dispersal events to the Antilles involving these species or their ancestors probably occurred at different times and under different geohistorical circumstances. As has been suggested by others for animals (Crother and Guyer 1996a; Williams 1989; Woods and Sergile 2001), this mixed dispersal/vicariance scenario may well be the norm in the historical biogeography of Antillean plants, but many more plant groups need investigation in a phylogenetic context before generalizations can be made in this context.

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