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A REVISION OF THE IMBRICATE GROUP OF *STYRAX* SERIES *CYRTA* (STYRACACEAE) IN ASIA[1]

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Abstract

Several taxonomic treatments of *Styrax* (Styracaceae) exist in regional floras of Asia, but the Asian species of the genus have not been comprehensively revised since 1907. To help rectify this, we conducted a taxonomic revision of the Asian species of *Styrax* series *Cyrta* with imbricate corolla aestivation. Our revision comprises 17 species with a combined distribution from Japan south to Sumatra and west to Nepal. The circumscriptions of the heretofore poorly defined species *S. hookeri* and *S. serrulatus* are clarified. *Styrax agrestis* var. *curvirostratus* is elevated to the species level, and lectotypes are selected for *S. duclouxii, S. floribundus, S. hemsleyanus, S. hookeri, S. hookeri* var. *yunnanensis, S. hypoglaucus, S. japonicus, S. limprichtii, S. macranthus, S. obassia, S. perkinsiae, S. serrulatus* var. *latifolius, S. shiraianus, S. supaii,* and *S. wilsonii.* Keys, descriptions, and distribution maps are provided for all species.
Key words: eastern Asia, Styracaceae, *Styrax, Styrax* series *Cyrta.*

Styrax L. comprises about 130 species of trees and shrubs distributed in eastern and southeastern Asia, the New World, and the Mediterranean region (Fritsch, 1999). The range of this genus is typical of many plant groups distributed among the refugia of Tertiary mixed-mesophytic forests in the Northern Hemisphere, except that it also includes a large Neotropical component that extends south to northern Argentina and Uruguay (Fritsch, 1999, 2001). *Styrax* is by far the largest and most widespread of the 11 genera in the Styracaceae sensu Fritsch et al. (2001) and Fritsch (in press a). Characters unique to *Styrax* in relation to the family include a stamen tube attached high (vs. low) on the corolla, the presence (vs. absence) of placental obturators, bitegmic (vs. unitegmic) ovules, and an indu-

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rate (vs. thin) seed coat; these have been identified as putative synapomorphies for the genus (Fritsch, 1999; Fritsch et al., 2001). The combination of the following characters also serves to delimit *Styrax* from other genera of Styracaceae: absence of bud scales, presence of pseudoterminal fertile shoots (except in *S. macrocarpus* W. C. Cheng; presumably a reversal), a short hypanthium, unarticulated pedicels, glossy stamen filament trichomes that are circular in cross section, a 3-carpellate ovary, the presence of mesocarp, and a seed-to-carpel ratio ≤ 1 (Fritsch et al., 2001; Fritsch, in press a). Like other Styracaceae, *Styrax* has a vestiture of stellate trichomes (in some cases modified to peltate scales or rarely simple trichomes), generally twice the number of stamens as petals, and introrsely dehiscent anthers with a large, linear connective (Fritsch et al., 2001; Fritsch, in press a).

Taxonomic History and Present Objectives

In the most recent worldwide monograph of the genus (Perkins, 1907), *Styrax* was divided into section *Styrax,* with 16- to 24-ovulate gynoecia (most of the genus) and section *Foveolaria* (Ruiz & Pav.) Perkins, with 3- to 5-ovulate gynoecia (2 Neotropical species). Section *Styrax* was in turn divided into series *Styrax* (= series *Imbricatae* Perkins, invalid name) and series *Valvatae* (Gürke) Perkins, each defined, as the names suggest, on the basis of corolla aestivation. Despite the use of aestivation type for infrageneric delimitation, Perkins (1907) acknowledged that some species of *Styrax* placed in series *Valvatae* are occasionally slightly imbricate (= "subvalvate"), whereby the edges of the corolla lobes are contiguous but oblique in cross section, with a mixed condition of valvate and subvalvate aestivation sometimes occurring within one and the same flower. On this basis, Steenis (1932), in a revision of the Malesian species of *Styrax,* did not recognize either series of Perkins and placed several imbricate-flowered species of series *Styrax* (*S. subpaniculatus* Jungh. & de Vriese, *S. porterianus* G. Don, and *S. subdenticulatus* Miq.) under *S. serrulatus* Roxb., a species with otherwise valvate to subvalvate aestivation.

Fritsch (1999) conducted a morphological phylogenetic analysis of *Styrax* and revised the infrageneric classification of the genus based on the results. In addition to corolla aestivation type, several other characters diagnosed the deep divergences of the *Styrax* topology, whereas clades diagnosed by a reduced number of ovules per gynoecium were highly nested. In the recircumscribed sectional and series classification, the clade corresponding to the deciduous section *Styrax* (about 33 species) was supported by the presence of young shoots with scattered stalked stellate trichomes distinct from the rest of the vestiture patterns (vs. without stalked trichomes unless accompanied by a dense tomentum consisting of trichomes of the same general type) and membranaceous (vs. subcoriaceous) corolla lobes, whereas the clade corresponding to section *Valvatae* Gürke (about 97 species) was supported by valvate (vs. imbricate or subvalvate) corolla aestivation, the evergreen (vs. deciduous) condition, sides of the corolla straight (vs. convex) in bud, and concave (vs. planar) stamen filaments. The delimitation of these two species groups corresponds roughly to a geographic distribution in warm-temperate versus humid-tropical regions, respectively. Within section *Styrax,* the clade corresponding to series *Styrax* (3 species, western North America, Mediterranean region) was supported by strictly pseudoterminal (vs. pseudoterminal and lateral) inflorescences, whereas that corresponding to series *Cyrta* (Lour.) P. W. Fritsch (about 30 species, eastern and southeastern Asia, southern North America) was supported by glandular-serrate (vs. entire) leaf margins.

The character states of corolla aestivation delimited in the morphological analysis reflected the distinction made previously (Perkins, 1907; Steenis, 1932) between a truly valvate type of corolla aestivation and the subvalvate type. The results of Fritsch (1999) demonstrated that valvate aestivation as defined by Perkins has evolved at least twice in *Styrax,* once in the most recent common ancestor of the evergreen species and once (as the subvalvate condition) in the deciduous species. Therefore, according to Fritsch's revision, valvate aestivation is possessed by all members of section *Valvatae,* imbricate aestivation is possessed by all members of series *Styrax* and some members of series *Cyrta,* and the remaining members of series *Cyrta* possess the subvalvate type. The morphological analysis of Fritsch (1999) supported the idea of Hwang (1999) that imbricate aestivation is the primitive state in *Styrax.*

A molecular phylogenetic analysis of *Styrax* based on DNA sequences from the internal transcribed spacer (ITS) region of nuclear ribosomal DNA, both separately and in combination with morphology, provided strong support for the series classification of Fritsch (1999, 2001). The ITS phylogeny was ambiguous as to the sectional classification, although a combined analysis recovered a topology consistent with it. A family-wide phylogenetic analysis based on DNA sequences of the chloroplast genes *rbc*L and *trn*L-F in combination with ITS sequences and morphology (Fritsch et al., 2001) provided some support for section *Styrax*, but support for section *Valvatae* was ambiguous. The placement of *Huodendron* Rehder as sister to *Styrax* with strong support rendered the original state for corolla aestivation in the genus ambiguous because both genera are polymorphic for this character. The monophyly of the subvalvate members of series *Cyrta* as predicted from morphology was not supported by the ITS results (Fritsch, 2001) because several major clades contained both subvalvate and imbricate species. For example, *S. japonicus* Siebold & Zucc., a species with imbricate aestivation, grouped strongly with *S. formosanus* Matsum., a species with subvalvate aestivation. Fritsch (2001) concluded that reticulate evolution may at least partly explain the discordance between morphological and molecular data in series *Cyrta* but cautioned that the absence of chromosome counts for most species hinders further progress on this issue.

During the course of our study it became clear that, despite the discordance between morphological and molecular data and the conclusions of Perkins (1907) and Steenis (1932), corolla aestivation is species-specific without exception in series *Cyrta* and apparently is one of the few discontinuous and potentially phylogenetically informative characters in the series. This indicated to us that the treatment of *S. serrulatus* by Steenis (1932), in which a mixture of distinctly imbricate and subvalvate types of aestivation was postulated, would require careful re-evaluation. Furthermore, our study of regional floristic treatments of the genus for Asia (Steenis, 1932, 1949; Hwang, 1987; Svengsuksa & Vidal, 1992; Yamazaki, 1993; Hwang & Grimes, 1996; Y. N. Lee, 1996; Long, 1999) suggested that the species of series *Cyrta* are often poorly understood taxonomically across political boundaries, likely through the lack of comprehensive examination of Asian types and other collections.

Here we provide a taxonomic revision of the members of *Styrax* series *Cyrta* in Asia with imbricate corolla aestivation (17 species). Restricting our revision to the species with imbricate aestivation provides a practical limit to the scope of the study and is not meant to suggest that the group is necessarily monophyletic. A revision of the remaining species of series *Cyrta* (i.e., those with subvalvate corolla aestivation) is anticipated as part of a comprehensive revision of *Styrax*. The four North American species of the series (*S. americanus* Lam., *S. glabrescens* Benth., *S. grandifolius* Ait., and *S. jaliscanus* S. Wats., all with imbricate aestivation) are treated in more taxonomic detail elsewhere (Gonsoulin, 1974; Fritsch, 1997; Fritsch, in prep.), but are included in the key to species and various discussion sections to provide complete coverage and facilitate identification of cultivated material.

Geographic Distribution and Endemism

The 30 or so species of *Styrax* series *Cyrta* occur in temperate lowland to tropical montane forests of eastern and southeastern Asia and North America with 80–300 cm mean annual precipitation and without a prolonged dry season (Fritsch, 2001). This intercontinentally disjunct distribution is common in many plant and animal groups, and is best explained by periods of relatively warm climate in the Tertiary that allowed widespread Northern Hemisphere distributions and transcontinental migration of lineages across the Bering and North Atlantic land bridges. Cooling and drying trends over the course of the Tertiary eventually restricted these lineages to "Tertiary refugia" today (Wolfe, 1975; Tiffney 1985a, b, 2000; Tiffney & Manchester, 2001). Most of the species in the series (ca. 26) occur in eastern and southeastern Asia, consistent with the general pattern of higher species richness in eastern Asia versus eastern North America in plant genera disjunct between these two regions (Wen, 1999). The remaining 4 species occur in the eastern United States (*S. americanus, S. grandifolius*), southwestern Mexico (Jalisco and Nayarit; *S. jaliscanus*), and eastern and southern Mexico to Costa Rica (*S. glabrescens*).

In Asia, the imbricate members of *Styrax* series *Cyrta* exhibit a combined distribution from Hokkaido, Japan, south to Sumatra, Indonesia, and west to Mechi, eastern Nepal. The 17 Asian species here recognized are all endemic to the region of interest. Most species possess a range that overlaps that of at least one other species in the group, except the southernmost species *S. curvirostratus* (B. Svengsuksa) Y. L. Huang & P. W. Fritsch, *S. porterianus*, and *S. subpaniculatus*. *Styrax japonicus* and *S. obassia* Siebold & Zucc. both exhibit a disjunct distribution among China, Korea, and Japan. *Styrax japonicus* extends along the Ryukyu Islands south to the northernmost islands of the Philippines, bypassing Taiwan. The most common and widespread species in more or less relative order are *S. japonicus, S. obassia, S. odoratissimus* Champ. ex Benth., *S. hookeri* C. B. Clarke, and *S. tonkinensis* (Pierre) Craib ex Hartwich. Species that can be considered narrow endemics are *S. buchananii* W. W. Sm., *S. chrysocarpus* H. L. Li, *S. curvirostratus, S. macrocarpus, S. porterianus, S. shiraianus* Makino, *S. sub-*

paniculatus, S. supaii Chun & F. Chun, and *S. wilsonii* Rehder, i.e., 53% of the Asian species of the group (Table 1).

Two other series of *Styrax* have representatives in Asia. *Styrax officinalis* L. of series *Styrax* occurs in the eastern Mediterranean region and extends into southwest Asia in Cyprus, Israel, Jordan, Lebanon, Syria, and Turkey. All ten or so species of series *Benzoin* P. W. Fritsch are endemic to eastern and southeastern Asia. The species of series *Benzoin* are easily distinguished from those of series *Cyrta* by the following characters: plants evergreen (vs. usually deciduous), bases of young shoots without stalked ferrugineous or fulvous stellate trichomes unless these accompanied by a dense tomentum consisting of trichomes of the same general color and type (vs. ferrugineous or fulvous stalked trichomes present, distinct from the rest of the vestiture), sides of the corolla straight or nearly so (vs. convex) in bud, corolla lobes subcoriaceous (vs. membranaceous or chartaceous), seeds depressed-globose (vs. generally ellipsoid, resting on the hilum on a flat surface instead of the sides between the hilum and apex), and seed coat crackled (i.e., coarsely reticulate-sutured; vs. generally smooth or with other types of patterns; see Fritsch, 1999). Although the geographic ranges of series *Cyrta* and series *Benzoin* overlap nearly completely, the species of series *Cyrta* tend to occur in warm-temperate regions, whereas those of series *Benzoin* tend to occur in subtropical to tropical regions.

Morphological and Taxonomic Characters

Here we discuss the principal diagnostic characters used in the systematics of the imbricate group of *Styrax* series *Cyrta* in Asia.

habit

All species herein are deciduous shrubs or trees except perhaps *Styrax curvirostratus* and *S. subpaniculatus*, which may be at least semi-evergreen. The tree species are typically less than 20 m tall but occasionally attain a height of greater than 30 m. Two species are known only as shrubs (*Styrax limprichtii* Lingelsh. & Borza and *S. wilsonii*). *Styrax rugosus* Kurz is typically a shrub but can occur as a small tree to 6 m, whereas *S. macrocarpus, S. obassia,* and *S. supaii* are typically small trees or rarely shrubs. *Styrax grandifolius* from the southeastern United States often forms colonies through root-suckering, but this habit is not known in any Asian species of *Styrax*.

leaves

Leaves are generally alternate but display two general patterns of phyllotaxis, one with more or less regularly spaced alternate leaves (*Styrax buchananii, S. chrysocarpus, S. curvirostratus, S. odoratissimus, S. porterianus, S. subpaniculatus,* and *S. tonkinensis*), the other with the two most basal leaves opposite or subopposite (sometimes one or both of these are replaced by scales). The latter condition, occurring on each new shoot, is nearly constant in *S. hemsleyanus* Diels, *S. macrocarpus, S. obassia,* and *S. supaii,* but less so in the remaining species, especially *S. limprichtii* and *S. rugosus.* The petioles of larger leaves are dilated at the base and completely cover the bud in two northern species (*S. obassia* and *S. shiraianus*); this feature is unique to these two species within *Styrax.* Petiole length differs greatly within and among species and is of diagnostic value in some instances (e.g., *S. macrocarpus*). The margins of the laminae are nearly always serrate or dentate, with each tooth tipped by a gland. Occasionally (e.g., *S. japonicus, S. porterianus, S. subpaniculatus*), some leaves are entire except for the tooth-like gland.

The size and shape of the leaves are variable within many species. The leaves of *Styrax hookeri, S. japonicus,* and *S. odoratissimus,* all relatively common and widespread species, are especially variable. The tertiary veins are more or less subparallel and perpendicular to the secondary veins in most species, but in *S. chrysocarpus, S. curvirostratus, S. japonicus, S. limprichtii,* and *S. supaii* they are more or less reticulate. Typically the leaves of sterile shoots are larger than those of fertile shoots.

vestiture

Although trichome types and the density of pubescence on various parts of the plants are useful characters for identifying some *Styrax* species, high infraspecific variation is common in the genus (Fritsch, 1996, 1997, in prep.). Many species in our revision exhibit such variation (*S. buchananii, S. hemsleyanus, S. hookeri, S. japonicus, S. limprichtii, S. odoratissimus,* and *S. subpaniculatus*). The lower laminar surface in these species can be essentially glabrous or sparsely to densely pubescent, the pubescence (if present) consisting of short or long stellate trichomes, or a mixture of both. In diagnostic terms, these differences are a matter of degree rather than kind and exhibit no correlated gaps with other characters, elevation, or geography (see discussions under each species in the Taxonomic Treatment section). The pubescence on reproductive parts of *Styrax* in our treatment can be

Table 1. Species distribution, richness, and endemism, by country. *, endemic.

Country	No. species/ No. endemics	Species
Bhutan	1/0	*S. hookeri*
China	12/7	**S. chrysocarpus*, **S. hemsleyanus*, *S. hookeri*, *S. japonicus*, **S. limprichtii*, **S. macrocarpus*, *S. obassia*, **S. odoratissimus*, *S. rugosus*, **S. supaii*, *S. tonkinensis*, **S. wilsonii*
India	1 [or 2]/0	*S. hookeri*, ? *S. japonicus*
Indonesia	1/1	**S. subpaniculatus*
Japan	3/1	*S. japonicus*, *S. obassia*, **S. shiraianus*
Laos	2/0	*S. japonicus*, *S. tonkinensis*
Malaysia	1/0	*S. porterianus*
Myanmar	5/1	**S. buchananii*, *S. hookeri*, *S. japonicus*, *S. porterianus*, *S. rugosus*
Nepal	1/0	*S. hookeri*
North Korea	2/0	*S. japonicus*, *S. obassia*
Philippines	1/0	*S. japonicus*
South Korea	2/0	*S. japonicus*, *S. obassia*
Thailand	2/0	*S. porterianus*, *S. rugosus*
Vietnam	3/1	**S. curvirostratus*, *S. japonicus*, *S. tonkinensis*

used to identify species such as *S. chrysocarpus* (with trichome color), *S. buchananii* (with trichome length), and *S. supaii* (with trichome type). Nonetheless, in some species pubescence presence and amount on reproductive parts varies continuously or sporadically, e.g., on the inner surface of the corolla lobes and style (*S. hookeri*), the pedicel and calyx (*S. japonicus*), or on the surface of seeds (*S. odoratissimus* and *S. tonkinensis*). In *S. japonicus*, the amount and density of pubescence is strongly associated with geography, whereby the most pubescent plants occur in the southernmost portion of the range and least pubescent and glabrous plants in the northernmost portion.

INFLORESCENCES

All inflorescences in members of series *Cyrta* are produced on the shoots of the current growing season except those of *Styrax macrocarpus,* which consist of single flowers produced on shoots of the previous growing season. The inflorescences of *S. macrocarpus* are unique within the genus in this respect, although several other genera of Styracaceae show the same pattern (Fritsch et al., 2001). This feature has presumably been derived independently in the ancestor of these genera and in *S. macrocarpus* because *Huodendron,* the sister group of *Styrax,* possesses the common state in *Styrax*. In species other than *S. macrocarpus,* inflorescences are both pseudoterminal and lateral; occasionally only pseudoterminal inflorescences are produced on some shoots of some species, but lateral inflorescences can always be found. Pseudoterminal inflorescences are always racemose or paniculate, sometimes two or more arising from the same node (e.g., *S. buchananii, S. hemsleyanus, S. obassia, S. odoratissimus, S. subpaniculatus,* and *S. tonkinensis*). Lateral inflorescences are 1- to 2-flowered or racemose; they are shorter than the pseudoterminal inflorescence and occur in the leaf axils immediately below it. We agree with Perkins (1902, 1907) that inflorescence length and flower number per inflorescence are relatively constant within most species of our revision, and have used these as fundamental key characters. Only *S. odoratissimus, S. tonkinensis,* and two North American species (*S. glabrescens* and *S. grandifolius*) exhibit significant variation in this respect (hence each must fall out twice in the key).

FLOWERS

Flowers are bisexual and actinomorphic with a short hypanthium (see Dickison, 1993) adnate to the basal third or less of the ovary wall. Flower length ranges from 0.7 to 3.2 cm. Some species (e.g., *Styrax curvirostratus, S. hemsleyanus, S. hookeri, S. japonicus, S. macrocarpus, S. obassia,* and *S. shiraianus*) have generally larger flowers than others, especially those whose flowers are consistently less than 1.5 cm long (e.g., *S. odoratissimus, S. porterianus, S. subpaniculatus,* and *S. wilsonii*).

The long pedicels (15–50 mm) of *Styrax japonicus* distinguish this species from all others in our revision. Except for most specimens of *S. japonicus,* the abaxial surface of the gamosepalous calyx in *Styrax* is always covered with stellate trichomes. Abaxial calyx pubescence can be used in species identification, e.g., the presence (vs. absence) of various amounts of scattered dark yellow, orange, or brown stiff stellate trichomes in addition to the base tomentum (*S. hemsleyanus, S. hookeri, S. limprichtii, S. obassia, S. rugosus, S. shiraianus,* and *S. wilsonii*), and a more sparsely pubescent to glabrous region than the rest of the calyx within 1 mm of the margin (*S. buchananii, S. curvirostratus, S. hookeri, S. japonicus, S. macrocarpus, S. odoratissimus, S. porterianus,* and *S. shiraianus*) versus a calyx that is evenly pubescent throughout. The calyx margin can be truncate, undulate, irregularly lobed, or distinctly dentate. If the margin is dentate, then the teeth are usually contiguous or separated by a shallow concave portion. *Styrax supaii* is distinguished from all other species by the long, simple or 2-armed trichomes covering the abaxial surface of the calyx, and long calyx teeth (4–5 mm long).

The gamopetalous corolla is completely white or rarely flushed with pink, and it is nearly always sparsely to densely stellate-pubescent on both sides. Some specimens of *Styrax hookeri* are glabrous adaxially. The corolla tube is almost always shorter than the lobes, usually ranging from 2 to 5 mm long. Only *S. shiraianus* possesses a corolla tube (10–12 mm long) longer than the lobes. In our species, the 5 (to 7) lobes range from 5 to 26 mm long and from 2.5 to 11 mm wide.

The stamens are adnate to the corolla tube proximally, free distally, and are twice the number of corolla lobes. The corolla lobes and stamen filaments become both free and distinct at approximately the same point along the floral axis in all species. Filaments range from 1.5 to 10 mm long and are usually equal or slightly unequal within a flower, but sometimes are distinctly alternately unequal in length, especially in *Styrax supaii.* The filaments are flexuous at mid-length in some species (*S. buchananii, S. curvirostratus, S. odoratissimus, S. subpaniculatus,* and sometimes *S. porterianus*). The filaments are of equal width throughout in *S. curvirostratus, S. hemsleyanus, S. obassia, S. rugosus, S. shiraianus,* and *S. tonkinensis,* and distally attenuate in the rest. Filament pubescence varies from absent (e.g., *S. obassia*) to proximally pubescent (e.g., *S. hemsleyanus*) or densely pubescent throughout (e.g., *S. buchananii, S. curvirostratus, S. odoratissimus, S. subpaniculatus*). The amount of filament pubescence is variable in *S. hookeri* and *S. tonkinensis.* Anthers are wider than the distal portion of the filament except in *S. curvirostratus, S. obassia, S. subpaniculatus,* and *S. tonkinensis,* where they are more or less the same width as the adjacent filament apex. The connectives are glabrous to stellate-pubescent. The length of the anthers, ranging from 2 to 7 (to 10) mm, is useful for species identification.

The ovary is always apically pubescent; it appears to hold little taxonomic value in the group under revision. The style is filiform and varies from glabrous (e.g., *Styrax hemsleyanus*) to densely hirsute (e.g., *S. buchananii, S. curvirostratus*). The amount of style pubescence varies substantially within some species, thus limiting its usefulness in species identification. The number of ovules per carpel in the group under study is often difficult to ascertain due to the small size of the placental region. The few samples that we have examined indicate that the number is variable, but is rarely less than 5 or more than 8 per carpel.

FRUIT

The fruit is usually globose, ovoid, or ellipsoid. *Styrax curvirostratus* has a cylindrical fruit, and that of *S. macrocarpus* is occasionally pyriform. The apex may be rounded (e.g., *S. subpaniculatus*), apiculate through persistence of the style base (e.g., *S. japonicus*), or rostrate (*S. curvirostratus* and *S. odoratissimus*). Fruit size ranges from 0.5 to 3 cm long and from 0.4 to 2.5 cm wide. The outer surface of the pericarp is white-gray to gray-yellow stellate-tomentose or -pubescent, except in *S. chrysocarpus,* in which it is golden yellow stellate-tomentose. The inner surface of the pericarp is typically glabrous or sparsely pubescent; only in *S. chrysocarpus* and *S. macrocarpus* is the pericarp densely pubescent inside. In both of these species the fruit is apparently indehiscent, although the limited material available for study leaves the constancy of this character in doubt. The fruit is unquestionably indehiscent in *S. porterianus* and *S. subpaniculatus*; the fruit is dehiscent by two or three valves in the other species. *Styrax porterianus* and *S. subpaniculatus* are similar in fruit dehiscence to the North American species *S. glabrescens* and *S. grandifolius,* which nearly always possess an indehiscent fruit. *Styrax porterianus* is the only species in our treatment with a fleshy pericarp (ca. 2 mm thick). The pericarp of all other species is dry. The thickness of the pericarp is variable within the dry-fruited species, but *S. macrocarpus* always has a pericarp greater than 1 mm thick, distinguishing this species from all other dry-fruited species in our revision.

SEEDS

The seeds of the imbricate group of series *Cyrta* are globose, ovoid, or ellipsoid, from beige to brown and smooth to finely reticulate-fissured or irregularly rugose (i.e., with a wrinkled appearance). Seed coat pubescence occurs in *Styrax curvirostratus, S.*

macrocarpus, S. odoratissimus, and *S. tonkinensis.* This pubescence is absent, however, in some individuals of each of these species. The seed coat is usually tuberculate in *S. tonkinensis.* These tubercles are sometimes arranged in a stellate pattern, in which case they often resemble stalked stellate trichomes.

CHROMOSOME NUMBERS

Only three species in our revision have been counted: *Styrax hookeri* ($n = 8$, Arora, 1961; Mehra & Bawa, 1969; Mehra, 1976), *S. japonicus* ($n > 20$, Manshard, 1936; $n = 8$, Yamazaki, 1993), and *S. obassia* ($n = 8$, Manshard, 1936; Yamazaki, 1993). Chromosome numbers of two North American species of series *Cyrta* have also been reported (*S. americanus*, $n = 8$; *S. grandifolius*, $n = 16$; Gonsoulin, 1974). From these numbers and reports for species in the other series, the base number of *Styrax* is inferred to be $x = 8$ (Fritsch, 2001). Polyploidy is thus far known with relative certainty only in series *Cyrta* (*S. grandifolius*; the old number for *S. japonicus* of $n > 20$ must be questioned in light of the more recent number of $n = 8$).

ECOLOGY AND ECONOMIC IMPORTANCE

According to herbarium specimen labels, species of the imbricate group of series *Cyrta* are found most often from 500 to 2700 m elevation in Asia. Several species (*Styrax japonicus, S. obassia, S. odoratissimus, S. porterianus, S. subpaniculatus, S. supaii,* and *S. tonkinensis*) occur additionally or exclusively at elevations less than 500 m; only *S. hookeri* extends to 3000 m or higher. Some species (*S. hemsleyanus, S. hookeri, S. japonicus, S. odoratissimus,* and *S. tonkinensis*) have a wide elevation range (2000 m or more in extent). Many of these species are found in a variety of habitats, such as open woodlands, pastures, mountain slopes, roadsides, high-elevation forests, and successional areas. Many species show a distinct preference for mesic microhabitats, such as canyons, draws, and other riparian situations.

Styrax species are most frequently pollinated by bumble bees and honey bees (Gonsoulin, 1974; Sugden, 1986; Kato & Hiura, 1999). Other pollinators reported for *Styrax* species are papilionoid butterflies, syrphid flies, sphingid moths, wasps, and other groups of bees (e.g., carpenter bees, halictids, anthophorids; Copeland, 1938; Gonsoulin, 1974; Sugden, 1986; Saraiva et al., 1988; Tamura & Hiura, 1998). Both nectar and pollen serve as floral rewards for pollinators, although there are no specialized structures recognizable as nectaries. The stellate trichomes present on the exterior surface of the corolla in most species of Styracaceae have been suggested as an adaptation for supporting large pollinators, which use them as "toe holds" to gather nectar and pollen (Sugden, 1986). The flowers of *Styrax* are sweetly fragrant (Perkins, 1907; Copeland, 1938; Fritsch, pers. obs.).

Nearly all species have exclusively hermaphroditic flowers. Partial self-incompatibility has been suggested for *Styrax obassia* (Tamura & Hiura, 1998), the only member of series *Cyrta* examined for breeding system. Obligate xenogamy is documented for several species of *Styrax* from other series (Sugden, 1986; Saraiva et al., 1988). Morphological gynodioecy is reported for ten species in series *Valvatae* (Wallnöfer, 1997; Fritsch, 1999, in press b), but experiments to confirm functional gynodioecy in these species have not been conducted.

Little data exist on the dispersal mechanisms of *Styrax.* Fruits of *S. obassia* are dispersed by ground mice and food-hoarding birds (Kato & Hiura, 1999). After the fruit wall has become detached, the seeds of the riparian species *S. faberi* Perkins, a valvate-flowered member of series *Cyrta,* remain attached to the receptacle by the hilum. The seeds, which would otherwise sink, can thus be transported in water by the floating infructescence (P. Fritsch, pers. obs.). The seeds of *S. japonicus,* an imbricate-flowered species of series *Cyrta* that exhibits the same type of seed attachment, may also be dispersed in this way. The seeds of *S. americanus* reportedly have been found attached to the feet of waterfowl (Ridley, 1930), but this is probably not a primary means of dispersal of *Styrax* species because the surface of the seeds is generally smooth and curved, and therefore not obviously adapted for attachment.

The benzofuran egonol and its glycosides occur in the seed oil of several species of *Styrax.* The fruit of *Styrax* contains significant amounts of jegosaponin, a potent defense chemical. Various species of *Styrax* also contain styracitol, β-phenyl ethyl alcohol, and coniferin (Hegnauer, 1962; Gibbs, 1974).

In many species of *Styrax,* a balsamic resin (benzoin, gum benjamin) exudes from the bark and wood tissues following injury to the cambium. This resin consists chiefly of coniferyl cinnamate, cinnamyl cinnamate (styracin), and coniferyl benzoate associated with cinnamic and benzoic acids; minor components are fragrant benzaldehyde, vanillin, and styrene (Hegnauer, 1962; Langenheim, 2003). It is used medicinally as an antiseptic and expectorant, and in the flavor and fragrance industries (Pratt & Youngken, 1951; Duke, 1985; Langenheim, 2003). The best known source of benzoin is *S. benzoin* Dryand., a species of series *Benzoin.* Within series *Cyrta,* three species have been reported as sources of benzoin (Burkill, 1966): *S. serrulatus, S. subpaniculatus,* and *S. tonkinensis,* the latter two of which are included in our revision. The benzoin from *S. tonkinensis* is called "Siam benzoin" because of its source in "the western parts of Indochina and eastern parts of Siam" (Burkill, 1966: 2146). We have not seen any specimens of *S. tonkinensis* from Thailand to confirm its occurrence there.

The oil extracted from the seeds of some species in our revision can be used to make soap or lubricating oil (e.g., *Styrax hemsleyanus, S. japonicus, S. obassia,* and *S. odoratissimus*; Tai & Pan, 1981; Hwang, 1987), or medicinally as an antiseptic to treat scabies (*S. tonkinensis*; Hwang, 1987). The young leaf of *S. japonicus* is used as tea in certain regions of China (*K. M. Feng 11082,* Yunnan), and the fruit of this species can be used as a source of sugar extract to brew wines (*P. C. Tam 63659,* Hunan). The flowers, leaves, fruits, and galls of some species are used as Chinese herbal medicines (e.g., *S. hemsleyanus* and *S. japonicus*; Tai & Pan, 1981). Several *Styrax* species of series *Cyrta* native to Asia are cultivated for ornament (Raulston, 1992). *Styrax japonicus* and *S. obassia* are most commonly cultivated, but also occasionally planted are *S. hemsleyanus, S. limprichtii, S. odoratissimus, S. shiraianus, S. tonkinensis,* and *S. wilsonii.* Many cultivars of *S. japonicus* have been developed (Raulston, 1992).

Most species of *Styrax* series *Cyrta* serve as the primary host for aphids of the family Hormaphididae (tribe Cerataphidini). These aphids produce conspicuous galls of various shapes on the vegetative and reproductive shoots of *Styrax.* Most individual cerataphidine aphid species use a single species of *Styrax* as primary host, although it is common for several species of aphid to parasitize the same species (Stern et al., 1997). Often the shapes of the galls produced by aphid species are characteristic of particular species of *Styrax,* e.g., spiral galls on *S. paralleloneurus* Perkins and coralline galls on *S. subpaniculatus.* The aphids produce a sterile soldier caste that defends the rest of the colony from predators. The morphology of these aphids and their galls, aphid behavior, and soldier production have been studied extensively (e.g., Docters van Leeuwen, 1922; Aoki, 1982; Kurosu & Aoki, 1990, 1991, 1997; Aoki & Kurosu, 1993; Aoki et al., 1998; Kurosu et al., 1998), and the evolution of soldier production has been investigated in ecological and phylogenetic contexts (Stern, 1994, 1998; Stern & Foster, 1996). Evidence for co-evolutionary patterns of host-switching comes from phylogenetic analyses of both the aphids (Stern, 1995) and *Styrax* (Fritsch, 1999). The four North American species of series *Cyrta* and *S. shiraianus* from Japan are apparently not parasitized by these aphids (P. Fritsch, pers. obs.; S. Aoki, pers. comm.); neither are any species of series *Styrax* or series *Valvatae* (P. Fritsch, pers. obs.). Thus, this interaction is apparently restricted to eastern and southeastern Asia and associated islands.

Materials and Methods

Nearly 5000 herbarium specimens from 22 herbaria (A, AAU, BM, BO, BR, C, CAS, DS, E, GH, IBK, IBSC, K, KUN, KYO, L, MO, P, PE, TAI, TI, and UC) were examined for this study. All descriptions were derived from examination of herbarium specimens. Flowering and fruiting times, elevation ranges, habitats, distributions, common names, and uses were derived from label information. Descriptions of leaves generally refer to those of the fertile branches; leaves of sterile branches are consistently larger and often possess more variation in trichome quantity and quality than those of fertile branches and thus are less useful for species identification. Leaf and petiole measurements were taken from the larger examples on each herbarium sheet. At the proximal ends of the twigs many deciduous species of *Styrax* have small leaves of roughly equivalent size among species, and the incorporation of these into descriptions would make species identification more difficult. Flowers are described at the stage of anthesis except where noted. Calyx dimensions are presented as height (from the end of the pedicel to the distal margin) times width at the apex, and thus include the short hypanthium. Fruit length was measured from the base of the fruiting calyx to the tip of the fruit (the calyx is persistent). Fruiting measurements were taken from mature fruits where possible. Often immature fruits are the only types available for examination on a herbarium sheet, in which case the larger fruits on the sheet were measured. Most observations were made by eye or with the aid of a dissecting microscope (maximum magnification = 64×).

Because our study is based primarily on herbarium specimens, we employ the morphological species concept, as discussed in Stuessy (1990), for species recognition. We base our species on the existence of correlated gaps in states among morphological characters, and treat clinal patterns as infraspecific variation that requires no formal taxonomic recognition. We explain our decisions on circumscription under each species, often in the context of the relevant taxonomic work of previous authors. We assume that the morphological differences among the species we recognize have a genetic basis, as can be inferred from examination of several species in a common garden setting (e.g., *Styrax japonicus, S. obassia,* and *S. odoratissimus* at the University of California Botanical Garden, Berkeley, California, U.S.A.), and regard the species we have recognized as hypotheses to be tested as new morphological data become available. Appendix 3 provides an alphabetic listing of species in the Taxonomic Treatment, including synonyms and excluded names.

The dots in the distribution maps are based on the specimens cited in this revision (see Taxonomic Treatment and Appendices 1 and 2). For collections in which geographic coordinates were not indicated on specimen labels (most collections), we estimated coordinates based on descriptive label information about the location of the collection. Our estimate was aided with a variety of published maps, atlases, and gazetteers, particularly the (United States) National Imagery and Mapping Agency (NIMA) database of foreign geographic feature names, with access provided by the GEOnet Names Server (GNS) at <http://www.nima.mil/gns/html/>. Mapped localities in China are resolved to the level of county (xian) or occasionally minutes; in all other countries, resolution is to the level of minutes unless more precise information was provided on labels. Geographic information provided on labels was often inadequate for estimation of locality, in which case the collection was not mapped. Some of these are listed at the beginning of collection citations in the Additional Specimens Examined sections, under the lowest-ranking political subdivision for which locality is known; otherwise they are listed under "Locality unknown." A database of all collection information used for this revision, including geographic coordinates linked to geographic information system software (ArcView, ESRI, Inc.), is available from the authors upon request.

Taxonomic Treatment

Styrax L., Sp. Pl. 444. 1753. TYPE: *Styrax officinalis* L. [as *S.* "*officinale*"].

Strigilia Cav., Diss. 7: 358, t. 201. 1789. TYPE: *Strigilia racemosa* Cav. [= *Styrax racemosus* (Cav.) A. DC.].

Foveolaria Ruiz & Pav., Fl. peruv. prodr. 57, t. 9. 1974. *Tremanthus* Pers., Syn. Pl. 1: 467. 1805. TYPE: *Foveolaria ferruginea* Ruiz & Pav., lectotype, designated by Fritsch (1999) [= *Styrax foveolaria* Perkins].

Epigenia Vell., Fl. flumin. 183. 1829. TYPE: *Epigenia integerrima* Vell., lectotype, designated by Fritsch (1999) [= *Styrax glabratus* Schott].

Pamphilia Mart. ex A. DC., in DC., Prodr. 8: 271. 1844. TYPE: *Pamphilia aurea* Mart. ex A. DC., lectotype, designated by Hutchinson (1967) [= *Styrax maninul* B. Walln.].

Darlingtonia Torr., Proc. Amer. Assoc. Advancem. Sci. 4: 191. 1851, nom. rej. TYPE: *Darlingtonia rediviva* Torr. [= *Styrax redivivus* (Torr.) L. C. Wheeler].

Evergreen or deciduous trees or shrubs; bark smooth or longitudinally fissured, gray to dark brown; twigs terete or subterete, outer layer of older twigs fibrous, dull brown or more often gray; inner layer yellow to dull maroon; buds superposed, stellate-pubescent or occasionally lepidote, naked (i.e., with a single outer scale that develops into the first leaf on new shoots). Vestiture consisting of stalked or unstalked, free or appressed stellate trichomes or less commonly scales, rarely also with simple trichomes. Leaves simple, pinnately nerved, estipulate, petiolate, generally alternate but sometimes basal leaves of the current year's growth opposite or subopposite, the margins glandular-serrate, glandular-dentate, or entire (but still glandular), rarely coarsely lobed. Inflorescences of bracteolate lateral and pseudoterminal (occasionally strictly pseudoterminal, rarely strictly lateral) racemes or panicles, essentially cymose but often appearing racemose, sometimes two or more arising from the same node, lateral inflorescences usually 1- to several-flowered; bracteoles small, positioned at various places along the pedicel or near the calyx base. Flowers actinomorphic, hermaphroditic, or (in gynodioecious species) female, fragrant, with a short hypanthium adnate to the basal third or less of the ovary wall; pedicel not articulated; calyx gamosepalous, campanulate, cupuliform or funnelform, teeth generally (4)5(6) or absent; corolla gamopetalous for ca. 2 mm or more, the petals distinct distally, the lobes (4)5(to 10), usually longer than the tube, imbricate, subvalvate, or valvate in bud, white, pink, or rarely yellow, pubescent, at least abaxially; stamens adnate to the corolla tube, free distally, (8 to)10(to 14), usually twice the number of the corolla lobes, uniseriate but often appearing biseriate in bud, the 5 inner, sepalad stamens often exceeding the 5 outer, petalad stamens, if 5 then all stamens petalad; filaments often connate proximally and distinct distally, sometimes completely distinct, flattened (but often auriculate ventrally), glabrous to stellate-pubescent or lepidote, the branches of the trichomes cylindrical in cross section, generally glossy; staminodia replacing the stamens in female plants; anthers linear, basifixed, 2-locular, introrse, longitudinally dehiscent, the anther sacs glabrous to moderately stellate-pubescent along the margins, the connective broad, tangentially thickened throughout the length, white, glabrous or stellate-pubescent; pollen light or golden yellow; ovary semi-inferior, 3-carpellate, 3-septate at the base but 1-locular through the distal attenuation of the septa, with essentially axile or near-basal placentation; style filiform, hollow; stigma terminal, obscure, capitate, punctiform or faintly 3-lobed; placental obturators usually present; ovules 1 to ca. 8 per carpel, anatropous, apotropous, bitegmic, tenuinucellate. Fruit a drupe, a capsule dehiscent by (2)3 valves, or nut-like (dry and indehiscent), globose, depressed-globose, ovoid, or ellipsoid, 1(to 3)-seeded, with persistent calyx; exocarp and endocarp thin, mesocarp dry, mealy, or juicy. Seeds ± globose, ovoid, or ellipsoid, beige to brown, completely filling the fruit cavity, with a broad hilum; seed coat 5 to 50 cells thick, usually smooth except for 3(to 6) longitudinal grooves, sometimes also finely reticulate-fissured to irregularly rugose, sometimes pubescent, rarely tuberculate; endosperm copious; embryo straight; cotyledons flattened. About 130 species. U.S.A to Argentina, eastern Mediterranean, eastern and southeastern Asia.

Styrax series **Cyrta** (Lour.) P. W. Fritsch, Syst. Bot. 24: 373. 1999. *Cyrta* Lour., Fl. cochinch. Ed. 1: 278. 1790. TYPE: *Cyrta agrestis* Lour. [= *Styrax agrestis* (Lour.) G. Don].

Adnaria Raf., Fl. ludov. 56. 1817. TYPE: *Adnaria odorata* Raf. [= *Styrax americanus* Lam.].

Anthostyrax Pierre, Fl. forest. cochinch. sub t. 260. 1892. TYPE: *Anthostyrax tonkinense* Pierre [= *Styrax tonkinensis* (Pierre) Craib ex Hartwich].

Deciduous (possibly at least semi-evergreen in *S. curvirostratus* and *S. subpaniculatus*) trees or shrubs; bases of young shoots with scattered stalked ferrugineous or rarely fulvous stellate trichomes distinct from the rest of the vestiture. Vestiture consisting of stalked or unstalked, erect to appressed stellate trichomes, rarely also with simple trichomes. Leaf margins of at least some leaves on sterile shoots (and often of fertile shoots) glandular-denticulate to glandular-serrate, rarely also lobed; occasionally margins of some leaves entire (but still glandular). Inflorescences produced laterally and pseudoterminally on at least some shoots (strictly laterally in *S. macrocarpus*), the lateral inflorescences often reduced to 1 to 3 flowers, the subtending leaves often reduced. Flowers hermaphroditic; corolla white or rarely white flushed with pink, the sides generally convex in bud; corolla lobes imbricate or subvalvate in bud, membranaceous to chartaceous; stamen filaments planar ventrally, straight or occasionally flexuous, glabrous or stellate-pubescent; placentation essentially axile, placental obturators present; ovules ca. 5 to 8 per carpel. Fruit a capsule dehiscent by (2)3 valves, or nut-like (dry and indehiscent), rarely (*S. porterianus*) a drupe; outer surface of pericarp smooth to irregularly rugose; endocarp at maturity adherent to the mesocarp, not the seed. Seeds ovoid, ellipsoid, subglobose to globose, resting on the side between the hilum and the apex when placed on a flat surface; seed coat usually smooth, sometimes finely reticulate-fissured to irregularly rugose, sometimes pubescent, rarely tuberculate (*S. tonkinensis*). About 30 species, eastern Asia (about 26 species, Japan to Indonesia and several island chains of the western Pacific, west to eastern Nepal) and North America (4 species, southeastern United States, Mexico, Central America).

Key to Species of the Imbricate Group of *Styrax* Series *Cyrta*
(* indicates species that fall out twice in the key)

1a. Outer surface of the pericarp golden yellow stellate-tomentose; inner surface of pericarp densely pale yellow appressed-pubescent .... 2. *S. chrysocarpus*
1b. Outer surface of the pericarp not golden yellow-stellate-tomentose; inner surface of pericarp glabrous or sparsely to densely white-pubescent.
  2a. Pseudoterminal inflorescences ≥ 7 cm long, often 8- to 20(to 23)-flowered.
    3a. Two most proximal leaves on each shoot of the current year subopposite to opposite.
      4a. Petiole of larger leaves dilated at base and covering the bud; rachis glabrous or nearly so; inner surface of calyx glabrous; pericarp coarsely and irregularly rugose .... 9. *S. obassia*
      4b. Petiole not dilated at base, not covering the bud; rachis stellate-tomentose; inner surface of calyx appressed-pubescent; pericarp smooth or slightly longitudinally rugose.
        5a. Vegetative end buds ≤ 3 mm long; calyx campanulate or broadly cupuliform; fruit globose, indehiscent or rarely dehiscent, not longitudinally rugose; North America.
          6a. Tree to 30 m, not suckering from roots; leaves membranaceous; corolla lobes 11–23 × 6–10 mm; fruit 10–17 × 9–19 mm; Mexico and Mesoamerica .... *S. glabrescens Benth.
          6b. Tree to 6 m, often suckering extensively from roots; leaves chartaceous; corolla lobes 8–16 × 3–7 mm; fruit 8–12 × 6–8 mm; southeastern United States .... *S. grandifolius Ait.

5b. Vegetative end buds 4–6 mm long; calyx narrow-cupuliform; fruit globose to ovoid, dehiscent, slightly longitudinally rugose; Asia .... 4. *S. hemsleyanus*

3b. Two most proximal leaves on each shoot of the current year alternate.

7a. Abaxial surface of the lamina completely concealed by the tomentum; calyx distinctly dentate, the teeth usually contiguous or separated by a shallow concave margin; filaments of equal width throughout, straight; seeds densely tuberculate, sometimes the tubercles arranged in stellate formations .... *16. *S. tonkinensis*

7b. Abaxial surface of the lamina visible through the pubescence, if present (rarely nearly concealed by the tomentum in *S. subpaniculatus*); calyx truncate, undulate, or irregularly lobed, the teeth not contiguous if present; filaments narrowing distally, flexuous at middle (occasionally straight in *S. subpaniculatus*); seeds smooth, glabrous, appressed-stellate-pubescent, or lepidote (seeds unknown in *S. buchananii*).

8a. Corolla lobes 1.7–2.2 times as long as wide; pseudoterminal inflorescences usually racemose, rarely paniculate; fruit apex rostrate, rarely merely apiculate; seeds usually appressed-stellate-pubescent or lepidote .... *10. *S. odoratissimus*

8b. Corolla lobes 2.3–3.0 times as long as wide; pseudoterminal inflorescences usually paniculate; fruit apex rounded or subacute, rarely also apiculate (fruit unknown in *S. buchananii*); seeds glabrous.

9a. Connectives (at least proximally) and style densely stellate-hirsute; anthers 5–7 mm long; flowers 1.3–1.6 cm long; calyx stellate-hirsute, arms of trichomes averaging ca. 1 mm long .... 1. *S. buchananii*

9b. Connectives and style glabrous; anthers 3–4 mm long; flowers 0.9–1.2 cm long; calyx tomentose, arms of trichomes < 0.2 mm long .... 14. *S. subpaniculatus*

2b. Pseudoterminal inflorescences < 7 cm long, $\leq$ 7-flowered (3- to 11-flowered in *S. shiraianus*).

10a. Petiole of larger leaves dilated at base, covering the bud; inflorescences distally congested; pedicel < 1 mm long; corolla tube 10–12 mm long .... 13. *S. shiraianus*

10b. Petiole not dilated at base, not covering the bud; inflorescences not distally congested; pedicel ≥ 2 mm long; corolla tube 2–5 mm long.

11a. Calyx teeth 4–5 mm long; calyx abaxially with simple or 2-armed trichomes ca. 1–1.5 mm long .... 15. *S. supaii*

11b. Calyx truncate or teeth < 3 mm long; calyx abaxially with stellate trichomes averaging $<$ 1 mm long or glabrous.

12a. Distalmost leaves on sterile shoots usually > 7 cm wide; fruit indehiscent (rarely dehiscent by 3 valves), with corolla 10–28 mm long; North America.

13a. Tree to 30 m, not suckering from roots; leaves membranaceous; corolla lobes 11–23 × 6–10 mm; fruit 10–17 × 9–19 mm; Mexico and Mesoamerica .... **S. glabrescens* Benth.

13b. Tree to 6 m, often suckering extensively from roots; leaves chartaceous; corolla lobes 8–16 × 3–7 mm; fruit 8–12 × 6–8 mm; southeastern United States .... **S. grandifolius* Ait.

12b. Distalmost leaves usually < 7 cm wide (occasionally > 7 cm wide in *S. jaliscanus, S. odoratissimus, S. subpaniculatus,* and *S. tonkinensis*); fruit dehiscent or if indehiscent, then corolla 5–9 mm long; Asia.

14a. Calyx truncate, undulate, irregularly lobed or toothed, if toothed then the teeth not contiguous; calyx abaxially glabrous, or if stellate trichomes present, within 1 mm of the margin more sparsely pubescent than the rest of the calyx or subglabrous to glabrous, somewhat scarious, brown when dry.

15a. Longer pedicels on each twig 15–50 mm long, usually equal to or longer than subtended flower .... 6. *S. japonicus*

15b. Longer pedicels on each twig 2–10(–13) mm long, usually shorter than subtended flower.

16a. All flowers solitary, arising from shoots of the previous growing season; petioles $< 1(–2.5)$ mm long; pericarp dry, (1–)1.5–3 mm thick; inner surface of pericarp densely appressed-pubescent .... 8. *S. macrocarpus*

16b. At least some flowers paired or in racemes arising from shoots of the current growing season; petioles > 2.5 mm long; pericarp < 1 mm thick or fleshy; inner surface of pericarp glabrous or sparsely pubescent.

17a. Stems of young fertile shoots generally < 0.6 mm wide at the narrowest points proximally; pedicels slender, 0.2–0.6 mm wide proximally; calyx toothed, the teeth linear-subulate at least at apex but often wider proximally, 0.5–1.2 mm long; corolla lobes 1–5 mm wide, apex acute; North America (eastern United States) .... *S. americanus* Lam.

17b. Stems of young fertile shoots generally ≥ 1 mm wide proximally (often narrower distally); pedicels stouter, (0.4–)0.6–1 mm wide proximally; calyx truncate, undulate, irregularly lobed, or toothed, if toothed the teeth deltoid to linear-deltoid; corolla lobes 3–13 mm wide, apex obtuse or acute-acuminate; Asia.

18a. Flowers (1.3–)1.5–2.5 cm long; corolla lobes (11–)12–18 mm long; calyx (3.5–)5–7(–9) × 4–7(–11) mm; filaments 4–7 mm long; pericarp at least faintly longitudinally striate.

19a. Tertiary and quaternary veins of lamina plane adaxially, the tertiaries subparallel; calyx often abaxially with various amounts of stiff stellate trichomes, especially proximally, scattered among the base tomentum; filaments 5–7 mm long, distally attenuate; anthers 3–5 mm long, wider than distal portion of filament; fruit subglobose or ovoid, (1.0–)1.5–2 cm long; apex acute, occasionally short-rostrate .... 5. *S. hookeri*

19b. Tertiary and quaternary veins of lamina conspicuously raised adaxially (as well as abaxially), the tertiaries irregularly reticulate; calyx abaxially without scattered stiff stellate trichomes; filaments 4–5 mm long, of equal width throughout; anthers 5–6 mm long, as wide as or narrower than distal portion of filament; fruit cylindrical to obliquely ovoid, 2–2.5 cm long; apex usually rostrate, rostrum up to 2 cm long. .... 3. *S. curvirostratus*

18b. Flowers < 1.5 cm long; corolla lobes 9–11 mm long; calyx 3–4(–5) × 3–4 mm; filaments 1.5–4 mm long; pericarp not longitudinally striate.

20a. Connectives (at least proximally) and style densely stellate-pubescent; pericarp dry, 0.5–1 mm thick, smooth or slightly rugose; seeds usually appressed-stellate-pubescent or lepidote, rarely glabrous; mature leaves light green to yellow-green when dry, chartaceous or thick-chartaceous .... *10. *S. odoratissimus*

20b. Connectives and style glabrous; pericarp fleshy, ca. 2 mm thick, deeply rugose when dried; seeds glabrous; mature leaves green to dark green when dry, membranaceous or thin-chartaceous .... 11. *S. porterianus*

14b. Calyx distinctly dentate, the teeth usually contiguous or separated by a shallow concave portion; calyx abaxially within 1 mm of the margin evenly pubescent, the color and texture ± similar to the rest of the calyx.

21a. Trees to 30 m tall; petiole 8–12(–15) mm long; pericarp not longitudinally striate, apex rostrate; seeds densely tuberculate, sometimes the tubercles arranged in stellate formations .... *16. *S. tonkinensis*

21b. Shrubs to 2.5 m tall (sometimes a tree to 6 m in *S. rugosus*); petiole ≤ 5 mm long; pericarp longitudinally striate, apex rounded or apiculate; seeds smooth or finely reticulate-fissured, glabrous.

22a. Lamina 1–2.5(–4) × 0.7–2(–2.5) cm; fruit 0.4–0.6 cm wide .... 17. *S. wilsonii*

22b. Lamina 3–13 × 2–8 cm; fruit ≥ 0.7 cm wide.

23a. Secondary veins of lamina 7–10 on each side of midvein; inflorescence rachis gray-green tomentose; calyx gray-green lanate throughout; North America (western Mexico) .... *S. jaliscanus* S. Wats.

23b. Secondary veins of lamina 4–7 on each side of midvein; inflorescence rachis yellow or orange tomentose; calyx yellow, yellow-brown, or orange tomentose, often also with various amounts of larger scattered dark yellow, orange, or brown stiff stellate trichomes, especially proximally; Asia.

24a. Quaternary as well as the tertiary veins of lamina abaxially prominent and raised in young leaves; rachis with stalked trichomes; fruit 0.8–0.9 cm wide .... 12. *S. rugosus*

24b. Only the tertiary veins of lamina abaxially prominent and raised in young leaves; rachis without stalked trichomes; fruit 1.0–1.5 cm wide .... 7. *S. limprichtii*

1. Styrax buchananii W. W. Sm., Notes Roy. Bot. Gard. Edinburgh 12: 234. 1920 [as *S.* "*Buchananii*"]. TYPE: Myanmar. Kachin State: Myitkyina in Mara Nantan forest, Kaukkwe Valley, 606 m, Mar. 1912, *E. M. Buchanan 51* (holotype, E!; isotype, E!). Figure 1.

Styrax serrulatus var. *latifolius* Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 37. 1907. TYPE: Myanmar. Mandalay Division: *W. Griffith 3670* (lectotype, designated here, K [loan accession no. H2000/01016-29]!; isotypes, GH!, K [loan accession no. H2000/01016-30]!).

Small trees. Young twigs densely yellow-brown stellate-pubescent; older twigs becoming gray, subglabrous. Petiole 3–4 mm long. Two most proximal leaves on each shoot alternate. Lamina of fertile shoots 6–11 × 4–6 cm, those of sterile shoots to 16 × 11 cm, chartaceous, ovate-oblong; apex slightly acuminate to obtuse, base rounded or broadly cuneate, rarely truncate; adaxially sparsely yellow-gray pubescent with 2- or 3-armed or stellate trichomes; abaxially sparsely to densely yellow-gray stellate-hirsute, the surface visible through the pubescence, the pubescence especially prevalent on veins; margin remotely irregularly serrulate apically; secondary veins 5 or 6 on each side of midvein, adaxially faintly prominent, abaxially prominent; tertiary veins parallel and perpendicular to the secondaries, plane or slightly sunken adaxially, abaxially prominent. Fertile shoots 19–30 cm long, 3- or 4-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences racemose, 2–5 cm long, 3- to 5-flowered, often with 1 or 2(to 4) flowers occurring in the same leaf axil; pseudoterminal inflorescences usually paniculate, sometimes racemose, 9–13 cm long, 10- to 22-flowered, lateral branches 2 to 5, sometimes with 2 or 3 short lateral racemes from the base of inflorescence, rachis and branches densely yellow stellate-pubescent. Pedicel (1–)3–5 mm long, densely yellow stellate-hirsute; bracteoles ca. 3 mm long, linear, usually positioned at the base of pedicels. Flowers 1.3–1.6 cm long. Calyx 4–5.5 × 4–5 mm, cupuliform; adaxially white appressed-pubescent with 2- or 3-armed or stellate trichomes; abaxially densely yellow stellate-hirsute, arms of trichomes averaging ca. 1 mm long, within 1 mm from the margin more sparsely pubescent, somewhat scarious, brown when dry; margin truncate, undulate, or irregularly lobed, the teeth minute and not contiguous if present. Corolla 0.8–1.1 cm long, white, tube ca. 3 mm long, glabrous, lobes 5, 9–13 × 3–4.5 mm, 2.4–3.0 × as long as wide, lanceolate or ovate-lanceolate, stellate-tomentose on both sides. Stamens 10; filaments 3–4 mm long, slightly flexuous at middle, distally attenuate, densely white to yellow stellate-hirsute throughout, arms of the trichomes predominantly pointing upward; anthers 5–7 mm long, wider than distal portion of filament; connectives (at least proximally) densely stellate-hirsute. Style densely white stellate-hirsute nearly throughout, thinning distally; stigma 0.4–0.7 mm wide, punctiform. Fruit unknown.

Illustrations. None previously published.

Phenology. Flowering: February–April. Fruiting: unknown.

Distribution. Myanmar (Kachin State, Mandalay Division, and Sagaing Division); Figure 2.

Habitat. In valley forests; 600–1500 m.

Styrax buchananii is geographically isolated in Myanmar from all other *Styrax* species except *S. hookeri* and *S. japonicus,* from which it can easily be distinguished by its longer inflorescences and more numerous flowers. It has been only rarely collected throughout its range and is only known from flowering collections.

This species was first described by Perkins (1907) as a variety of *Styrax serrulatus.* Perkins suggested that it likely represented a new species, but the available material at the time of description (*Griffith 3670* from the Ruby Mines District (Smith, 1920) of Mandalay Division, Myanmar) was inadequate for a proper assessment of species status. Similarly, Smith (1920), in describing *S. buchananii* based solely on *Buchanan 51,* was uncertain whether *S. serrulatus* var. *latifolius* Perkins should be listed as a synonym. With the benefit of additional material available to us, we affirm that *Griffith 3670* and *Buchanan 51* represent one and the same species, based on the combination of imbricate corolla aestivation, pubescent style, many-flowered inflorescences, and other key characters present in these collections. Furthermore, the general locality of *Griffith 3670* lies in the vicinity of all other collections of *S. buchananii.* Smith (1920) described *S. buchananii* with valvate corolla aestivation, but our observations confirm that all specimens cited in the protologue of *S. buchananii* have distinctly imbricate aestivation.

Several shared characteristics, e.g., the two most proximal leaves on each shoot of the current year subopposite to opposite and stellate pubescence covering nearly the whole length of the filaments and styles, suggest that *Styrax buchananii* is a close relative of *S. odoratissimus. Styrax buchananii* can be distinguished from *S. odoratissimus* by the shorter petioles (3–4 vs. 5–12 mm), the typically paniculate (vs. typically racemose) inflorescences, corol-

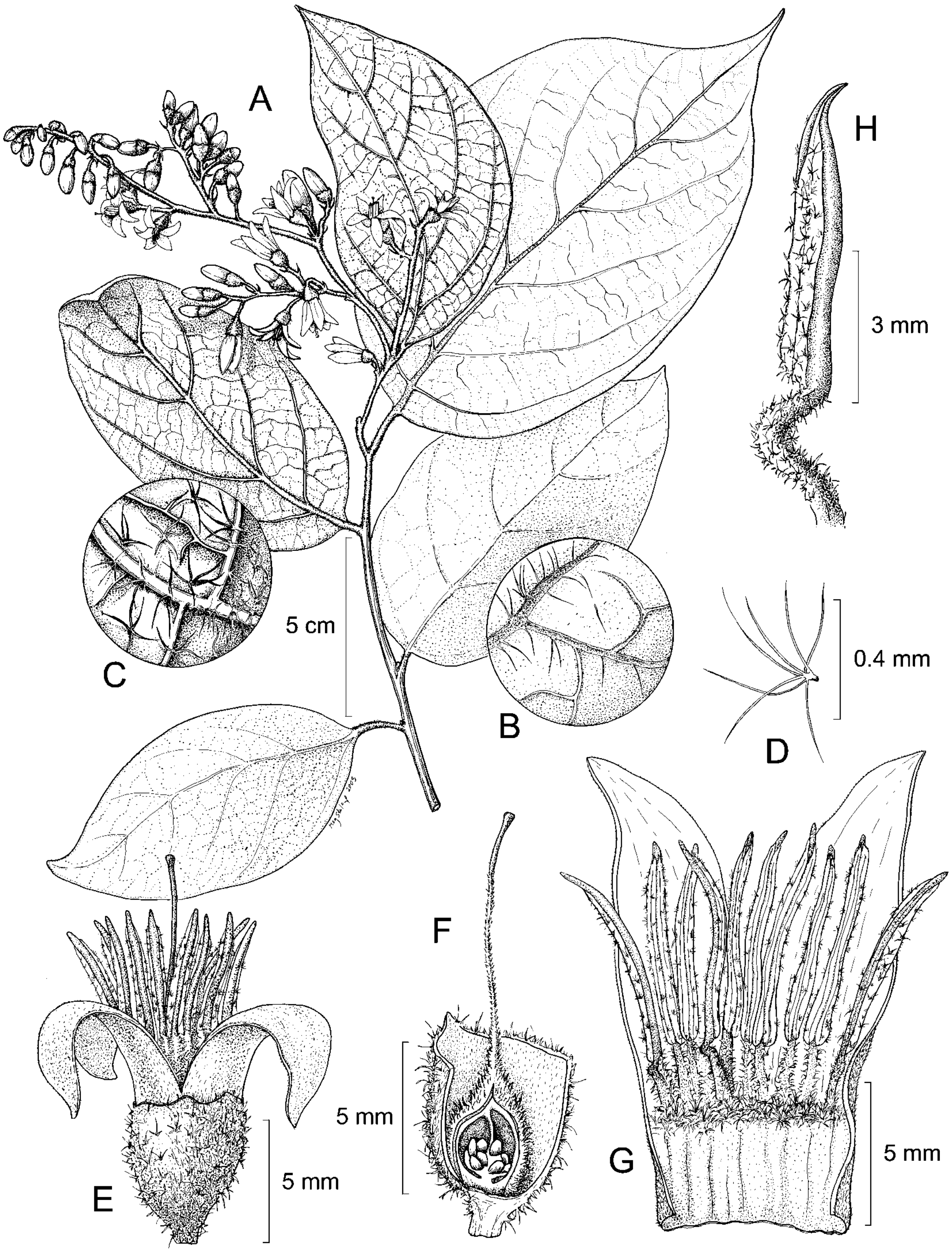

Figure 1. *Styrax buchananii.* —A. Flowering branch. —B. Leaf surface, adaxial view. —C. Leaf surface, abaxial view. —D. Stellate trichome from the abaxial side of the leaf. —E. Flower. —F. Calyx + gynoecium, median long-section. —G. Part of corolla + androecium, opened. —H. Stamen, lateral view. Based on *Kingdon-Ward 20550.*

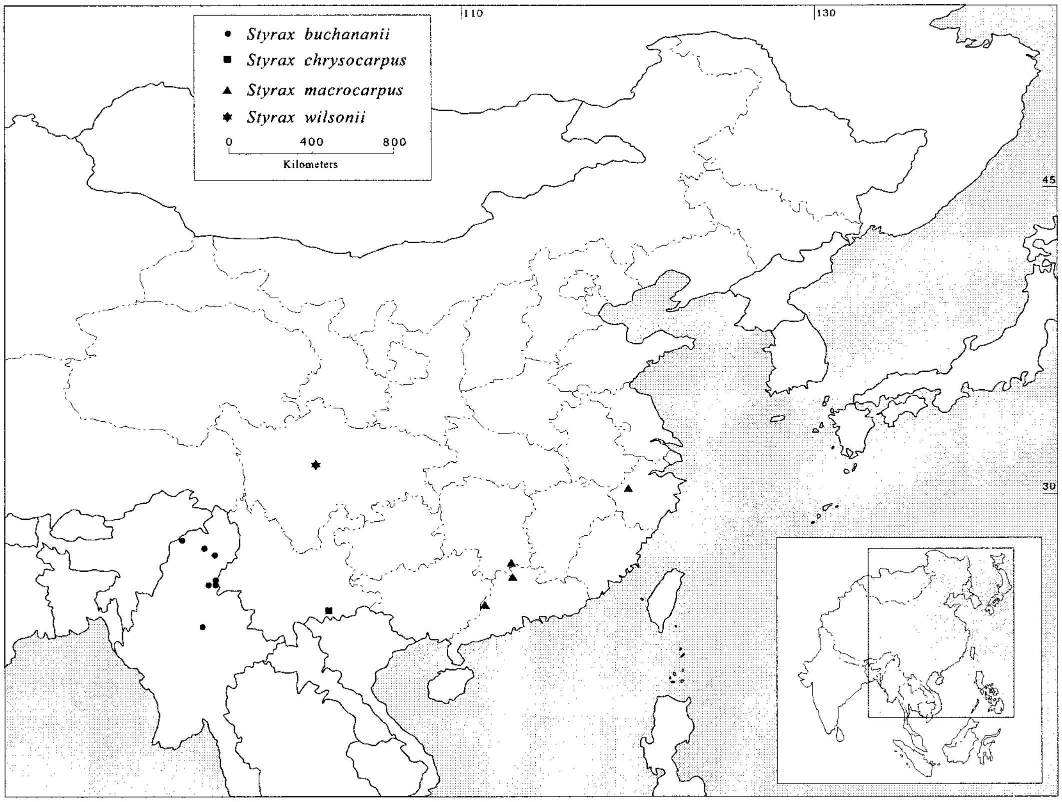

Figure 2. Geographic distribution of *Styrax buchananii*, *S. chrysocarpus*, *S. macrocarpus*, and *S. wilsonii*.

la lobes 2.4–3 (vs. 1.7–2.2) times as long as wide, and a distribution (northern Myanmar) that is outside the known range of *S. odoratissimus* (China).

Another probable close relative of *Styrax buchananii* is *S. chrysocarpus,* a species whose range in Yunnan Province is located between those of *S. buchananii* and *S. odoratissimus*. *Styrax chrysocarpus* has a leaf texture and average petiole length (5–8 mm) similar to the other two species, and in all three the two most proximal leaves are alternate. The differences between *S. buchananii* and *S. chrysocarpus* are not entirely clear in the absence of data from flowers (*S. chrysocarpus*) and fruits (*S. buchananii*).

The protologue of *Styrax serrulatus* var. *latifolius* cites both B and K specimens of *Griffith 3670*. The B specimen has presumably been destroyed, and thus we have chosen one of the two K specimens that we have seen as a lectotype. Neither sheet harbors Perkins's annotation, but that with loan accession number H2000/01016–29 has better flowering material. Thus, we have chosen this sheet as the lectotype.

Additional specimens examined. MYANMAR. **Kachin State:** Myitkyina at Lamaing, *E. M. Buchanan 21* (E); Japing Valley, *G. Forrest 21083* (E); Myitkyina Dist., Sumprabum Subdivision, Hlingnan, *Y. Hla & C. Koko 3746* (K); Bhamo Dist., road to Sinlumkaba, *J. H. Lace 5737* (E); Bhamo Dist., *J. H. Lace 5774* (E, K); Sumpra Bum, *F. F. K. Ward 20550* (A, BM). **Sagaing Division:** Patkoi Range, border betw. Burma [Myanmar] & India, *R. S. Hole 17* (K).

2. Styrax chrysocarpus H. L. Li, J. Arnold Arbor. 25: 312. 1944. TYPE: China. Yunnan: Pingbian Miaozu Zizhixian, 1400 m, 9 July 1934, *H. T. Tsai 62505* (holotype, A!; isotypes, IBSC!, KUN!, PE!).

Trees 7–20 m tall. Young twigs yellow-brown stellate-tomentose; older twigs dark brown, subglabrous. Petiole 5–8 mm long. Two most proximal leaves on each shoot alternate. Lamina 10–20 × 5.5–11 cm, chartaceous, oblong-ovate to oblong; apex acute to slightly acuminate; base rounded or broadly cuneate; adaxially sparsely yellow-gray stellate-pubescent, arms of the trichomes up to 0.2–0.3 mm long, the pubescence especially prevalent on veins; abaxially densely yellow-gray stellate-hirsute, arms of the trichomes up to 0.5–0.6 mm long, the surface remaining visible through the pubescence; margin subentire or remotely irregular serrulate apically; secondary veins 5 to 10 on each side of midvein, adaxially plane or slightly sunken, abaxially prominent; tertiary veins reticulate, abaxially prominent. Flowers unknown. Infructescences arising from shoots of the current growing season, apparently racemose, 1- to 5-fruited, yellow stellate-tomentose. Fruiting pedicel 4–5 mm long. Fruiting calyx 5–6 × 10–15 mm, cupuliform, red-brown, the margin not appressed to the fruit, glabrous adaxially, densely stellate-pubescent abaxially; margin irregularly 5- or 6-crenately lobed, lobes ca. 4 × 10 mm. Fruit 1.6–1.8 × 1.0–1.2 cm, ovoid, apex shortly pointed, apparently indehiscent; pericarp dry, 0.3–0.5 mm thick, outside golden yellow stellate-tomentose, inside densely pale yellow appressed-pubescent. Seeds dull dark-brown, ovoid, smooth, glabrous.

Illustrations. C. Y. Wu, Fl. Yunnan. 3: 430, pl. 123 (1–3). 1983.

Phenology. Flowering: unknown. Fruiting: July.

Distribution. China (Yunnan); Figure 2.

Habitat. In ravine forests; 1400–1500 m.

Vernacular names. Huang-guo-an-xi-xiang (Hwang & Qi, 1985), Mao-guo-an-xi-xiang (Wu, 1983).

Styrax chrysocarpus is known with certainty only from Pingbian Miaozu Zizhixian, southeastern Yunnan Province. This species is easily distinguished from other members of *Styrax* by its golden yellow fruit and densely pale yellow pubescent inner surface of the pericarp. A sterile specimen with aphid galls collected between 1550 and 1650 m elevation in Yongshan Xian, extreme northeastern Yunnan Province (*H. T. Tsai 51156*), might be this species. Its leaves, however, are glabrous, unlike the densely hirsute upper and lower surfaces of those in the type. More fertile material from the vicinity of Tsai's localities is highly desirable to better understand the taxonomy of this species.

Although only fruits are available for comparison, careful analysis of vegetative and fruit morphology suggests that *Styrax chrysocarpus* is most likely allied to other deciduous species with imbricate aestivation. Sterile specimens of *S. chrysocarpus* are similar to some specimens of *S. buchananii* and *S. odoratissimus* in the relatively large leaves, the lower laminar surface somewhat rough to the touch, and the strictly alternate leaves. *Styrax chrysocarpus* consistently differs from *S. odoratissimus,* however, in its shorter infructescences and larger yellow stellate-hirsute fruit, and differs from most specimens of *S. odoratissimus* in its glabrous seeds (differences between *S. chrysocarpus* and *S. buchananii* are addressed in the discussion under *S. buchananii*). Furthermore, none of the distributional ranges of these three species overlap: *S. buchananii* is restricted to Myanmar, *S. odoratissimus* to southeastern China, and *S. chrysocarpus* to eastern Yunnan Province, China.

Additional specimens examined. CHINA. **Yunnan:** Pingbian Miaozu Zizhixian, *H. T. Tsai 62522* (A, KUN, PE), *62766* (A, IBSC, KUN, PE); Yongshan Xian, *H. T. Tsai 51156* (A, BO).

3. Styrax curvirostratus (B. Svengsuksa) Y. L. Huang & P. W. Fritsch, stat. nov. Basionym: *Styrax agrestis* var. *curvirostratus* B. Svengsuksa, Flore du Cambodge du Laos et du Viêtnam 26: 176. 1992. TYPE: Vietnam. Lam Dong: Massif du Lang Bian, between Dankia and Dangle, 1000–1200 m, 25 Oct. 1930, *E. Poilane 18626* (holotype, P not seen; isotype, P!). Figure 3.

Trees to 15(–20) m tall. Young twigs dark gray or brown, sparsely gray-white stellate-pubescent; older twigs dark brown or nigrescent, glabrescent. Petiole 7–10 mm long. Two most proximal leaves on each shoot alternate. Lamina 6–11 × 3–4.5 cm, thick-chartaceous, elliptic to oblong; apex short-acuminate to acuminate; base rounded to broadly cuneate; glabrous, rarely abaxially sparsely short-stellate-pubescent on the veins and vein axils, both surfaces glossy, bright green when dry; margin entire or slightly undulate, rarely irregularly denticulate; secondary veins 5 or 6 on each side of midvein; tertiary and quaternary veins irregularly reticulate and conspicuously raised on both sides. Fertile shoots 8–15 cm long, 3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1(2)-flowered; pseudoterminal inflorescences 1- or 2-flowered or racemose, 1–3 cm long, (1- to)3- to 5-flowered, rachis yellow stellate-tomentose. Pedicel 8–9 mm long, yellow stellate-tomentose; bracteoles 1–2 mm long, linear, positioned at various places along the pedicel but mostly near the base. Flowers 1.6–1.8 cm long. Calyx 6–7 × 6.5–7 mm, cupuliform; adaxially densely white appressed-stellate-pubescent, proximally becoming sparsely pubescent with white 2- or 3-armed trichomes; abaxially densely yellow stellate-pubescent, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin truncate, undulate, or irregularly lobed, the teeth minute, not contiguous if present. Corolla 0.9–1.2 cm long, white, tube ca. 4 mm long, slightly pubescent, glabrous

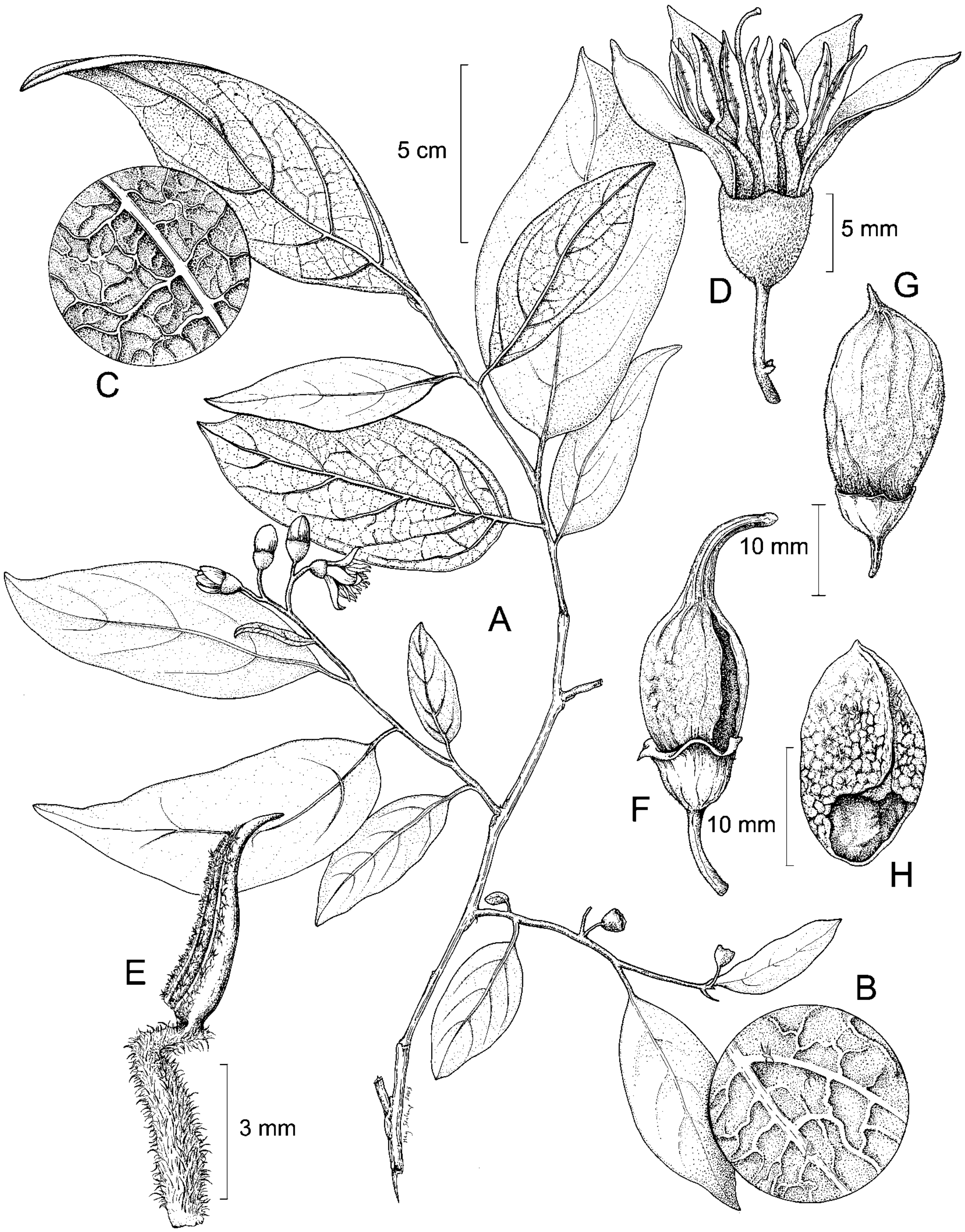

Figure 3. *Styrax curvirostratus.* —A. Flowering branch. —B. Leaf surface, adaxial view. —C. Leaf surface, abaxial view. —D. Flower. —E. Stamen, lateral view. —F, G. Fruit. —H. Seed. A–E based on *Averyanov et al. VH 4544*; F based on *Poilane 18626*; G, H based on *Chevalier 38674.*

proximally, lobes 5, 12–13 × 5–6 mm, obovate to obovate-elliptic, apex acute, densely pale yellow stellate-hirsute on both sides. Stamens 10; filaments 4–5 mm long, strongly flexuous at middle, of equal width throughout, densely white stellate-villous throughout, arms pointing upward; anthers 5–6 mm long, as wide as or narrower than distal portion of filament; connectives glabrous. Style densely

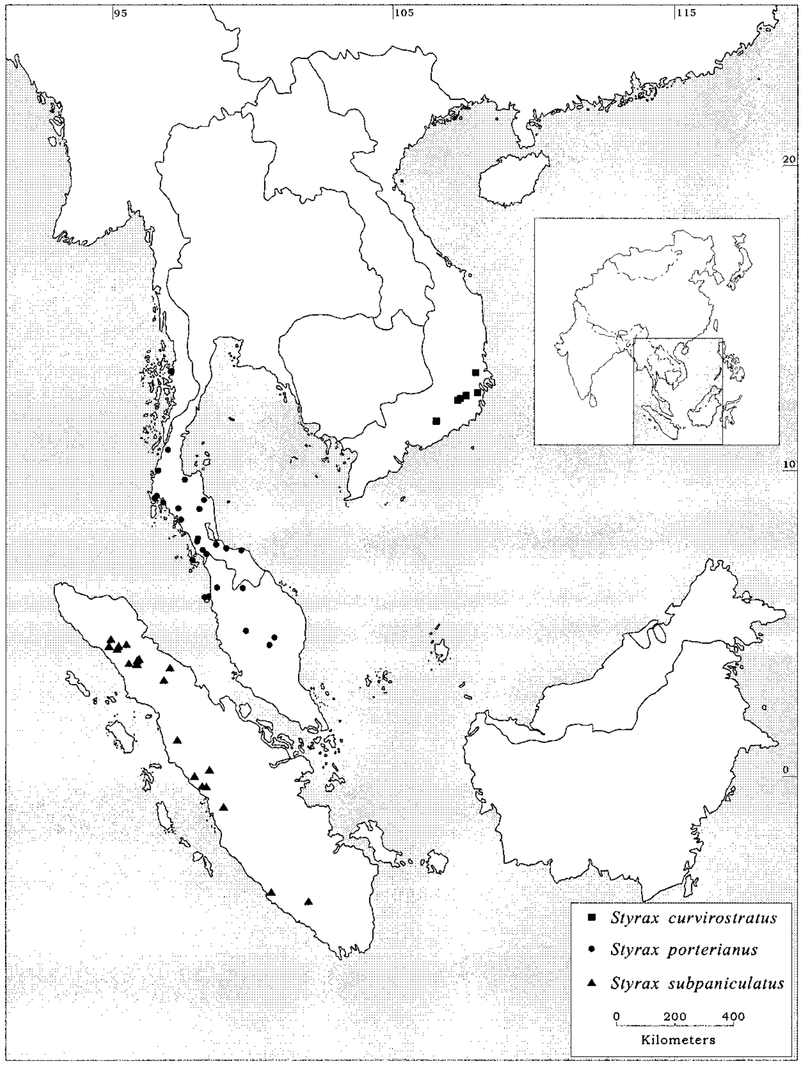

Figure 4. Geographic distribution of *Styrax curvirostratus, S. porterianus,* and *S. subpaniculatus.*

white stellate-pubescent throughout, conspicuously 3-angular and 3-furrowed, stigma ca. 0.2 mm wide, capitate. Fruit 2.0–2.5 × 1.1–1.5 cm, cylindrical to oblique-ovoid, apex usually rostrate, rostrum up to 2 cm long, dehiscent; pericarp dry, 0.3–0.4 mm thick, outside irregularly longitudinally striate, gray stellate-tomentose, inside minutely downy-pubescent. Seeds brown, ellipsoid, smooth to finely reticulate-fissured, glabrous or occasionally appressed-stellate-pubescent.

Illustrations. B. Svengsuksa & J. E. Vidal, *Flore du Cambodge du Laos et du Viêtnam* 26: 173, pl. 31 (10–11). 1992 (as *S. agrestis* var. *curvirostratus*).

Phenology. Flowering: April, May. Fruiting: January, September, October.

Distribution. Vietnam (Binh Thuan, Dac Lac, Khanh Hoa, and Lam Dong); Figure 4.

Habitat. In primary, closed, evergreen broad-leaved mountain forests; 1000–1700 m.

Styrax curvirostratus is the only imbricate species of *Styrax* documented in southern Vietnam; it is thus easily distinguishable from the several sympatric members of the genus with valvate aestivation. This species is distinguished from most other imbricate species by its long-rostrate, cylindrical to oblique-ovoid fruit 2–2.5 × 1.1–1.5 cm. The other species in this group with at least some rostrate-fruited individuals are *S. hookeri, S. odoratissimus,* and *S. tonkinensis*. These species possess smaller (less than 2 cm long) fruit with a shorter rostrum (typically less than 2 mm long) than *S. curvirostratus*. Features of *S. curvirostratus* shared with *S. odoratissimus* and *S. buchananii* are the (1) densely white stellate-villous filaments and style, (2) truncate, undulate, or irregularly lobed calyx with noncontiguous teeth if present, and (3) sparsely pubescent or subglabrous calyx within 1 mm of the margin, without larger stiff stellate trichomes. In addition, *S. curvirostratus* and *S. buchananii* have longer anthers (5–6 mm long) than the other imbricate species of series *Cyrta*. *Styrax curvirostratus* occasionally possesses appressed-stellate-pubescent seeds, as in most individuals of *S. odoratissimus*. *Styrax curvirostratus* can be distinguished from both *S. buchananii* and *S. odoratissimus* by its larger calyx (6–7 × 6.5–7 mm), longer flowers (1.6–1.8 cm long), and longer, wider, straight (vs. flexuous) filaments of equal width throughout (vs. narrowing distally). Moreover, *S. curvirostratus* is easily separable from *S. buchananii* by its shorter inflorescences (1–3 cm vs. 9–13 cm long) with fewer (1 to 5 vs. 10 to 22) flowers. *Styrax curvirostratus* can be recognized when sterile by the reticulate and distinctly raised quaternary veins on both surfaces of the lamina.

This species was first collected in Lam Dong in 1930 (*Poilane 18626*), but was left undescribed until Svengsuksa and Vidal (1992) assigned this specimen and several others to *Styrax agrestis* (Lour.) G. Don, a species with valvate corolla aestivation, as a new variety. The variety was based on fruiting specimens only, as no flowering material was available. *Styrax curvirostratus* typically shares with *S. agrestis* a rostrate fruit, which separates these two species from most others in Southeast Asia, and the ranges of the two taxa overlap, with that of *S. agrestis* the larger. It was thus not unreasonable for Svengsuksa and Vidal to place *S. curvirostratus* as a variety of *S. agrestis*, distinguishable in fruit from the typical variety by its shorter petioles and pedicels, usually glabrous seeds, and more conspicuous rostrum. Recently, however, a flowering specimen (*Averyanov et al. VH4544*) was collected at a locality within the range of *S. curvirostratus* that matches the vegetative morphology of this taxon in every respect, yet has distinctly imbricate, rather than valvate, corolla aestivation and fewer flowers per inflorescence than *S. agrestis* (1 to 5 vs. 5 to 10). These features clearly distinguish *S. curvirostratus* from *S. agrestis*. Furthermore, the conspicuously reticulate quaternaries on both surfaces, long anthers, and other features listed above distinguish this taxon from all other species of *Styrax*, thus warranting its recognition at the species level.

Additional specimens examined. VIETNAM. **Dac Lac:** N de Ninh-Hoa, Massif de la Mère et l'Enfant, *E. Poilane 6578* (P). **Khanh Hoa:** Phu Khanh, Massif du Hon Ba, *A. J. B. Chevalier 38674* (P). **Lam Dong:** Lac Duong, Mun. Da Chay, 35 km NE from Dalat City, *L. Averyanov et al. VH4544* (AAU, CAS); Massif du Haut Donai, betw. Dankia & Dangle, *E. Poilane 23457* (P), *23569* (P).

4. Styrax hemsleyanus Diels, Bot. Jahrb. Syst. 29: 530. 1900 [as *S.* "*Hemsleyana*"]. TYPE: China. Sichuan: Wushan Xian, 1885–1888, *A. Henry 5676* (lectotype, designated here, A!; isotypes, BM!, GH!, IBSC[2]!).

Styrax hemsleyanus var. *griseus* Rehder, in Sarg., Pl. Wilson. 1: 291. 1912. TYPE: China. Hubei: Changyang Tujiazu Zizhixian, 1212–1818 m [1300–2000 m, protologue], June 1907, *E. H. Wilson 2574a* (holotype, A!; isotypes, BM!, E!, K!).

Styrax huanus Rehder, J. Arnold Arbor. 11: 167. 1930 [as *S.* "*Huanus*"]. TYPE: China. Sichuan: Nanchuan Shi, 2273–2576 m [1200–2700 m, protologue], 3 June 1928, *W. P. Fang 1376* (holotype, A!; isotypes, BM!, DS!, E!, IBSC!, K!, PE[4]!).

Trees to 12 m tall. Young twigs densely gray-brown stellate-pubescent; older twigs dark brown, glabrescent. Petioles 10–24 mm long, neither dilated nor covering the bud. Two most proximal leaves on each shoot subopposite to opposite. Lamina 7–15 × 4–9 mm, chartaceous, elliptic or ovate-elliptic, rarely broadly elliptic, gray-green to dark green when dry; apex acute to short-acuminate; base oblique and subrounded to broadly cuneate, often shortly decurrent into petiole; adaxially sparsely gray-white pubescent with 2- or 3-armed or stellate trichomes; abaxially glabrous or sparsely to densely gray-white stellate-pubescent or -tomentose; margin subentire or serrate apically; secondary veins 7 to 10 on each side of midvein, tertiary veins subparallel, abaxially prominent. Fertile shoots (12–)15–20 cm long, 2- to 4-leaved. Inflorescences arising from shoots of the current growing season, racemose; lateral racemes 4- to 9(to 13)-flowered, often with solitary flowers occurring in the same leaf axil; pseudoterminal racemes 1(to 3), 8–15 cm long, 8- to 15(to 20)-flowered, rachis yellow-brown stellate-tomentose. Pedicel 2–4 mm long, yellow-brown stellate-tomentose; bracteoles 2–3 mm long, subulate or linear, positioned at the base or middle part of pedicel, sometimes those toward the base of the inflorescence leaf-like. Flowers 1.5–2.5 cm long. Calyx 4–8 × 3–6 mm, narrow-cupuliform; adaxially densely appressed-pubescent, proximally becoming sparsely pubescent with white

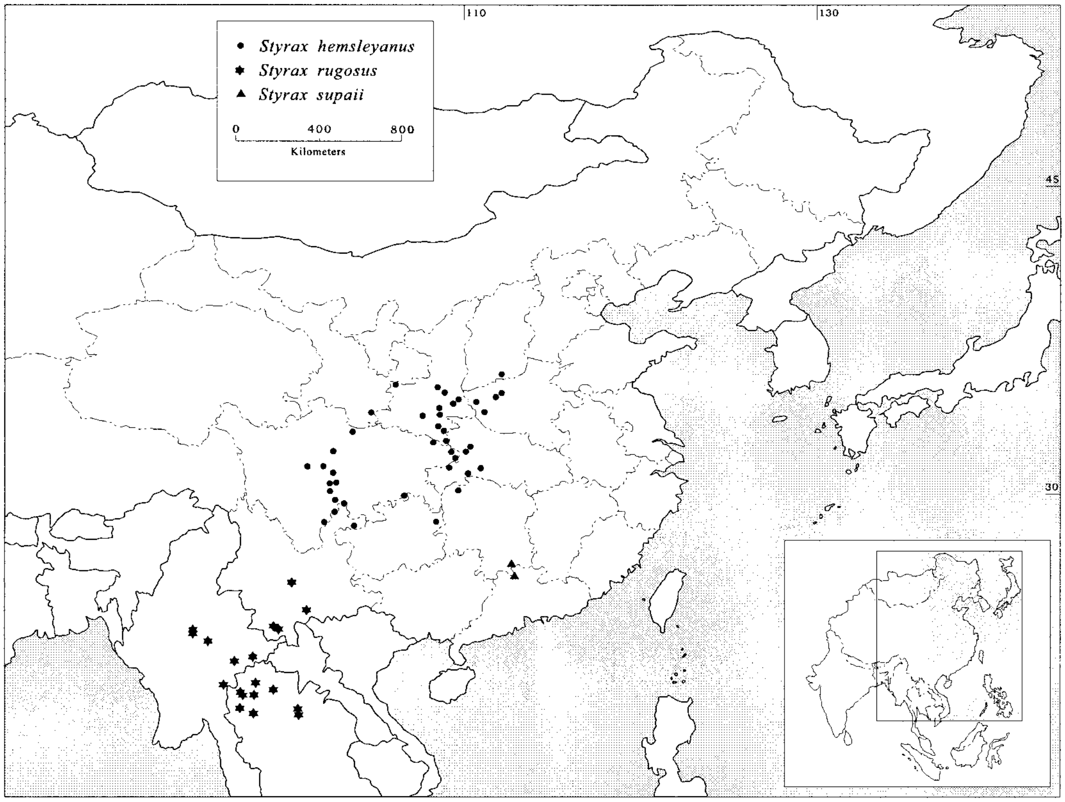

Figure 5. Geographic distribution of *Styrax hemsleyanus*, *S. rugosus*, and *S. supaii*.

2- or 3-armed trichomes; abaxially yellow-brown stellate-tomentose throughout, often also with various amounts of larger dark brown stiff stellate trichomes especially proximally; margin with 5 unevenly distributed teeth 2–3 mm long, unequal, subulate or deltoid, contiguous, densely pubescent on both sides. Corolla 1.1–1.7 cm long, white, tube 4–5 mm long, glabrous, lobes 5 or 6, 12–15 × 4.5–5 mm, elliptic to elliptic-obovate, apex acute, adaxially subglabrous except distally, abaxially pale yellow stellate-tomentose. Stamens 10 to 12; filaments 6–7 mm long, straight, relatively broad, of equal width throughout, ventrally ± pubescent proximally, glabrous distally; anthers 3.5–4.5 mm long, wider than distal portion of filament; connective subglabrous. Style glabrous; stigma 0.4–0.5 mm wide, capitate. Fruit 0.8–1.3(–1.6) × 1–1.5 cm, globose to ovoid, apex apiculate, dehiscent; pericarp dry, 0.1–0.4 mm thick, outside slightly longitudinally rugose, yellow-brown to gray-yellow stellate-tomentose, inside sparsely appressed-stellate-pubescent or glabrous. Seeds brown, ovoid, nearly smooth, sometimes irregularly rugose or finely reticulate-fissured, glabrous.

Illustrations. Prain, Bot. Mag. 136: t. 8339. 1910; W. P. Fang, Ic. Pl. Omei. 1(1): t. 47. 1942; Anonymous, Ic. Cormophyt. Sin. 3: 337, fig. 4628. 1974; F. T. Tai & T. C. Pan in W. P. Fang, Fl. Sichuan. 1: 418, fig. 161. 1981 (as *S. huanus*); ibid.: 426, pl. 165. 1981; C. Y. Wu, Fl. Yunnan. 3: 430, pl. 123 (4–7). 1983; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1602, fig. 797. 1985 (as *S. huanus*); ibid.: 1619, fig. 812. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 85, pl. 28 (6–7). 1987 (as *S. huanus*); ibid.: 96, pl. 32 (8–14). 1987; W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 896, pl. 472 (1–6). 1990; S. Y. Wang in B. Z. Ding, Fl. Henan 3: 230, fig. 1775 (5–8). 1997; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 197, fig. 197 (6–7). 2000 (as *S. huanus*); ibid.: 201, fig. 201 (8–14). 2000.

Phenology. Flowering: March, May, June. Fruiting: February, May–September.

Distribution. China (Gansu, Guizhou, Henan, Hubei, Hunan, Shaanxi, Shanxi, Sichuan, and Yunnan); Figure 5.

Habitat. In relatively mesic, semi-open mixed forests on mountain slopes and in ravines; 700–2700 m.

Vernacular names. He-si-li-ye-mo-li (China, Sichuan; Fang, 1942), Hui-mao-lao-gua-ling (China, Yunnan; Wu, 1983), Jin-shan-an-xi-xiang (China, Sichuan; Tai & Pan, 1981), Lao-gua-ling (China, Henan; Anonymous, 1974), Ma-lin-guang (China, Shaanxi; *J. Q. Xiang 6053*), Mai-pao (China, Sichuan; *J. H. Xiong et al. 91179*), Mo-pao (China, Henan; Anonymous, 1974), Nan-chuan-an-xi-xiang (China, Sichuan; Tai & Pan, 1981).

Styrax hemsleyanus is a relatively common species, occurring mainly in the mountains at middle elevations surrounding the Sichuan basin. It can be distinguished from sympatric imbricate-flowered species by the combination of the subopposite to opposite two most proximal leaves on each shoot, long, multi-flowered pseudoterminal racemes, and prominent calyx teeth. *Styrax hemsleyanus* is similar in these respects only to *S. obassia,* a species ranging farther to the east, but these two species are easily distinguished even when sterile by the petiole base of the larger leaves, which covers the bud in *S. obassia* but not in *S. hemsleyanus.* Furthermore, the rachis of the raceme is pubescent in *S. hemsleyanus* and glabrous or nearly so in *S. obassia.*

Rehder (1930) described *Styrax huanus* from Nanchuan Shi in southeastern Sichuan, considering the white-stellate tomentum on the lower laminar surface and the longer and glabrous stamen filaments as distinguishing it from *S. hemsleyanus.* Rehder (1912) also differentiated *S. hemsleyanus* var. *griseus* from the typical variety by the presence and quantity of pubescence on the lower laminar surface. Hwang (1987) treated this variety as a synonym of *S. hemsleyanus,* but agreed with Rehder on the status of *S. huanus,* citing the leaf pubescence difference and the type of trichomes as justification for recognizing two species.

Contrarily, we have found no basis for recognizing any taxon other than a single species among these entities. Filament length and pubescence quantity exhibit a complete range of variation among individuals of *Styrax hemsleyanus* and *S. huanus.* Pubescent-leaved individuals of *S. hemsleyanus* have a combined distribution largely overlapping that of glabrous-leaved individuals, occurring from Yangcheng Xian, Shanxi Province (e.g., *T. W. Liu & Z. F. Zeng 226, 245, 1285,* and *1393*), at the extreme northern edge of the species' range, south to Zhenxiong Xian, Yunnan Province (*Exp. NE Yunnan 1161*), whereas glabrous-leaved individuals occur throughout the range of the group. The pubescent-leaved individuals also exhibit no obvious elevation or habit distinctions, and seem to occur sporadically, often near collection localities of glabrous-leaved individuals. Furthermore, several collections show an intermediate amount of pubescence between the types of *S. hemsleyanus* and *S. huanus,* even among collections from the vicinity of the type locality of *S. huanus.*

In addition to the density of pubescence on the abaxial leaf surface, Hwang (1980) considered *Styrax huanus* distinguishable from *S. hemsleyanus* based on leaf trichome types. We consider this difference to reflect merely the length of the stellate trichomes. The arms of the trichomes on the abaxial surface of the leaves are small (averaging ca. 0.15 mm long) in *S. huanus* versus some specimens of *S. hemsleyanus* (averaging ca. 0.5 mm long), but careful inspection of all collections of this group available to us indicates that arm length varies continuously.

In the protologue of *Styrax hemsleyanus,* three collections (syntypes) are cited by Diels: *A. Henry 5676, A. Henry 6895,* and *B. von Rosthorn 2078.* Because Diels's herbarium was B, we assume that the material on which the description of *S. hemsleyanus* was based has been destroyed. We therefore have designated the A specimen of *A. Henry 5676* as the lectotype because duplicates are apparently more widely distributed than those of the other two syntypes (in particular, *A. Henry 5676* is represented by two duplicates in a Chinese herbarium (IBSC), unlike either of the other syntypes), and only the *A. Henry 5676* specimen from A possesses collection locality data. There is no evidence of Diels's handwriting on the type material that we have examined.

Selected specimens examined. CHINA. **Gansu:** Kang Xian, Yang-ba-xiang, *Z. Y. Zhang 16612* (PE). **Guizhou:** Jiangkou Xian, Niu-wei-he, *Exp. Fan-jin-shan & Feng-huang-shan 402110* (IBSC, PE). **Henan:** Lushi Xian, Lao-chun-shan, *K. M. Liou 4421* (K, PE); Song Xian, Sang-shi, Long-di-man, *Henan Forestry Dept. 1074* (PE); Xixia Xian, *T. L. Dai 1296* (PE); Yichuan Xian, *Pu-cha-biao-ben 20304* (PE). **Hubei:** Changyang Tujiazu Zizhixian, *T. P. Wang 11480* (KUN); Jianshi Xian, Hua-guo-ping, *W. B. Lin 91* (PE); Shennongjia Linqu, Shen-nong-jia Forest Dist., *Sino-Amer. Bot. Exp. (1980) 1133* (A, E, KUN, UC); Wufeng Tujiazu Zizhixian, *H. J. Li 5861* (IBSC, PE). **Hunan:** Sangzhi Xian, Ba-mao-xi-xiang, Tian-ping-shan, *B. G. Li 750286* (PE). **Shaanxi:** Ankang Xian, Tao-he-gong-she, *P. Y. Li 7778* (KUN); Fuping Xian, He-tao-ping, *K. T. Fu 4849* (PE); Long Xian, Shen-si, Lung-chow, Kuan-shan, *collector unknown 2346* (A); Luonan Xian, *P. C. Kuo 342* (KUN); Ningshan Xian, Jiang-kou-xiang, *J. Q. Xing 6053* (IBK); Pingli Xian, Da-dang-fu-shan, *P. Y. Li 1380* (KUN); Shangzhou Shi, Long-ju-xiang, *Z. C. Zhu et al. 34* (IBSC); Weinan Shi, Qing-gang-ping, Zhu-zi-gou, *Z. B. Wang 15652* (IBSC, KUN, PE); Zhashui Xian, Qing-ling-shan., *collector unknown 66*

(PE); Zhen'an Xian, *X. X. Hou et al. 601* (IBSC); Zhenping Xian, Zhong-hong-xiang, *P. Y. Li 2209* (KUN). **Shanxi:** Yangcheng Xian, Sang-lin, Shu-pi-gou, Gan-qi-tong, *T. W. Liu & Z. B. Zeng 1285* (CAS). **Sichuan:** Chengkou Xian, Hou-ping-xiang, *T. L. Dai 105634* (KUN, PE); Ebian Yizu Zizhixian, Wa-shan, *E. H. Wilson 2578* (A, BM, E); Emeishan Shi, E-mei-shan, *W. P. Fang 14826* (A, KUN); Dujiangyan Shi, *W. P. Fang 2225* (A, E, IBSC, K); Jinyang Xian, *Sichuan Economic Pl. Exp. 2483* (PE); Kangding Xian, near Ta-chien-lu, *A. E. Pratt 406* (BM, K); Leibo Xian, *Z. T. Guan 411* (IBSC); Mabian Yizu Zizhixian, *F. T. Wang 23029* (A, KUN, PE); Nanchuan Shi, *W. P. Fang 1401* (A, E, IBSC, K, PE); Pingshan Xian, *Sichuan Economic Pl. Exp. 1206* (PE); Pingwu Xian, *H. L. Tsiang 19* (IBSC); Tianquan Xian, *F. C. Tai & C. M. Teng 4215* (KUN); Wushan Xian, *A. Henry 5676A* (IBSC); Wuxi Xian, Hong-chi-ba, *G. H. Yang 59375* (IBSC, KUN, PE). **Yunnan:** Zhenxiong Xian, Hua-shan, *Exp. NE Yunnan 1161* (KUN).

5. Styrax hookeri C. B. Clarke, in Hook. f., Fl. Brit. India 3: 589. 1882 [as *S.* "*Hookeri*"]. TYPE: India. Sikkim: 1828–2121 m, *J. D. Hooker s.n.* (lectotype, designated here, K! [loan accession no. H2000/01016, fl branch]; isotypes, BM!, BR!, C!, K!, L[2]!).

Styrax macranthus Perkins, Bot. Jahrb. Syst. 31: 487. 1902. TYPE: China. Yunnan: Lüchun Xian, region of Feng Chun Ling, 2121 m [2000 m, protologue], S of the Red River, *A. Henry 10644* (lectotype, designated here, K!; isotypes, A!, BM!, E[2]!, IBSC[2]!, MO!, PE!).

Styrax caudatus Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 74. 1907. TYPE: India. Assam: Mt. Sillet (Perkins, 1907), *Wallich 4400B* (holotype, B destroyed; isotype, K not seen; digital image of K specimen!).

Styrax hookeri var. *yunnanensis* Perkins, Repert. Spec. Nov. Regni Veg. 8: 84. 1910. TYPE: China. Yunnan: Zhaotong Shi, Hay Tse Pa, 6 July 1906, *F. Ducloux 4626* (lectotype, designated here, P!).

Styrax roseus Dunn, Bull. Misc. Inform. Kew 1911: 273. 1911. TYPE: China. Sichuan: Ebian Yizu Zizhixian, Mt. Wu [from protologue], Wa-shan (Rehder, 1912), 2424 m [2600 m, protologue], July 1903, *E. H. Wilson 4065* (holotype, K!; isotypes, A[2]!, BM!, IBSC!).

Styrax perkinsiae Rehder, in Sarg., Pl. Wilson. 1: 292. 1912 [as *S.* "*Perkinsiae*"]. TYPE: China. Sichuan: Ebian Yizu Zizhixian, Wa-shan, 1828–2121 m [2000 m, protologue], 1908, *E. H. Wilson 2576* (lectotype, designated here, A [July 1908]!; isotypes, BM!, E!).

Styrax shweliensis W. W. Sm., Notes Roy. Bot. Gard. Edinburgh 12: 236. 1920. TYPE: China. Yunnan: Tengchong Xian, Tengyueh-Shweli divide; 25°N, 2121 m, May 1913, *G. Forrest 9869* (holotype, E!; isotypes, A!, K!).

Shrubs or trees to 10 m tall. Young twigs gray-brown stellate-puberulent; older twigs purplish brown, glabrescent. Petiole (2.5–)4–6(–10) mm long. Two most proximal leaves on each shoot subopposite to opposite. Lamina 6–8(–12) × 3–4(–6) cm but sometimes distalmost lamina smaller, chartaceous to thick-chartaceous, oblong, lance-ovate, or narrowly elliptic, often dark green when dry; apex acuminate to caudate, rarely acute, slightly oblique; base often slightly oblique, rounded to broadly cuneate, rarely shallowly cordate or narrowly cuneate; adaxially sparsely gray-white (rarely yellow-brown) pubescent with simple or 2- or 3-armed to stellate trichomes, glabrescent; abaxially glabrous or sparsely to gray-white stellate-pubescent to -tomentose, pubescence especially prevalent on the veins and especially longer on the axils of the midvein and secondary veins; margin glandular-serrulate and slightly revolute; secondary veins 5 to 7 on each side of midvein, tertiary veins subparallel and perpendicular to the secondary nerves, together with the quaternaries adaxially plane and abaxially prominent. Fertile shoots 4–12 cm long, 3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- to 3-flowered; pseudoterminal inflorescences 1- or 2-flowered or racemose, 2–4 cm long, (1)2- or 3(to 6)-flowered, rachis yellow stellate-tomentose. Pedicel (2–)5–8(–13) mm long, yellow-brown stellate-tomentose; bracteoles 3–4 mm long, subulate or linear, positioned at various places along the pedicel but mostly near the middle, more rarely near the base, sometimes those toward the base of the inflorescence leaf-like. Flowers (1.3–)1.5–2.5 cm long. Calyx (3.5–)5–7(–9) × 4–6(–11) mm, cupuliform; adaxially covered with 2- or 3-armed to stellate appressed trichomes, becoming glabrous proximally; abaxially yellow stellate-tomentose, often also with various amounts of larger scattered gray, tawny, orange, or brown stiff stellate trichomes especially proximally, within 1 mm from the margin more sparsely pubescent, somewhat scarious, brown when dry; margin truncate, undulate, irregularly 2- or 3-lobed, or toothed, the teeth if present minute to 1 mm, deltoid to linear-deltoid, not contiguous. Corolla (0.8–)1.2–1.9 cm long, white or pink, tube 3–4 mm long, glabrous, lobes 4(5), (11–)12–18 × (4–)5–10 mm, obovate to obovate-elliptic, adaxially appressed-stellate-pubescent or nearly glabrous, abaxially densely pale yellow stellate-pubescent. Stamens 8 to 10; filaments 5–7 mm long, straight, distally attenuate, densely pubescent proximally, glabrous or sparsely stellate-pubescent distally, pubescence especially prevalent along the margin; anthers 3–5 mm long, wider than distal portion of filament; connectives glabrous. Style usually ± white stellate-pubescent throughout, occasionally subglabrous; stigma 0.2–0.5 mm wide, capitate. Fruit (1.0–)1.5–2 × (0.7–)1–1.5 cm, subglobose or ovoid, apex acute, occasionally short-rostrate, dehiscent; pericarp dry, 0.1–0.3(–0.6) mm thick, rarely up to 0.9 mm thick, outside at least

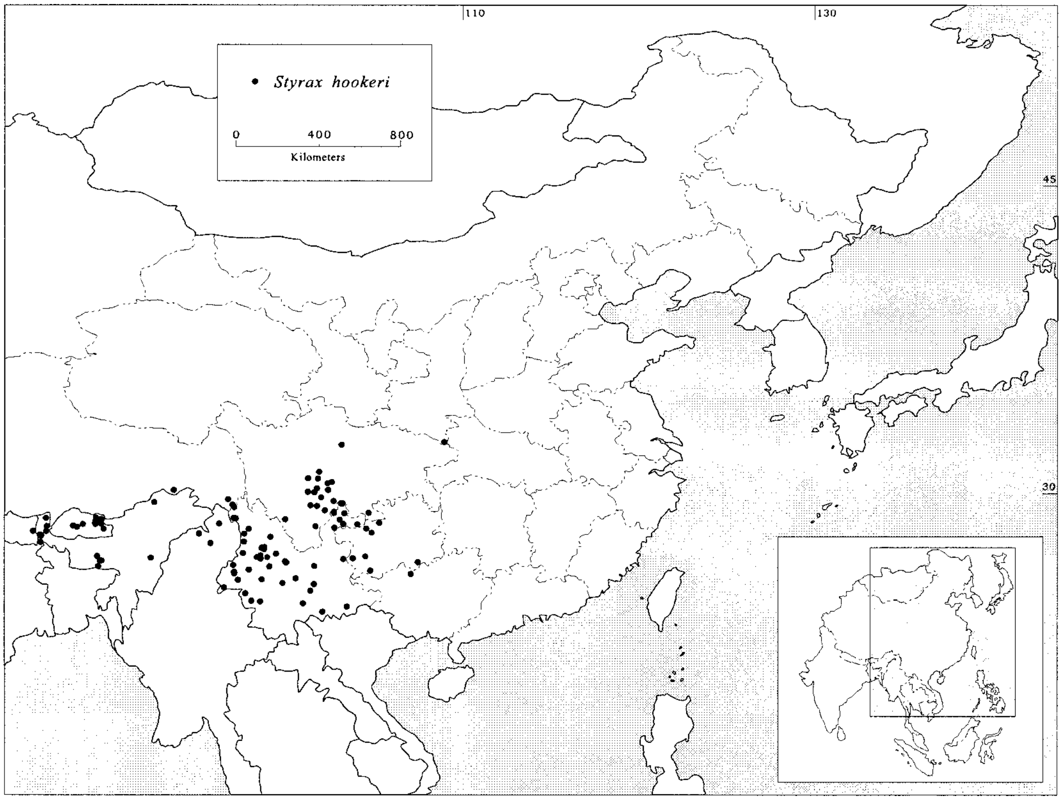

Figure 6. Geographic distribution of *Styrax hookeri.*

faintly longitudinally striate and ± rugose when dry, gray-yellow stellate-tomentose, inside glabrous. Seeds beige or brown, subglobose or ovoid, smooth, glabrous.

Illustrations. Anonymous, Ic. Cormophyt. Sin. 3: 337, fig. 4627 (as *S. roseus*). 1974; F. T. Tai & T. C. Pan in W. P. Fang, Fl. Sichuan. 1: 428, fig. 166. 1981 (as *S. roseus*); C. Y. Wu, Fl. Yunnan. 3: 424, pl. 120 (7–10). 1983 (as *S. perkinsiae*); ibid.: 433, pl. 124. 1983 (as *S. roseus* and *S. macranthus*); S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1607, fig. 802. 1985 (as *S. perkinsiae*); ibid.: 1621, fig. 814. 1985 (as *S. macranthus*); ibid.: 1622, fig. 815. 1985 (as *S. roseus*); T. L. Ming in C. Y. Wu, Fl. Xizang. 3: 869, fig. 335 (1–3). 1986; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 90, pl. 30 (6–9). 1987 (as *S. perkinsiae*); ibid.: 101, pl. 34 (6–10). 1987 (as *S. macranthus*); ibid.: 103, pl. 35 (1–6). 1987 (as *S. roseus*); W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 894, pl. 471 (7–12). 1990 (as *S. roseus*); D. G. Long in Grierson & D. G. Long, Fl. Bhutan 2(2): 577, fig. 58(e–g). 1999 (as *S. grandiflorus*); Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 199, fig. 199 (6–9). 2000 (as *S. perkinsiae*); ibid.: 203, fig. 203 (7–12). 2000 (as *S. macranthus*); ibid.: 204, pl. 204 (1–7). 2000 (as *S. roseus*).

Phenology. Flowering: March–September. Fruiting: April–November, January.

Distribution. Bhutan (Lhun Tshi, Tashigang, Tongsa, and Wangdi Phodrang), China (Guangxi, Guizhou, Sichuan, Xizang, and Yunnan), India (Arunachal Pradesh, Assam, Meghalaya, Nagaland, Sikkim, and West Bengal), Myanmar (Kachin State), and Nepal (Mechi); Figure 6.

Habitat. In a variety of open or semi-open wooded habitats and forest edges on mountain slopes; 730–3352 m.

Vernacular names. Da-rui-ye-mo-li (China, Sichuan; *Exp. E-shan 155*), Fen-hua-an-xi-xiang (Hwang, 1980), Fen-hua-ye-mo-li (SW China; Anonymous, 1974), Feng-chun-an-xi-xiang (Hwang, 1980), Lü-chun-an-xi-xiang (Hwang, 1987), Mai-mu (China, Sichuan; *Z. T. Guan 8448*), Mao-zhu-ye-mo-li (China, Yunnan; Wu, 1983), Qing-ye-dong-gua-shu (China, Guangxi; *S. Q. Chen 14376*), Rui-li-an-xi-xiang (Hwang, 1980), Rui-li-ye-mo-li (China, Yunnan; Anonymous, 1974), Shui-liang-zi (China, Sichuan; *Sichuan Economic Pl.*

Exp. 169), Trali Shing (Bhutan; *F. Ludlow et al. 18802*), Wa-shan-an-xi-xiang (Tai & Pan, 1981), Xi-shu-mai-mu (China, Sichuan; *Z. T. Guan 8197*), Yun-nan-ye-mol-li (China, Yunnan; Wu, 1983).

Styrax hookeri is a common and widespread species, occurring at relatively high elevations from eastern Nepal along the Himalayas through Assam, India, and extending into southwestern China. It is apparently most common in Yunnan Province.

Our treatment of *Styrax hookeri* differs from those of Perkins (1907) and Hwang (1987). We agree with Perkins (1907) that this species is not an extreme variant of *S. serrulatus*, as suggested by Clarke (1882). Perkins (1907) treated *S. hookeri* narrowly by simultaneously recognizing *S. caudatus* Perkins (Assam, India) and *S. macranthus* Perkins (southern and eastern Yunnan Province). Later, Perkins (1910) distinguished *S. hookeri* var. *yunnanensis* Perkins from the typical variety by its smaller and narrower leaves. This collection is geographically isolated (northeastern Yunnan Province) from variety *hookeri* sensu Perkins (Himalayas). Three new species of *Styrax* from the provinces of Yunnan and Sichuan (*S. perkinsiae* Rehder, *S. roseus* Dunn, and *S. shweliensis* W. W. Sm.) were subsequently described by various authors. Their types, along with that of *S. macranthus,* are centrally located between the apparently disjunct localities of *S. hookeri* sensu Perkins (i.e., its known range as of 1910). These species were delimited primarily by poorly defended features of the leaves, inflorescence, and calyx. Hwang (1987) considered *S. macranthus, S. perkinsiae,* and *S. roseus* to be separate species, and treated *S. shweliensis* as a synonym of *S. perkinsiae.* Because Hwang's treatment was in a regional flora of China, Hwang apparently did not examine collections of *S. hookeri* sensu Perkins from outside China. She may also not have had access to the type of *S. hookeri* var. *yunnanensis,* which she cited as a synonym of *S. grandiflorus* Griff. (= *S. japonicus*). *Styrax hookeri* var. *yunnanensis* has a shorter pedicel and a calyx with scattered orange stiff trichomes, among other features, that clearly distinguish it from *S. japonicus* and establish its placement within our concept of *S. hookeri.*

Access to many more collections than were available to either Perkins or Hwang has allowed us to reassess these high-elevation taxa. We interpret the highly overlapping range of morphological variation exhibited by this group as warranting only a single widely distributed species. Although trichome type and the amount of pubescence on various parts of the plants are diagnostic characters in the delimitation of some *Styrax* species, these features are highly variable in *S. hookeri.* The vestiture on the inner surface of the corolla lobes and the lower laminar surface consists of either long or short stellate trichomes, or else is lacking; that on the lower laminar surface can be sparse to dense. The styles are usually densely stellate-pubescent nearly throughout, at least proximally, but in some specimens from northeastern Yunnan Province and the Khasi Hills in Meghalaya, India, they are glabrous. Several other characters are also variable across the range of *S. hookeri* (e.g., leaf shape and size, flower and fruit size, petiole and pedicel length). We detect no gaps in character state variation, either associated with gaps in other characters or with geographic or ecophysiographic variables, for use in recognizing any of the synonyms of *S. hookeri.*

Although recognizing species segregates of *Styrax hookeri* is not warranted, there has clearly been some regional isolation among populations of this species resulting in geographically correlated (although not discontinuous) morphological trends. For example, individuals with the most densely pubescent abaxial leaf surfaces occur in western and central Yunnan Province, with consistently glabrous or sparsely pubescent populations to the west in the Himalayas. Some collections from the edge of the species' range exhibit slightly atypical features. The collections from the Khasi Hills (e.g., *C. B. Clarke 43631A*) have leaf margins with more numerous and prominent serrations than are typical in the species. This variation, however, also appears in other areas scattered throughout the species' range. Perhaps the most distinctive morphological variants within *S. hookeri* come from the provinces of Guangxi and Guizhou (e.g., *X. H. Song 272* and *907, C. Wang 41180, S. Q. Chen 14376,* and *Exp. Guizhou 6836*). These specimens have narrowly lance-elliptic, subcoriaceous leaves and/or relatively small fruits ca. 7 mm wide. We have opted against the formal recognition of these populations of *S. hookeri* at an infraspecific level because many specimens collected from areas scattered throughout the range of the species exhibit intermediacy in these characters.

Differences between *Styrax hookeri* and all sympatric imbricate-flowered species of *Styrax* are addressed in the discussions under *S. buchananii, S. hemsleyanus, S. limprichtii, S. odoratissimus,* and *S. rugosus.* Flowering individuals of *S. hookeri* with a pedicel length approaching that of *S. japonicus* can usually be distinguished by the presence of scattered orange or brown stiff long-stellate trichomes on the calyx. Fruiting individuals are more easily distinguished, because the pericarp of *S. hookeri* is usually thinner and at least faintly longitudinally striate (vs. irregularly rugose), and the seeds are smooth (vs. usually finely reticulate-fissured or irregularly rugose). Sterile specimens of *S. hookeri* can be distinguished from those of *S. japonicus* by a tendency toward elliptical leaves with acuminate to caudate apices and subparallel tertiary veins that are conspicuously raised only abaxially, versus a tendency toward subrhombic leaves with acute to slightly acuminate apices and narrowly reticulate tertiary veins that are conspicuously raised on both surfaces. These characters, however, exhibit some degree of overlap.

The closest putative relatives of *Styrax hookeri* (i.e., *S. limprichtii, S. rugosus,* and *S. wilsonii*) occur at relatively high elevations scattered throughout southwestern China and northern Myanmar. These species share with *S. hookeri* a typically subglobose or ovoid fruit rounded or apiculate at the apex and with usually at least a faintly longitudinally striate pericarp, seed surfaces that are smooth or irregularly rugose, and a calyx with usually various scattered orange or brown stiff stellate trichomes larger than those of the base tomentum. *Styrax hookeri* is easily distinguished from them, however, by the characters in couplet 14 of the key. The presence of abaxially glabrous or sparsely pubescent leaves and a densely pubescent style can often be used to distinguish *S. hookeri* from these species as well but are not as reliable.

According to the protologue, the type locality of *Styrax roseus* is Mt. Wu ("Wushan" in Pinyin) in Sichuan Province. Hwang (1987) interpreted this as Wushan Xian in eastern Sichuan, but the label on the type indicates that the locality is in western Sichuan. Rehder (1912) confirmed that the western Sichuan locality is correct by citing the type locality as Mt. Wa (a variant of Mt. Wu) in western Sichuan, also the type locality of *S. perkinsiae.*

The type material of *Styrax hookeri* at K consists of two sheets of *J. D. Hooker s.n.* from Sikkim, both of which possess flowering and fruiting branches. Individuals of *S. hookeri* flower and fruit at different times of the year within the same geographic region, indicating that these branches were collected on different dates. Thus, we interpret the material as consisting of four syntypes. This conclusion is supported by the writing "2 Styrax Sikkim" followed by Hooker's initials in his handwriting on each of the sheets, implying that there are two *Styrax* specimens on each sheet. There appears to be no basis for a decision regarding selection of the most appropriate specimen as the lectotype other than the condition of the material and the fact that one of the sheets possesses what is likely to be a field label in Hooker's handwriting. Thus, we have lectotypified on the largest branch with the most reproductive material on this sheet. In further support of our selection, this branch is also the largest and most floriferous of those on either sheet.

The holotype of *Styrax macranthus* at B is presumably destroyed. It is possible that Perkins only saw the specimen at B; none of the other sheets of *A. Henry 10644* that we have examined possess Perkins's annotation label, and no herbarium other than B is mentioned in either Perkins (1902) or Perkins (1907) to confirm Perkins's examination of additional material. On this basis, we have chosen the K specimen of *A. Henry 10644* as the lectotype, because Kew was the location of Henry's headquarters.

The holotype of *Styrax hookeri* var. *yunnanensis* at B is presumably destroyed. We have designated the specimen at P as the lectotype because it is the only duplicate specimen that we have seen, and it possesses Perkins's annotation.

The protologue of *Styrax perkinsiae* cites *E. H. Wilson 2576* as the type. There are two sheets of this number at A, but each has a different date. The word "holotype" is written on one of the sheets, but this is apparently not in Rehder's handwriting and it is not clear who wrote it. As such, these sheets must be considered syntypes. We have chosen the specimen that was collected in July 1908 as the lectotype because the material has more flowers for examination than the 17 September 1908 collection. Also, because the word "holotype" is written on this sheet, designating this sheet as the lectotype will avoid the risk of undue confusion.

Selected specimens examined. BHUTAN. **Lhun Tshi:** Dengchung, Khoma Chu, *F. Ludlow et al. 18802* (A, BM). **Tashigang:** Yonpu La, near Tashigong Dzong, *F. Ludlow et al. 12593* (BM, E). **Tongsa:** 1 km S of Tongsa, *A. J. C. Grierson & D. G. Long 1107* (E, K). **Wangdi Phodrang:** Mara Chu Valley, *F. Ludlow & G. Sherriff 3133* (BM, E). CHINA. **Guangxi:** Nandan Xian, *C. Wang 41180* (A, CAS, IBSC); Rongshui Miaozu Zizhixian, San-fang-xiang, Jiu-wan-da-shan, *S. Q. Chen 14376* (IBK, IBSC, KUN, PE). **Guizhou:** Anlong Xian, Long-shan-xiang, *Exp. Guizhou 4737* (KUN); Bijie Shi, Sheng-ji-xiang, *P. H. Yu 240* (KUN); Dafang Xian, Bai-na-qu, Jiu-long-shan, *Exp. Bi-jie 847* (PE); Libo Xian, Dong-ting, *X. H. Song 272* (K, MO); Panxian Tequ, Ba-da-shan, *Exp. An-shun 890* (KUN); Qinglong Xian, *Exp. S Guizhou 205* (KUN); Xingyi Shi, Ding-xiao-xiang, *Exp. Guizhou 6836* (IBSC, PE). **Sichuan:** Baoxing Xian, Er-lang-shan, Tuan-niu-ping, *Nan-shui-bei-diao-dui 1871* (PE); Ebian Yizu Zizhixian, *T. T. Yü 853* (A, IBSC, PE); Emeishan Shi, E-mei-shan, *G. H. Yang 55400* (IBSC, KUN, PE); Ganluo Xian, Hai-tang, *Sichuan Economic Pl. Exp. 4086* (KUN, PE); Hanyuan Xian, *Y. X. Zhao 511* (PE); Leibo Xian, Ma-hu-xiang, Tang-jia-shan, *Sichuan Economic Pl. Exp. 315* (KUN, PE); Mabian Yizu Zizhixian, Da-zhu-bao, Shan-mu-gang, *T. H. Tu 5494* (PE); Mao Xian, *S. K. Wu 840104* (KUN); Meigu Xian, Shu-dang-xiang, *Sichuan Economic*

Pl. Exp. 13556 (PE); Mianning Xian, from Guanling Xian to Muli Xian, *S. K. Wu 2204* (KUN); Muli Zangzu Zizhixian, from Guanling Xian to Muli Xian, *S. K. Wu 2203* (KUN, PE); Pingshan Xian, Wu-zhi-shan, *Q. S. Zhao 504* (PE); Puge Xian, You-jia-ping, *Z. T. Guan 8059* (PE); Shimian Xian, *C. C. Hsieh 39893* (IBSC, PE); Tianquan Xian, Er-lang-shan, *H. L. Tsiang 35129* (IBSC, PE); Xuyong Xian, Yi-shui-qu, *Sichuan Economic Pl. Exp. 351* (KUN); Yanyuan Xian, Ni-ba-shan, *Q. S. Zhao 309* (PE); Yuexi Xian, Bao-an, Da-long-tang, *Sichuan Economic Pl. Exp. 3813* (PE). **Xizang (Tibet):** Motuo Xian, Han-mi, Duo-xiong, Qu-lan, *B. S. Li & S. Z. Cheng 5062* (PE). **Yunnan:** Baoshan Shi, San-dao-qiao, *China-USSR team 6268* (IBSC, PE); Binchuan Xian, Ji-zhu-shan, *S. Y. Bao 4* (KUN); Daguan Xian, Lian-he, Tang-jia-shan, *B. S. Sun 676* (IBSC, KUN, PE); Dali Shi, He-yang, Cang-shan, *R. C. Ching 22673* (KUN, PE[2]); Eryuan Xian, N end of Cang-shan, *Sino-British Exp. Cang-shan 850* (A, E, K, KUN); Eshan Yizu Zizhixian, Huang-cao-ling, *Exp. E-shan 88155* (KUN); Fengqing Xian, Shun-ning, Wu-mu-lung, *T. T. Yü 16624* (A, E, KUN, PE); Fugong Xian, Fenquan, *Exp. Qinghai & Xizang 7245* (KUN); Fumin Xian, Djiunienping, *H. F. Handel-Mazzetti 6119* (A, E); Fuyuan Xian, Shi-ba-lian-shan, Xiao-nao-chang, *Exp. Hong-shui-he 2356* (KUN); Gengma Daizu Wazu Zizhixian, Xi-shan, *China-USSR team 5570* (IBSC, PE); Gongshan Dulongzu Nuzu Zizhixian, from Gong-shan to Du-long, Da-ba-di, Gao-li-gong-shan, *P. Y. Mao 427* (KUN, PE); Jingdong Yizu Zizhixian, Feng-kua-shan, *M. K. Li 3493* (IBSC, KUN); Lanping Baizu Pumizu Zizhixian, Bing-zhong, Luo-he, *X. F. Deng 791361* (KUN); Lijiang Naxizu Zizhixian, Lichiang Range, *H. D. McLaren L100A* (BM); Longling Xian, Salwin-Kiukiang divide, *T. T. Yü 20294* (A, E, PE); Lüchun Xian, Feng-chun-ling, S of Red River, *A. Henry 10644* (A, BM, E[2], IBSC[2], K, MO, PE); Lushui Xian, from Ya-kou to Pian-ma, *S. K. Wu 8478* (KUN); Ruili Shi, Luckoag-Salween divide, *G. Forrest 18249* (A, E, K); Shuangbai Xian, Shuang-bai-si-qu, Bai-zhu-shan, *W. C. Yin 490* (IBSC, KUN[2], PE); Shuangjiang Lahuzu Wazu Bulangzu Daizu Zizhixian, Tai-ping-xiang, *J. S. Xing 832* (IBSC, KUN, PE); Suijiang Xian, Luo-han-ping, *B. S. Sun 359* (IBSC, PE); Tengchong Xian, Lang-ya-shan, *D. Y. Xia BG58* (KUN); Weishan Yizu Huizu Zizhixian, Wu-liang-shan, Menghwa, *Y. Tsiang 12204* (IBSC); Weixi Lisuzu Zizhixian, Wei-deng-xiang, *Exp. Qinghai & Xizang 6603* (KUN); Wenshan Xian, Lao-jun-shan, *K. M. Feng 22401* (IBSC, KUN); Yangbi Yizu Zizhixian, Shi-zhong-xiang, Shang-chang, *Sino-British Exp. Cang-shan 269* (A, E, K, KUN); Yanjin Xian, Cheng-feng-shan, *Exp. NE Yunnan (1970s) 1163* (KUN); Yao'an Xian, Tai-ping-xiang, *Y. Chen & B. Bai 562* (KUN); Yiliang Xian, Cao-tian-ma, *Exp. NE Yunnan (1970s) 568* (KUN, PE); Yongping Xian, betw. Sha-yang & Chu-tong, *G. Forrest 21112* (A, BM, E, K, PE[2], UC); Yongshan Xian, *H. T. Tsai 50936* (A, IBSC[2], KUN, PE); Yuanjiang Hanizu Yizu Daizu Zizhixian, Hou-shan, *Qin Lin 770497* (KUN); Yuxi Shi, Gao-lu-shan, *S. K. Wu 57* (KUN); Zhaotong Shi, Tang-lang-pa, *F. Ducloux 4951* (P); Zhenkang Xian, Snow Range, *T. T. Yü 17074* (A, E, KUN, PE); Zhenxiong Xian, Mo-dong, *X. W. Li 173* (IBSC). INDIA. **Arunachal Pradesh:** Pachakshiri Dist., Lalung, *F. Ludlow et al. 3713* (BM, E). **Assam:** *Dr. King's collector s.n.* (BM, L). **Meghalaya:** Khasi Hills, *J. D. Hooker & J. J. Hooker s.n.* (BM, C, E, K, L). **Nagaland:** Naga Hills, Kohima, *W. N. Koelz 25269* (L, UC). **Sikkim**: *J. D. Hooker s.n.* (BM, BR, C, K, L[2]). **West Bengal:** Takdah, Darjeeling, *H. Hara & M. Togashi 2141* (BM, K, KYO). MYANMAR. **Kachin State:** N Triangle (Camp III Tama Bum), *F. F. K. Ward 20990* (A, BM, E). NEPAL. **Mechi:** Salpa Dara, *J. D. A. Stainton 8332* (BM).

6. Styrax japonicus Siebold & Zucc., Fl. Jap. 1: 53. 1837–1838 [as *S.* "*japonicum*"]. *Cyrta japonica* (Siebold & Zucc.) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 279. 1859. TYPE: Japan. Kyushu: Kumamoto Pref., Simabara, *I. Keiske s.n.* (lectotype, designated here, L [accession no. 908240–682] not seen; digital image of lectotype!).

Styrax grandiflorus Griff., Not. Pl. Asiat. 4: 287. 1854 [as *S.* "*grandiflora*"]. TYPE: Myanmar [Sagaing Division] or India [Assam]: Naga Hills, Namtuzceh [Mar. 1837, protologue] and Nempea [19 Mar. 1837, protologue], *W. Griffith 3671* (Perkins, 1907) (holotype, K!; isotype, GH!).

Styrax japonicus var. *calycothrix* Gilg, Bot. Jahrb. Syst. 34 (Beibl. 75): 58. 1904. TYPE: China. Shandong: Qingdao Shi, Lao-shan, Aug. 1907, *O. Nebel s.n.* (holotype, B destroyed).

Styrax cavaleriei H. Lév., Repert. Spec. Nov. Regni Veg. 4: 331. 1907 [as *S.* "*Cavaleriei*"]. TYPE: China. Guizhou: Longli Xian, 7 May 1903, *J. Cavalerie 997* (holotype, E!; isotype, A!).

Styrax bodinieri H. Lév., Repert. Spec. Nov. Regni Veg. 4: 332. 1907 [as *S.* "*Bodinieri*"]. TYPE: China. Guizhou: Guiyang Shi, vicinity of Guiyang, Collège Mt., Apr. 1898, *E. Bodinier 2221* (holotype, E!; photo of holotype, A!).

Styrax duclouxii Perkins, Repert. Spec. Nov. Regni Veg. 8: 83. 1910 [as *S.* "*Duclouxii*"]. TYPE: China. Yunnan: Nanjian Yizu Zizhixian, near Lanngy Tsin, 20 Apr. 1904, *F. Ducloux 2716* (lectotype, designated here, P!).

Styrax touchanensis H. Lév., Repert. Spec. Nov. Regni Veg. 11: 64. 1912. TYPE: China. Guizhou: Dushan Xian, Apr. 1902, *E. Bodinier s.n.* (holotype, E!; isotypes, A!, E!).

Styrax kotoensis Hayata, Icon. Pl. Formos. 5: 121. 1915. *Styrax japonicus* var. *kotoensis* (Hayata) Masam. & Suzuki, Annual Rep. Taihoku Bot. Gard. 3: 65. 1933. TYPE: China. Taiwan: Taitung Xian, Kotosho [Lanyu Island], July 1912, *Y. Tashiro, T. Kawakami & S. Sasaki 44* [collection number not indicated in protologue] (holotype, TI!; isotype, IBSC!).

Styrax jippei-kawamurai Yanagita, J. Soc. Forest. 15: 693. 1933 [as *S.* "*Jippei-Kawamurai*"]. *Styrax japonicus* var. *jippei-kawamurai* (Yanagita) H. Hara, Enum. Sperm. Jap. 1: 111. 1948 [as *S.* "*japonicus* var. *Jippei-Kawamurai*"]. *Styrax japonicus* f. *jippei-kawamurai* (Yanagita) T. Yamazaki, Fl. Japan 3a: 104. 1993 [as *S.* "*japonicus* f. *jippei-kawakamii*"]. TYPE: Japan. Honshu: Shizuoka Pref., O Shima Island, Jan. 1930, *J. Kawamura s.n.* (type material missing).

Styrax japonicus var. *iriomotensis* Masam., Trans. Nat. Hist. Soc. Taiwan 25: 250. 1935. TYPE: Japan. Ryukyu Islands: Okinawa Pref., Iriomote, Oct. 1923, *Ipse s.n.* (holotype, TAI not seen).

Styrax philippinensis Merr. & Quisumb., Philipp. J. Sci. 56: 313. 1935. TYPE: Philippines. Babuyan: Camiguin Island, Mt. Malabsing, 9 Mar. 1930, *G. E. Edaño 79248* (holotype, NY not seen; isotype, L!).

Styrax japonicus var. *zigzag* Koidz., Acta Phytotax. Geobot. 6: 212. 1937. TYPE: Japan. Honshu: Iwate Pref., Rikuchiu, Higashiiwaigun, Ohtsuhomura, *G. Toba s.n.* (holotype, KYO not seen).

Styrax japonicus f. *parviflorus* Y. Kimura, J. Jap. Bot. 16: 59. 1940 [as *S.* "*japonica* f. *parviflora*"]. TYPE: Japan. Kyushu: Fukuoka Pref., Buzen, Tikuzyô-gun, Iwaya-mura, 30 May 1937, *S. Yosioka 23* (holotype, TI!).

Styrax japonicus var. *angustifolius* Koidz., Acta Phytotax. Geobot. 10: 55. 1941 [as *S.* "*japonicum* var. *angustifolia*"]. TYPE: Japan. Honshu: Wakayama Pref., Kii, Koyasan, 1 June 1940, *G. Koidzumi s.n.* (holotype, KYO!; isotype, KYO!).

Styrax japonicus var. *tomentosus* Hatus., J. Jap. Bot. 29: 230. 1954 [as *S.* "*japonicum* var. *tomentosum*"]. *Styrax japonicus* f. *tomentosus* (Hatusima) T. Yamazaki, Fl. Japan 3a: 104. 1993. TYPE: Japan. Ryukyu Islands: Kagoshima Pref., Tokara Islands Group, Nakanoshima Island, Apr. 1936 and 18 Aug. 1933 [1934 from protologue], *T. Naito s.n.* (holotype, FU not seen; photo of holotype, TI!).

Styrax japonicus f. *rubicalyx* Satomi, J. Geobot. 6: 110. 1957. TYPE: Japan. Honshu: Ishikawa Pref., Kaga, Yokotani-pass, Asakawa-mura, Kahoku-gun, 20 July 1952, *N. Satomi s.n.* (holotype, KANA not seen).

Styrax japonicus var. *longipedunculatus* Z. Y. Zhang, Fl. Tsinlingensis 1(4): 395. 1983 [as *S.* "*japonica* var. *longipedunculata*"]. TYPE: China. Gansu: Wen Xian, Bi-kou-zhen, Bi-shan-gou, Quai-miao, 750 m, 31 Aug. 1967, *C. L. Tang 1739* (holotype, HW not seen).

Styrax japonicus var. *nervillosus* Z. Y. Zhang, Fl. Tsinlingensis 1(4): 395. 1983 [as *S.* "*japonica* var. *nervillosa*"]. TYPE: China. Shaanxi: Shiquan Xian, Gangtie-gong-she, Lu-jia-gou, 1010 m, 21 June 1959, *J. Q. Xing 9028* (holotype, HW not seen; isotype, IBK!).

Styrax japonicus f. *pendulus* T. Yamazaki, Fl. Japan 3a: 104. 1993. TYPE: Japan. Honshu: Tokyo Pref., Tokyo, cultivated, 18 Sep. 1991, *T. Yamazaki s.n.* (holotype, TI not seen).

Shrubs or trees to 8(–10) m tall. Young twigs brown, sparsely gray-yellow or pale yellow stellate-pubescent; older twigs gray or nigrescent, glabrescent. Petiole (2–)4–7(–10) mm long. Two most proximal leaves on each shoot (when both present) subopposite to opposite. Lamina 3–11 × 2–5(–7) cm, chartaceous to thick-chartaceous, oblong-elliptic, ovate-elliptic, ovate to ovate-lanceolate, or subrhombic; apex acute to slightly acuminate; base cuneate to broadly cuneate or subrounded, often decurrent into petiole; adaxially sparsely stellate-pubescent when young, especially prevalent on veins, glabrescent; abaxially glabrous except along the vein and the axils of the secondary veins; margin entire to apically remotely serrate; secondary veins 5 to 8 on each side of the midvein, tertiary veins reticulate, conspicuously raised on both surfaces. Fertile shoots 2–9 cm long, 1- to 4-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- or 2-flowered; pseudoterminal inflorescences 2-flowered or racemose, 1–4 cm long, 2- to 5-flowered; rachis glabrous or pubescent. Pedicels (10–)15–50 mm long, the longer pedicels on each twig ≥ 15 mm long, usually equal to or longer than subtended flower, slender, glabrous or stellate-pubescent; bracteoles 3–5 mm long, linear or subulate, usually positioned at the base of pedicels, sometimes those toward the base of the inflorescence leaf-like. Flowers (1.2–)1.5–2.5(–3) cm long. Calyx 4–7 × 3–5 mm, cupuliform to funnelform; adaxially glabrous; abaxially glabrous or sparsely to densely white or gray-yellow stellate-pubescent, if stellate trichomes present, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin with 5 irregularly spaced triangular-ovate teeth 0.5–1 mm long or sometimes less, not contiguous. Corolla (0.8–)1.0–1.6(–2.3) cm long, white, occasionally pink, tube 3–5 mm long, glabrous, lobes 5 or 6, 11–20 × (3–)5–7(–9) mm, ovate, oblong-ovate, obovate, or ovate-lanceolate, apex obtuse, densely appressed-stellate-pubescent on both sides, sometimes sparsely pubescent adaxially. Stamens 10 to 12; filaments 5–6 mm long, straight, slightly broadened proximally and white-villous, distally attenuate and glabrous; anthers 4–5(–10) mm long, wider than distal portion of filament; connective glabrous. Style proximally white stellate-pubescent, distally glabrous; stigma 0.2–0.4 mm wide, punctiform. Fruit 0.8–1.5 × 0.8–1 cm, ovoid or ellipsoid, apex apiculate, usually dehiscent by 3 valves from the base; pericarp dry, 0.4–1.0 mm thick, dry, outside coarsely and irregularly rugose when dry, gray or gray-yellow stellate-tomentose, inside glabrous. Seeds brown, ellipsoid, smooth or finely reticulate-fissured to irregularly rugose, glabrous.

Selected illustrations. Siebold & Zucc., Fl. Jap. 1: t. 23. 1835; Griff., Ic. Pl. Asiat. 4: t. 423. 1854 (as *S. grandiflorus*); Regel, Gartenfl. 17: t. 583. 1868; Hook. f., Bot. Mag. 98: t. 5950. 1872 (as *S. serrulatus* Roxb.); Gard. Chron. ser. 2, 24: fig. 166. 1885; Gartenflora 36: fig. 89. 1887; Dippel, Handb. Laubholzkunde 1: fig. 207. 1889; Gard. Chron. ser. 3, 65: 279, fig. 140. 1919; Addisonia 7: t. 231. 1922; Merr. & Quisumb., Philipp. J. Sci. 56: 316, pl. 1. 1935 (as *S. philippinensis*); W. P. Fang, Ic. Pl. Omei. 1(1): t. 48. 1942; Anonymous, Ic. Cormophyt. Sin. 3: 336, fig. 4625. 1974; F. T. Tai & T. C. Pan in W. P. Fang, Fl. Sichuan. 1: 424, fig. 164. 1981; C. Y. Wu, Fl. Yunnan. 3: 428, pl. 122 (1–10). 1983 (7–10 as *S. grandiflorus*); L. Yang in Y. K. Li, Fl. Guizhou. 2: 541, fig. 231. 1984 (including *S. japonicus* var. *calycothrix*); S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1614, fig. 808.

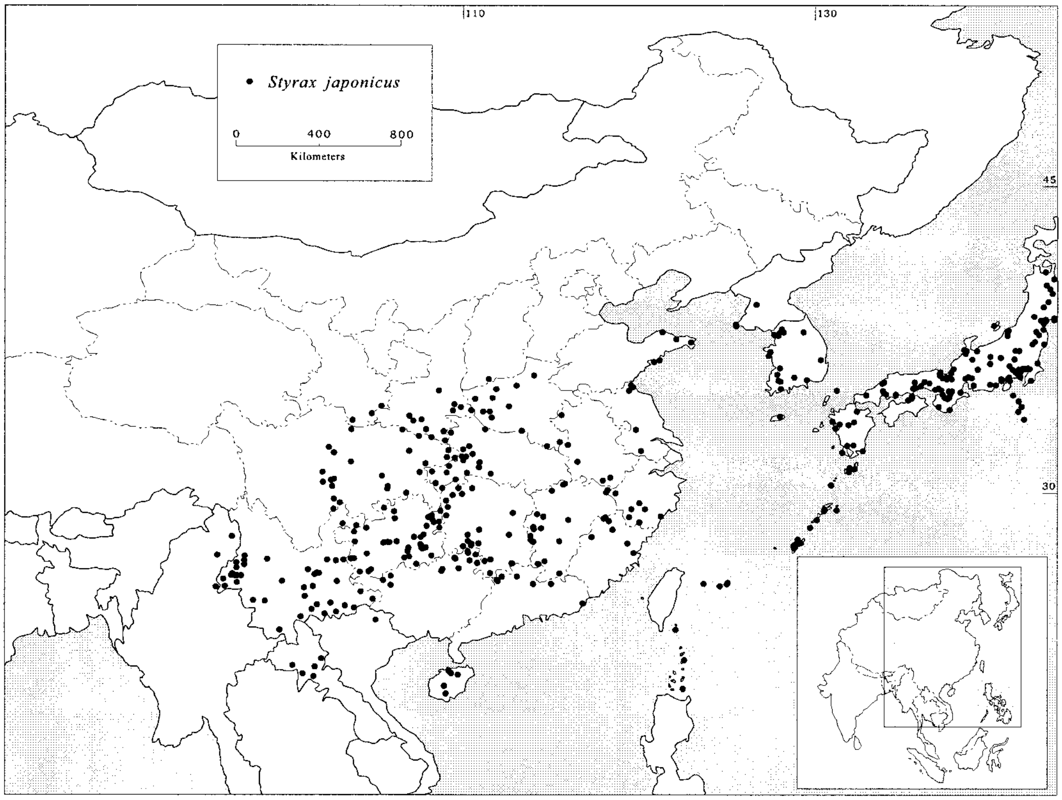

Figure 7. Geographic distribution of *Styrax japonicus.*

1985; ibid.: 1616, fig. 809. 1985 (as *S. grandiflorus*); S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 93, pl. 31. 1987 (1–11; 8–11 as *S. grandiflorus*); S. M. Hwang in F. H. Chen, Fl. Guangdong 1: 387, fig. 419. 1987; ibid.: 387, fig. 420. 1987 (as *S. grandiflorus*); J. Q. Liu in L. G. Lin, Fl. Fujian. 4: 351, fig. 284. 1989; X. M. Liu in X. H. Qian, Fl. Anhui 4: 65, fig. 1769. 1991; S. Y. Wang in B. Z. Ding, Fl. Henan 3: 230, fig. 1775 (1–4). 1997; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 200, fig. 200 (1–11). 2000 (8–11 as *S. grandiflorus*).

Phenology. Flowering: January–October, December. Fruiting: February–November.

Distribution. China (Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hainan, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Shandong, Shanxi, Sichuan, Taiwan, Yunnan, and Zhejiang), Japan (Honshu, Kyushu, Ryukyu Islands, and Shikoku), Laos (Houaphan and Xiangkhoang), Myanmar (Kachin State), North Korea (Pyongyang City), Philippines (Babuyan Islands and Batan Islands), South Korea (Cheju, Inchon City, Kangwon, Kyonggi, North Cholla, North Kyongsang, Seoul City, South Cholla, South Chungchong, and South Kyongsang), and Vietnam (Cao Bang); Figure 7.

Habitat. In a variety of open wooded habitats, in woodlands and forest edges, successional habitats, rarely in dense shade, mostly in mesic microhabitats, such as canyons, draws, ravines, and other riparian situations; 3–2700 m.

Vernacular names. Benigaku-egonoki (Japan; Satomi, 1957), Chun-shu (China, Sichuan; *Sichuan Economic Pl. Exp. 12*), Da-hua-an-xi-xiang (Hwang, 1980), Da-hua-ye-mo-li (Anonymous, 1974), Diao-gong-zai (China, Guangxi; *Z. F. Hunag 15*), Egonoki (Japan; *Shigetaka Suzuki AA1108*), Er-wan-tao (China, Guangdong; *X. Q. Liu 24221*), Ganboku-egonoki (Japan; Koidzumi, 1937), Gou-bi-zi-shu (China, Hunan; *L. H. Liu 1877*), Gou-luan-zi (China, Zhejiang; *Zhejiang Bot. Res. Team 26071*), Hei-Cha-hua (China, Sichuan; Tai & Pan, 1981), Hime-egonoki (Japan; Anonymous, 1940), Hosoba-yegonoki (Japan; Koidzumi, 1941), Hou-feng-teng (Hwang & Qi, 1985), Hui-lu-tui (China, Henan; *collector unknown 334*), Jun-qian-zi (China, Shaanxi; *P. C. Kuo 2180*), Kôtô-egonoki (Japan; Masamune & Suzuki, 1933), Lai-xiang-mei (China, Hunan; *P. C. Tam 63659*), Lan-yu-an-xi-xiang (Li, 1978), Lan-yu-ye-mo-li (Li, 1978), Li-jia (China, Hunan; *P. C. Tam 62899*), Ling-dang-hua (China, Guizhou; *R. B. Jiang 521*), Mao-e-ye-mo-li (Anonymous, 1974), Mo-li-bao (China, Guizhou; *P. C. Tsoong 1032*), Mu-jie-zi (China, Hubei; Hwang & Qi, 1985), Mu-xin-zi (China, Sichuan; *Z. R. Zhang 25145*), Ni-chi-yang (China, Jiangxi; *Jiangxi Normal Univ. 1243*), Padong mao (Laos; *A. F. G. Kerr 20941*), Ru-xiang-shu (China, Yunnan; *Y. Y. Hu 580582*), Sa-ye-shu (China, Hunan; *P. C. Tam 61328*), Sei-ton-kwa (Japan; Siebold, 1835–1841), Shui-dong-gua (China, Guangxi; *Q. H. Lu 2441*), Tsisjano-ki (Japan; Siebold, 1835–1841), Ttaejuk namu (South Korea; *B. R. Yinger et al. 2525*), Yang-huai-zi (China, Yunnan; *L. S. Xie & M. Cai 440*), Yang-jiao-shu (China, Sichuan; *H. F. Zhou 11150*), Yao-bai-he (China, Shaanxi; *J. Q. Xing 9018*), Ye-hua-bei (Hwang, 1987), Ye-mo-li (China, Guizhou; *K. M. Lan 351*), Ye-ping-guo (China, Hubei; *K. R. Liu 142*), Ye-wu-wei-zi-shu (China, Guangxi; *Z. F. Hunag 19*), Ye-xun-zi (China, Henan; *P. C. Kuo 3945*), Zhuang-shu (China, Sichuan; Tai & Pan, 1981).

Probably the most common species of *Styrax* in Asia, *S. japonicus* occurs from Japan to Myanmar south to Vietnam and Laos, with a few outliers in the far northern Philippines and the islands of Lanyu and Hainan, China.

Styrax japonicus is distinguished from all other species of *Styrax* by pedicels that are usually greater than 1.5 cm long (vs. $\leq$ 1.3 cm long) and equal to or longer (vs. shorter) than the subtended flower. Populations on Hainan Island and in several localities in Yunnan Province, China, have the shortest pedicels (as short as 10 mm, although pedicels on specimens from these areas can be found that are at least 15 mm). Also, some specimens of *S. hookeri* in Yunnan Province have unusually long pedicels that approach the length of the shortest pedicels of *S. japonicus*.

This species is highly variable across its range. The pubescence on the calyx consists of a sparse to dense layer of stellate trichomes, or is absent. Like other widespread species of *Styrax* on other continents (e.g., *S. americanus*, *S. glabrescens*, *S. sieberi* Perkins), *S. japonicus* exhibits variation in the size and shape of the flowers, fruits, and especially leaves. Consequently, many varieties and forms of this species have been recognized. Our study, however, does not reveal consistent combinations of characters for use in delimiting infraspecific taxa in *S. japonicus*. For example, the type of *S. japonicus* f. *parviflorus* Y. Kimura has extremely small flowers and leaves, but collections with one or both of these features have also been collected in Yunnan Province (e.g., *H. T. Tsai 55793*). Such a pattern suggests that this extreme represents a sporadic variant rather than a taxonomically significant geographic entity. Other populations in the Ryukyu Islands and Honshu Island, Japan, and Lanyu Island, China, have flowers and leaves that are larger than is typical for the species. These populations have been recognized in some works as varieties *kotoensis* (Hayata) Masam. & Suzuki, *jippei-kawamurai* (Yanagita) H. Hara, and *iriomotensis* Masam. Although the presence of a relatively high percentage of individuals with these features in insular East Asia might prompt the question of why such a pattern exists, the individuals themselves merely possess extremes of completely continuous characters that can be found in other parts of Asia. We therefore do not formally recognize such plants.

Perkins (1907) and Hwang (1987) maintained *Styrax grandiflorus* as a species distinct from *S. japonicus* by its densely pubescent pedicel and calyx and apparently its general range, extending farther south than *S. japonicus*. The leaves of *S. grandiflorus* also tend to be elliptic (vs. subrhombic) with an acute (vs. slightly acuminate) apex, but these features are apparently only weakly correlated with pedicel and calyx pubescence from south to north. Several specimens from Japan, Korea, and Shandong Province, China, possess a densely pubescent calyx, whereas specimens with glabrous pedicels occur sporadically throughout southern China (e.g., Yunnan Province and Hainan Island). Furthermore, many collections exhibit an intermediate amount of pubescence. The pubescent phase also exhibits no obvious elevation or habit distinctions and seems to occur sporadically, often near collection localities of the glabrous phase. A similar pattern of variation in pubescence density unaccompanied by geographic or ecological separation occurs in *S. hemsleyanus* and *S. hookeri*, and those species have not been subdivided in this revision. For the same reason, we have subsumed *S. grandiflorus* under *S. japonicus*.

The distribution of *Styrax japonicus* exhibits some notable patterns. No specimens from mainland China have been collected south of the Nanling Mountains, which extend along the northern border of Guangxi and Guangdong Provinces, but the species has been collected south of the mainland on Hainan Island. Long-distance dispersal is not likely as an explanation for this distribution because the fruit of *S. japonicus* appears not to possess high vagility (Fritsch, 1999). A more likely explanation is that intervening populations have gone extinct due to habitat changes (vicariance).

Hainan was connected with mainland China until the early Quaternary (Chang, 1962), and insofar as Hainan Island is considered part of the Guangdong floristic region (Chang, 1962), the appearance of the Qiongzhou Strait separating Hainan Island from the mainland seems not to have had a major influence on the flora of Hainan. It is also possible that populations have become extirpated through human disturbance.

The disjunct distribution of *Styrax japonicus* between Lanyu Island (Taiwan) and the Philippines is paralleled in about 110 other flowering plant species, suggesting that land connections between the two islands are likely to have existed previously (Chang, 1994). The flora of Lanyu Island appears to have greater similarity to the flora of the Philippines than to Taiwan in that 46 genera not appearing on Taiwan are shared by Lanyu and the Philippines (Chang, 1994). The Taiwan Strait may have first appeared in the late Mesozoic, after which Taiwan contacted Mainland China several times (Chang, 1994). Although the floras of Taiwan and the mainland share many species, Taiwan does possess some distinctive floristic characteristics. The absence of *S. japonicus* from Taiwan suggests that the evolution of *Styrax* has proceeded in isolation on this island. *Styrax japonicus* is very similar to the Taiwanese endemic species *S. formosanus,* differing mainly by imbricate (vs. valvate) corolla aestivation and a slightly longer pedicel. Phylogenetic analysis of DNA sequences of the ITS region (Fritsch, 2001) strongly suggests that *S. japonicus* and *S. formosanus* are sister species. Thus, it appears that *S. formosanus* on Taiwan has speciated from *S. japonicus* ancestral stock and that the imbricate-flowered species of *Styrax* do not constitute a clade (see Taxonomic History and Present Objectives).

The locality of *W. Griffith 3671* (the type of *Styrax grandiflorus*) is in the Naga Hills, either in the Sagaing Division of Myanmar or Nagaland, India. We could not determine the geographic coordinates of the specific localities mentioned in the protologue of this species ("Nempea" and "Namtuzceh") with sufficient precision to map them. The collection appears to represent the westernmost locality of *S. japonicus* known.

No specimens were cited in the protologue of *Styrax japonicus.* New species in volume 1 of *Flora Japonica* were described by J. G. Zuccarini based on data supplied by von Siebold. The only material that we have seen from the von Siebold herbarium consists of on-line images of two L collections from a database of the von Siebold collections maintained by the National Herbarium Nederland (<http://www.nationaalherbarium.nl>). We chose *I. Keiske s.n.,* accession number 908240-682, as the lectotype because it has better flowering material than *I. Keiske 64* (accession number 908240-688). Furthermore, the *I. Keiske s.n.* collection bears insect galls of the same general type as those that appear on the illustration accompanying the protologue, whereas *I. Keiske 64* does not possess galls.

The type material of *Styrax jippei-kawamurai* Yanagita (*J. Kawamura s.n.*) is missing. Yanagita worked at the National Forestry Agency in Tokyo, the herbarium of which is now part of the herbarium of the Tama Forest Museum, Tokyo. None of Yanagita's specimens can be found in this herbarium or are known elsewhere (H. Ohba, TI, pers. comm.).

Selected specimens examined. CHINA. **Anhui:** Huangshan Shi, Huang-shan-qu, Huang-shan, *M. P. Deng & K. Yao 79022* (A); Jinzhai Xian, Bai-ma-zhai, Guan-cai-gou, *K. Yao 8965* (A, CAS, K, MO); Qimen Xian, Mao-peng-dian, *Z. W. Xue 830187* (IBSC); Yuexi Xian, Yao-luo-ping, *Z. W. Xie & L. Zheng 97133* (CAS). **Fujian:** Chong'an Xian, Xin-chun-xiang, *Exp. Wu-yi-shan 912* (PE); Fuzhou Shi, Gu-shan, Bai-yun-dong, *L. G. Lin 48* (CAS); Gutian Xian, *L. G. Lin 1406* (PE); Taining Xian, Xin-qiao-xiang, *G. L. Cai 464* (IBSC, KUN). **Gansu:** Hui Xian, Fan-ba, *Z. B. Wang 19392* (KUN); Kang Xian, Yang-ba-xiang, from Nao-hui-ba to Yang-ba, *Z. Y. Zhang 16760* (PE); Wen Xian, Xiao-wan-li, Bi-feng-gou, Bi-kou, *X. Wang 98* (MO). **Guangdong:** Heping Xian, *G. C. Zhang 35* (IBSC); Liannan Yaozu Zizhixian, Jin-keng-xiang, *P. C. Tam 59492* (IBSC, KUN, PE); Lianshan Zhuangzu Yaozu Zizhixian, *P. C. Tam 58283* (KUN); Ruyuan Yaozu Zizhixian, Xi-shan-xiang, Ba-bao-shan, *C. Wang 44043* (IBSC, KUN, MO, PE); Shantou Shi, Wu-king-fu, 1906, *J. M. Dalziel s.n.* (E); Wengyuan Xian, Long-xian, *X. Q. Liu 24221* (IBSC). **Guangxi:** Guanyang Xian, Dou-yan-lin, *Z. Z. Chen 52458* (IBK, IBSC, KUN); Leye Xian, Niu-wei, Ba-wang-shan, *Exp. Hong-shui-he 89–1109* (KUN); Lingui Xian, Huang-sha-xiang, *Z. Z. Chen 50983* (IBK, IBSC, KUN[2]); Lingyun Xian, Loe-hoh-tsuen, *A. N. Steward & H. C. Cheo 415* (A, BM); Longsheng Gezu Zizhixian, San-men-xiang, *D. A. Huang 60211* (IBK, IBSC); Rongshui Miaozu Zizhixian, Luo-dong-xiang, Jiu-wan-da-shan, *S. Q. Chen 14442* (IBK, IBSC, KUN, PE); Xing'an Xian, Liang-jin-kuang-xiang, Mao-er-shan, *Z. Z. Chen 51257* (IBK, IBSC, KUN); Zi-yuan Xian, Shuen-yuen, *T. S. Tsoong 81668* (A). **Guizhou:** Anlong Xian, Long-shan-xiang, *Exp. Guizhou 4481* (KUN, PE); Bijie Shi, Bao-he-xiang, *P. H. Yu 331* (KUN, PE); Dushan Xian, Shui-li-guang-li-qu, *Exp. Li-bo 1115* (KUN); Duyun Shi, Yun-fou-shan, Tuyun, *Y. 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Fung 491* (BM, IBSC, PE). **Henan:** Baofeng Xian, *Pu-cha-biao-ben 18727* (PE); Lushi Xian, from Da-quai-di to Qi-he, *J. Q. Fu 2210* (KUN); Neixiang Xian, Bao-tian-man Nature Reserve, Da-hong-si River, *D. E. Boufford et al. 26287* (AAU, E); Shangcheng Xian, *Pu-cha-biao-ben 10363* (PE); Song Xian, Hong-luo-he, *K. J. Guan et al. 1905* (PE[2]); Tongbai Xian, Fu-niu-shan, *Henan Forestry Dept. 59* (PE); Weihui Shi, Long-chi, *Pu-cha-biao-ben 34393* (PE); Xin Xian, Wu-ma, *Pu-cha-biao-ben 8269* (PE); Xingyang Shi, Ji-gong-shan, *China-USSR team 346* (PE); Xixia Xian, Tai-ping-zhen, *K. J. Guan et al. 1405* (PE[2]); Yiyang Xian, *Pu-cha-biao-ben 6239* (PE). **Hubei:** Badong Xian, *A. Henry 1430* (K); Baokang Xian, *E. H. Wilson 2134* (K); Changyang Tujiazu Zizhixian, Huo-jia-ping, *T. P. Wang 11375* (PE); Enshi Shi, He-wan-chang, *L. Y. Dai & C. H. Qian 616* (PE); Hefeng Xian, *H. J. Li 5516* (KUN); Jianshi Xian, Hua-guo-ping, *W. B. Lin 70* (PE); Lichuan Shi, Shui-shan-ba, Yang-he-xiang, *W. C. Cheng & C. T. Hwa 559* (A, PE, UC); Shen-nongjia Linqu, Shen-nong-jia Forest Dist., NE of Guan-men-shan along the S side of the Shi-cao River, *Sino-Amer. Bot. Exp. (1980) 763* (A, E, KUN, UC); Songzi Xian, Mo-pan-zhou, *Père C. Silvestri 17704* (A); Wufeng Tujiazu Zizhixian, *H. J. Li 6802* (KUN, PE); Xianfeng Xian, Qing-shui-kuang-qu, *W. B. Lin 575* (PE); Xingshan Xian, Yan-tang-ping, Hing-shan, *H. J. Li 1064* (PE); Yichang Shi, Nan-T'O, *A. Henry 3926* (K); Yun Xian, Wu-dang-shan, *K. R. Liu 142* (PE); Zhuxi Xian, *K. M. Liou 8776* (PE); Zigui Xian, *H. J. Li 318* (PE). **Hunan:** Baojing Xian, *X. L. Yu 91440* (KUN); Changsha Shi, *collector unknown 27495* (PE); Chengbu Miaozu Zizhixian, Jin-tong-shan, *Q. Z. Lin 11145* (IBSC); Cili Xian, Suo-xi-luo Nature Reserve, *Exp. W Hunan 1087* (PE); Dao Xian, Lan-zhu-ping, *P. C. Tam 61328* (IBK, IBSC); Dayong Xian, Zhang-jia-ba, *Z. H. Shen 1577* (IBSC); Dongkou Xian, *X. D. 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Tsai 55793* (A, B, IBSC, KUN, PE); Lüchun Xian, Fen-shui-ling, Lei-bo Valley, *D. D. Tao 238* (IBSC, KUN[2]); Lufeng Xian, W of Lufeng City, *Sino-Amer. Bot. Exp. (1984) 1307* (A, CAS, KUN); Luxi Xian, Lo-shiueh-shan, *H. D. McLaren U219* (C, E); Malipo Xian, Chung-dzai, *K. M. Feng 12740* (A, KUN, PE[2]); Mengzi Xian, Yang-cao-tang-xiang, *Y. Y. Hu 580574* (KUN); Nanjian Yizu Zizhixian, *F. Ducloux 2716* (P); Pingbian Miaozu Zizhixian, Liang-zi-xiang, Yao-shan-qu, *P. Y. Mao 4154* (IBSC[3], KUN, PE); Qujing Shi, Ma-xiong-shan, *Exp. Hong-shui-he 2065* (KUN); Shuangjiang Lahuzu Wazu Bulangzu Daizu Zizhixian, from Shuang-jiang to Tai-ping-xiang, *J. S. Xing 763* (IBSC, KUN[2]); Suijiang Xian, Mo-dao-xi, *B. S. Sun 141* (IBSC, KUN); Tengchong Xian, Dong-shan-xiang, Qing-cai-tang, *H. Li 11357* (CAS); Wenshan Xian, Lao-jun-shan, *K. M. Feng 11082* (A, KUN, PE); Xinping Yizu Daizu Zizhixian, Mao-er-shan, *Exp. Yuxi 2992* (KUN); Xundian Huizu Yizu Zizhixian, Hay tien, *F. Ducloux 2717* (P); Yiliang Xian, from Cao-tian-ma to Niu-jie, *Exp. NE Yunnan 905* (KUN); Yingjiang Xian, *G. D. Tao 13063* (KUN); Yuanjiang Hanizu Yizu Daizu Zizhixian, Er-qu, He-ping-shui-ku, *Y. H. Li 5739* (KUN); Yuanyang Xian, *S. C. Ho 85196* (IBSC); Zhanyi Xian, Xiao-ma-la, *Y. H. Li 148* (KUN, PE); Zhenxiong Xian, Shi-jia-wan, *P. H. Yu 1096* (IBSC, KUN, PE). **Zhejiang:** Jinyun Xian, Yan-ling-keng, Wen-yang, *S. Y. Chang 1740* (MO); Kaihua Xian, Gu-tian-miao, *J. X. Wang 2123* (PE); Longquan Shi, Feng-yang-shan, *S. Y. Chang 3319* (MO); Rui'an Shi, Shi-yang, *S. Y. Zhang 6613* (MO, PE); Suichang Xian, Shui-chang, *Zhejiang Bot. Res. Team 25807* (MO, PE); Taishun Xian, Wu-ling-yan, *S. Y. Zhang 5667* (KUN, PE); Wuyi Xian, Xi-lian-xiang, *Z. W. Zhang J8311260* (IBSC). JAPAN. **Honshu:** Aichi Pref., Seto-shi, *M. Ito 675* (KYO); Aomori Pref., Hachinohe, *Père U. J. Faurie 13031* (K, MO); Chiba Pref., Matsudo-shi, Takatsuka, *Y. Tateishi 816* (TI); Fukuoka Pref., Buzen, Tikuzyô-gun, Iwaya-mura, *S. Yosioka 23* (TI); Fukushima Pref., Ishikawa-gun, Ishikawa-cho, *H. Iketani 1117* (MO); Gifu Pref., Mizunami-shi, Matsuno-ko, *S. Tsugaru et al. 23572* (KYO); Gumma Pref., Usui-gun, Matsuida-machi, Usuitooge, *J. Murata & T. T. Chen 7672* (TI); Hiroshima Pref., Saeki-gun, Yuki-cho, Hontada-gawa, 1979, *T. Nakano s.n.* (AAU); Hyogo Pref., Mt. Rokko, *H. Muroi 3092* (A); Ishikawa Pref., Enuma-gun, Natani, *H. Muroi 2243* (A); Iwate Pref., Morioka, Mt. Iwayama, *H. Muroi 5010* (A); Kanagawa Pref., Musashi, Yokohama, Totsuka, *S. Kobayashi 16251* (BR); Kyoto Pref., Funai-gun, Wachi-cho, Mt. Choro-ga-dake, *S. Tsugaru et al. 18431* (MO); Mie Pref., Itsushi-gun, *M. Hiroe 16424* (UC); Miyagi Pref., Matsushima-cho. W side of Mt. Otakamori, *E. W. Wood & D. E. Boufford 3967* (A, CAS); Nagano Pref., Nishichi-kumagun, Okuwa-mura, betw. Noziri & Mt. Aterayama, along the River Ayera-gawa, *G. Murata & H. Nishimura 122* (AAU, KYO); Nagasaki Pref., Tsushima Island, Shimoagata-gun, Mitsushima-cho, Sumo, *K. Mimoro 1840* (MO); Nara Pref., Nara-shi, Ninnikusen-cho, *H. Iketani 2256* (MO); Nigata Pref., Morimachi, Minami-Kambara, *Y. Ikegami 17502* (A); Okayama Pref., Maniwa-gun, *M. Hiroe 16409* (UC); Osaka Pref., Kawachinagano City *N. Fukuoka 5852* (AAU, C, E, K, L, UC); Saitama Pref., Kitaadachi-gun, Niiza-machi, Heirinzi, 1966, *H. Ohashi s.n.* (TI); Shiga Pref., Takashima-gun, Makino-machi, Minamimakino, *H. Ohashi et al. 8653* (A); Shimane Pref., Yatsuka-gun, Shimane-cho, Kukedo-bana, *K. Deguchi & S. Tsugaru 3819* (MO); Shizuoka Pref., Izu Peninsula, Ito-shi, *K. Nakayama & F. Konta 1433* (KUN); Tochigi Pref., *P. A. Savatier 810* (P); Tokyo Pref., Hachioji-shi, *H. T. Im & T. Karahara 9714* (A, AAU, C, E, K, KUN, MO, PE); Toyama Pref., Mt. Tonami in town of Isurugi, *S. Kirino 360* (MO); Wakayama Pref., Kii, Koyasan, *G. Koidzumi s.n.* (KYO[2]); Yamagata Pref., Higashine-shi, Inosawa, *H. Ohashi et al. 10779* (A); Yamaguchi Pref., Mukaidoi, Tukuyama, 1954, *H. Migo s.n.* (A). **Kyushu:** Kagoshima Pref., Phsumi, Yaku-shima Island, Mt. Motchomu Hara Yaku-choo, *F. Miyoshi 10778* (K); Kumamato Pref., Aso-gun, Aso-machi, Futae Pass, 1983, *Y. Endo s.n.* (MO); Miyazaki Pref., Cape Toi, *K. Kondo 2228* (TI). **Ryukyu Islands:** Okinawa Pref., Okinawa Island, Kunigami, Nago-dake, *E. H. Walker et al. 6157* (E, GH, K, L, UC). **Shikoku:** Kagawa Pref., Mitoyo-gun, Toyono-mura, *M. Takahashi 1197* (A, KUN, PE). LAOS. **Houaphan:** Muang awin, Clueng Kwang, *A. F. G. Kerr 20941* (BM, K, L). **Xiangkhoang:** betw. Muong Hom & Ta Thom, *J. Vidal 880B* (P). MYANMAR. **Kachin State:** N Triangle (Hkunlum), *F. F. K. Ward 20632* (A, BM, E). NORTH KOREA. **Pyongyang City:** Chonbuk, Chonju, Wansan Chilbong, 1988, *B. Y. Sun s.n.* (A). PHILIPPINES. **Babuyan Islands:** Camiguin Island, Mt. Malabsing, *G. E. Edaño 79248* (L). **Batan Islands:** Batan Island, Mt. Matarem, *M. Ramos 80424* (BO, L). SOUTH KOREA. **Cheju:** Nam-cheju-gun, Shinye-ri, *D. E. Boufford et al. 25729* (CAS, E). **Kangwon:** Kogen, *E. H. Wilson 9328* (A). **Kyonggi:** Keiki, Kosyo *E. H. Wilson 8754* (A, K). **North Cholla:** Wanju-gun, Moak san, *D. E. Boufford et al. 25808* (CAS, E, KUN). **North Kyongsang:** Daegwannim, 1987, *Y. S. Kim s.n.* (A, MO). **Seoul City:** Sammaksa Temple, *R. Moran 4327* (BM, BR, E, GH, MO, UC). **South Cholla:** Mt. Moodung, 1984, *Y. S. Kim s.n.* (A). **South Chungchong:** Sosan Gun, Anmyon Island, *B. R. Yinger et al. 2525* (A). **South Kyongsang:** Chilean Keisyonando Chosen Nippon, *K. Uno 23243* (A). VIETNAM. **Cao Bang:** Mt. Pia Oac, 1997, *U. Kurosu s.n.* (CAS).

7. Styrax limprichtii Lingelsh. & Borza, Repert. Spec. Nov. Regni Veg. 13: 386. June 1914 [as *S.* "*Limprichtii*"]. TYPE: China. Yunnan: Chuxiong Shi, Tschu-hsiung-fu, 2000 m, 24 Aug. 1913, *K. G. Limpricht 920* (lectotype, designated here, WRSL not seen; photo of lectotype, A!, PE!; isotype, A!).

Styrax langkongensis W. W. Sm., Notes Roy. Bot. Gard. Edinburgh 8: 208. September 1914. TYPE: China. Yunnan: xian unknown, hills at the S end of the Lang-kong Valley, 26°10′N, 2121–2727 m, May 1910, *G. Forrest 5585* (holotype, E!; isotypes, BM[2]!, IBSC!, K[2]!, PE!, UC!).

Shrubs to 2.5 m tall. Young twigs gray-yellow or yellow-brown stellate-tomentose; older twigs dark purple, glabrescent. Petiole 1–3 mm long. Two most proximal leaves on each shoot alternate or more often subopposite to opposite. Lamina 3.5–7(–9.5) × 2–4.5 cm, chartaceous, elliptic to obovate; apex obtuse to slightly acuminate; base rounded to broadly cuneate; adaxially densely stellate-pubescent when young, becoming sparsely pubescent; abaxially white stellate-tomentose, rarely subglabrous, often with additional scattered orange or dark brown stellate pubescence especially prevalent on veins and the two most proximal leaves on each shoot; margin serrate or nearly entire (but still glandular), often irregularly dentate apically; secondary veins 5 or 6 on each side of midvein, tertiary veins reticulate, plane or slightly sunken, abaxial surface of the secondary and tertiary veins obscured by the tomentum, only the tertiaries abaxially prominent and raised in young leaves. Fertile shoots 1–7 cm long, 3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1(2)-flowered; pseudoterminal inflorescences 2-flowered or racemose, 1–2 cm long, 2- or 3(4)-flowered, rachis yellow or orange stellate-tomentose, stalked trichomes absent. Pedicel 3–4 mm long, densely pubescent; bracteoles 3–5 mm long, subulate, positioned at various places along the pedicel but mostly near the middle, more rarely near the base, sometimes those toward the base of the inflorescence leaf-like. Flowers 1.5–2.0 cm long. Calyx 5–6 × 5–6 mm, cupuliform; adaxially sparsely appressed-pubescent with white 2- or 3-armed or stellate trichomes, becoming glabrous proximally; abaxially yellow-brown or orange stellate-tomentose throughout, often also with various amounts of larger scattered orange or brown stiff stellate trichomes, especially proximally; margin distinctly dentate, the teeth (0.6–)1–1.5(–2) mm long, subulate to deltoid, unequal, usually contiguous or separated by a shallow concave portion. Corolla 1.0–1.4 cm long, white, tube ca. 4 mm long, glabrous, lobes 5, 9–11 × 4–6 mm, elliptic to ovate-elliptic, short-stellate-pubescent on both sides. Stamens 10; filaments 5–6 mm long, straight, proximally broadened, densely white stellate-pubescent, trichomes up to 0.5 mm long, distally subulate-attenuate and glabrous; anthers 4–5 mm long, wider than distal portion of filament; connectives glabrous. Style proximally stellate-pubescent and distally glabrous, sometimes sparsely stellate-pubescent or glabrous throughout; stigma 0.2–0.4 mm wide, capitate. Fruit 1.4–1.6 × 1–1.5 cm, globose, apex rounded or apiculate, dehiscent by 3 valves from apex; pericarp dry, 0.3–0.6 mm thick, outside regularly longitudinally striate throughout, rugose, gray stellate-tomentose, inside glabrous or minutely downy-pubescent. Seeds brown, ovoid, finely reticulate-fissured, glabrous.

Illustrations. Anonymous, Ic. Cormophyt. Sin. 3: 339, fig. 4631. 1974; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1606, fig. 801. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 90, pl. 30 (1–5). 1987; W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 892, pl. 470 (7–10). 1990; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 199, fig. 199 (1–5). 2000.

Phenology. Flowering: February–October. Fruiting: April, June–November.

Distribution. China (Sichuan and Yunnan); Figure 8.

Habitat. In relatively sunny, dry stony pastures, more often in forests on open rocky slopes; 1400–2750 m.

Vernacular names. Chu-xiong-an-xi-xiang (Hwang, 1980), Chu-xiong-ye-mo-li (Anonymous, 1974).

Styrax limprichtii, a much-branched shrub that rarely exceeds 2.5 m, occurs only in northeastern Yunnan Province and adjacent southwestern Sichuan Province.

The ranges of *Styrax limprichtii* and *S. rugosus* are contiguous. These two species are morphologically similar in many respects, as demonstrated by their adjacency in the key, and are probably sister taxa. They nonetheless exhibit enough differences throughout their ranges to justify the recognition of these two entities as species (see couplet 24 of the key). Furthermore, *S. rugosus* usually occurs at lower elevations (700–1650 m) than *S. limprichtii* (1400–2750 m). Besides these differences, *S. limprichtii* differs from *S. rugosus* by a tendency toward shorter calyx teeth, shorter bracteoles, shorter shoots, and less rugose leaves. These characters, however, exhibit some degree of overlap. Also similar to *S. limprichtii* is *S. wilsonii* (see comparisons under that species).

Styrax limprichtii, *S. rugosus*, *S. wilsonii*, and the western Mexican endemic *S. jaliscanus* are all similar morphologically, sharing a shrubby habit, a calyx that is densely pubescent throughout abaxially and distinctly dentate with the teeth contiguous or nearly so, a petiole ≤ 5 mm long, and an evenly longitudinal-striate pericarp. The striate pericarp appears to be restricted to these species within *Styrax*. Phylogenetic analysis of DNA sequences of the ITS region, however, places *S. limprichtii* at the base of series *Cyrta*, and *S. jaliscanus* groups with the rest of the North American species of series *Cyrta* (Fritsch, 2001). Nonetheless, support for these positions is weak, and this group is in need

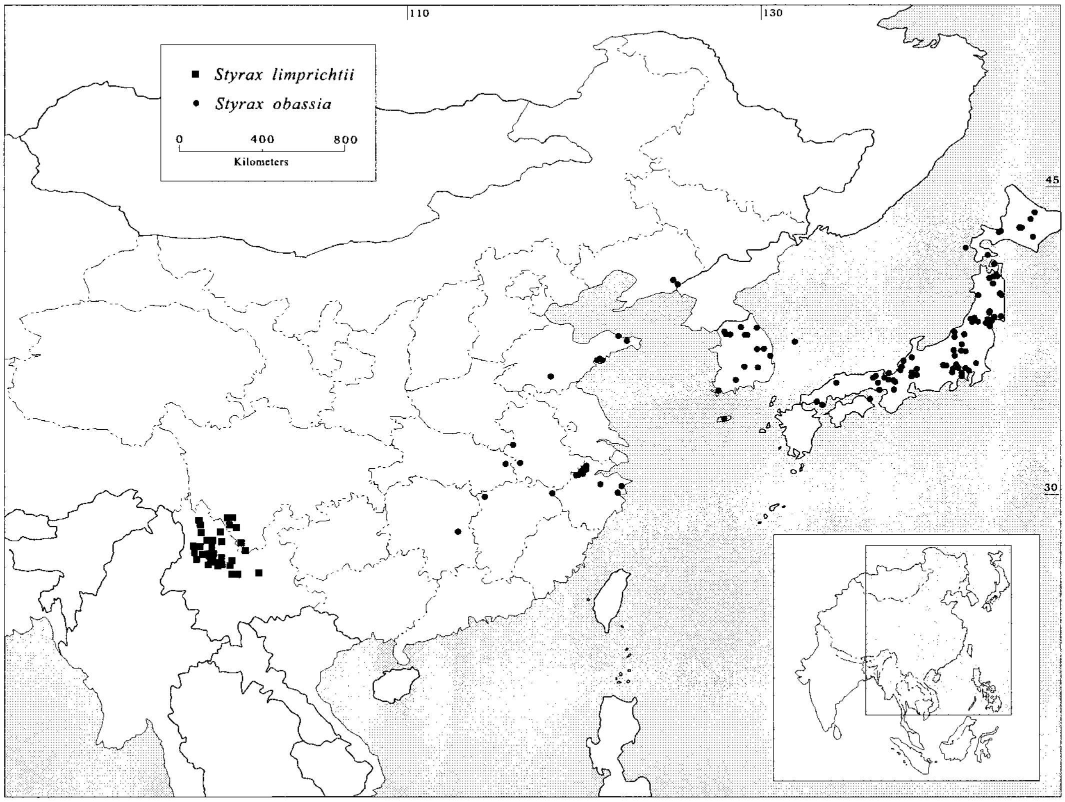

Figure 8. Geographic distribution of *Styrax limprichtii* and *S. obassia.*

of more detailed study to resolve the apparent discrepancy between molecular and morphological data.

Only two imbricate-flowered species of *Styrax* are sympatric with *S. limprichtii. Styrax hookeri* is normally easily distinguished from *S. limprichtii* by its tree (vs. shrub) habit. *Styrax limprichtii* can be further distinguished from small individuals of *S. hookeri* by its distinctly dentate (vs. usually truncate or undulate) calyx, which is ± pubescent throughout (vs. more sparsely pubescent within 1 mm of the margin). *Styrax limprichtii* also tends toward leaves with acute to blunt (vs. acuminate to caudate) apices, coarsely serrate margins, especially distally (vs. more finely serrate), and a rugose (vs. smooth) surface abaxially. Moreover, *S. limprichtii* also usually has densely pubescent laminae abaxially, and anthesis often occurs before the full expansion of the leaves, whereas the leaves of *S. hookeri* can be densely pubescent to glabrous abaxially and anthesis occurs at the same time as or after full leaf expansion. The only other species of imbricate-flowered *Styrax* sympatric with *S. limprichtii* is *S. japonicus,* occurring near Dali Shi and Kunming Shi, Yunnan Province. This species is readily distinguished from *S. limprichtii* by its longer pedicels and nonstriate (vs. longitudinally striate) pericarp.

The collections of K. G. Limpricht numbers 896, 920, and 973 are all cited in the protologue of *S. limprichtii* without a clear indication of type, and thus are all syntypes of this name. We have chosen the *K. G. Limpricht 920* specimen at WRSL as the lectotype because it is apparently the most widely distributed of the three collections.

Selected specimens examined. CHINA. **Sichuan:** Muli Zangzu Zizhixian, *G. Forrest 22394* (A, E, K); Luo-boxiang, *Nan-shui-bei-diao-dui 5709* (KUN, PE); Mu-li Valley, mtns. betw. Mu-li & Ku-lu, *J. F. Rock 24150* (A, E, UC); from Ke-tze to Ku-ba-dian, *T. T. Yü 7216* (A, KUN, PE); from Tuo-li-gou to Ke-tze, *T. T. Yü 14198* (A, KUN, PE); Panzhihua Shi, Da-bao-ding, *Exp. Qinghai & Xizang 11362* (KUN); Yanyuan Xian, *H. F. Handel-Mazzetti 2068* (A, E), *Nan-shui-bei-diao-dui 5584* (PE); Wei-luo-he, Mao-niu-shan, *Nan-shui-bei-diao-dui 5967* (KUN, PE). **Yunnan:** Binchuan Xian, Hi-zu-shan, *S. Y. Bao 1* (KUN); Sin-tien, Pin-tchouan, *F. Ducloux 4627* (P); Ji-zhu-shan, *H. Li 503* (KUN); Gan-dian, *Y. Q. Lin 11* (KUN); from Xia-yang to Wa-xi, *T. N. Liou 21495* (IBSC, PE); Niu-jing, *T. N. Liou 21688* (IBSC, PE); Simeon Yen, *S. Ten 351* (E, UC); Ji-shan, *H. C. Wang 1988* (KUN, IBSC, PE); Chuxiong Shi, Guang-ba-he Reservoir, *S. C. Huang 20* (KUN);

Long-tang, *Sino-Amer. Bot. Exp. (1984) 1256* (A, CAS, KUN, MO); Dali Shi, Kong-ti, *J. M. Delavay 2782* (A, P); Pu-peng, *Exp. NW Yunnan 4010* (KUN, PE), *Exp. Qinghai & Xizang 20* (KUN); W slopes of the Sung-kuiei Range, *G. Forrest 23057* (A, E, K); Xiao-tuan-shan, Erhai Park, *Sino-British Exp. Cang-shan 1* (A, E, K, KUN), *Y. Tsiang 11337* (IBSC, KUN); Wu-tai-feng, Shi-tou-cun, *H. C. Wang 1740* (IBSC[2], KUN[2]); Yang-tze divide, E of Dali lake, *J. K. Ward 3831* (E); Dayao Xian, Shi-yang-qu, *Coll. Team for Oil Pl. (1965) 650302* (KUN); Kang-jia-shan, *P. Di 60022* (KUN); Eryuan Xian, San-ying-qu, Jiao-shi-he, *Exp. NW Yunnan 6389* (KUN, PE); Heqing Xian, Bai-yan, *R. C. Ching 24523* (KUN, PE); from Sarchatze to Chiang-Ing near Sung-kuei, *K. M. Feng* 801 (A, IBSC, KUN); Dsolin-ho, *H. F. Handel-Mazzetti 6224* (A, E); Li-chiang Range, *H. D. McLaren S114* (BM); Jsu-yung, *H. D. McLaren 114F(AA)* (C, E); Pai-ching, *H. D. McLaren F199* (AAU, E); Sung-kuei, *H. D. McLaren e233* (E); He-chuan-xiang, *W. C. Wang 390* (KUN); Kunming Shi, Yi-ping-lang, *T. N. Liou 16614* (IBSC[2], PE); Lanping Baizu Pumizu Zizhixian, in the Lang-kong Valley, *G. Forrest 9954* (BM, E, K, PE, UC); Lijiang Naxizu Zizhixian, Tze-li on Yang-tze River, *R. C. Ching 20264* (A, KUN, PE); Tai-ngo-koo, *R. C. Ching 21670* (KUN); Tze-li on Yang-tze, *R. C. Ching 22139* (A); Shu-di-du-kou, *Exp. Qinghai & Xizang 638* (KUN[2]); near Jin-sha-jiang, *Exp. SW China (Guizhou, Sichuan & Yunnan) 200* (PE); Jia-zi-xiang, Bai-shui-he, *K. M. Feng 21567* (KUN, PE); Li-chiang Range, *H. D. McLaren 46No.2* (BM); high plateau betw. Ta-li-fu & Li-kiang, *J. F. Rock 3198* (A, E, UC); betw. Li-kiang & Ta-li-fu, *J. F. Rock 6397* (A, UC); S Li-kiang-shan, Sung-kwe-ho-chin Range, *J. F. Rock 8268* (A, UC); betw. Li-kiang, Tung-shan, Tui-nao-ko, & Tsi-li-kiang, *J. F. Rock 8520* (A, UC); Yulung-shan, *C. K. Schneider 3965* (IBSC); Da-dong-qu, *H. Sun 771038* (KUN); *C. Y. Zhao 21670* (KUN, PE); Shi-er-lan-gan-ban-shan, *Y. X. Zhao 22139* (KUN); Ninglang Yizu Zizhixian, from Ku-ba-dian to Tuo-li-gou, *T. T. Yü 7309* (A, KUN, PE); Yangbi Yizu Zizhixian, betw. Li-kiang, Young-ning & Young-pei, *J. F. Rock 5058* (A, UC); Yao'an Xian, Da-jian-shan, 1965, *Exp. SW China (Guizhou, Sichuan & Yunnan) s.n.* (PE); Yao-chou, *H. D. McLaren 205F* (C); Yongsheng Xian, Song-ping-xiang, *Exp. Qinghai & Xizang 692* (KUN); Jong-shan, *G. Forrest 16929* (E); Xin-liang-gong-she, *C. X. Lü 62168* (KUN); Yunlong Xian, Jin-yue-liang, *Xiang-liao-dui (Coll. Team for Perfume Pl.) 156* (KUN); Zhongdian Xian, mtns. NE of Yang-tze Bend, *G. Forrest 10696* (A, BM, PE, UC); Chung-tien plateau, *G. Forrest 12653* (AAU, BM, E, PE).

8. Styrax macrocarpus W. C. Cheng, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 10: 242. 1938 [as *S.* "*macrocarpa*"]. TYPE: China. Hunan: Yizhang Xian, Mang-shan, 800 m, 21 Aug. 1937, *W. C. Cheng 7000* [from protologue] (holotype, PE!; isotype, PE! [no collection number indicated on either sheet]).

Styrax zhejiangensis S. M. Hwang & L. L. Yu, Acta Bot. Austro Sin. 1: 75. 1983. TYPE: China. Zhejiang: Jiande Xian, 27 June 1958, *Y. Y. Ho 29344* (holotype, IBSC!; isotype, IBSC!).

Shrubs to 2 m tall or trees to 9 m tall. Young twigs densely gray-brown stellate-pubescent, older twigs becoming gray, glabrescent. Petiole < 1(–2.5) mm long. Two most proximal leaves on each shoot subopposite to opposite. Lamina 2.5–17 × 2–7.5 cm, chartaceous, elliptic to obovate-elliptic; apex acute; base cuneate, broadly cuneate or rounded; sparsely stellate-pubescent on veins when young, otherwise glabrous; margin subentire or apically slightly serrate, secondary veins 6 to 10 on each side of midvein; tertiary veins subparallel, adaxially plane or slightly sunken, abaxially raised. Pedicel 7–12 mm long, white stellate-tomentose; bracteoles 3–5 mm long, ovate-lanceolate, positioned at the base or middle part of pedicel. Flowers 2.3–3.2 cm long, solitary, arising only laterally from shoots of the previous growing season, opening before the leaves. Calyx 5–7 × 7–9 mm, cupuliform; adaxially glabrous; abaxially gray stellate-tomentose, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin with 4 to 6 broadly deltoid teeth, subglabrous on both sides. Corolla 1.6–2.6 cm long, white, tube 3–4 mm long, glabrous, lobes 5–7, 1.6–2.3 × 0.8–1.1 cm, elliptic or narrowly elliptic, apex obtuse to acute, sparsely white stellate-pubescent on both sides. Stamens 10 to 12; filaments 8–10 mm long, straight, proximally broadened and ventrally densely white stellate-villous, distally attenuate and glabrous; anthers 5–6 mm long, wider than distal portion of filament; connectives glabrous. Style proximally sparsely white stellate-pubescent proximally, distally glabrous; stigma 0.2–0.4 mm wide, punctiform. Fruit 1.8–3 × 1.0–2.5 cm, ovoid to pyriform, apex rounded or apiculate, apparently indehiscent; pericarp dry, (1–)1.5–3 mm thick, outside smooth, gray or pale brown stellate-tomentose, inside densely appressed-pubescent with long simple, 2-armed, or stellate white trichomes. Seeds brown or dark brown, ellipsoid to ovoid-ellipsoid, irregularly rugose, glabrous, sometimes sparsely white stellate-villous.

Illustrations. W. C. Cheng, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 10: 243, fig. 25. 1938; S. M. Hwang, Acta Bot. Austro Sin. 1: 76, fig. 1. 1983 (as *S. zhejiangensis*); S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1618, fig. 811. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 98, pl. 33 (1–2). 1987; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 98, pl. 33 (3–5). 1987 (as *S. zhejiangensis*); Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 202, fig. 202 (1–5). 2000 (3–5 as *S. zhejiangensis*).

Phenology. Flowering: April, May. Fruiting: June, July, September, October.

Distribution. China (Guangdong, Hunan, and Zhejiang); Figure 2.

Habitat. In shady mountain forests, and along the margins of mixed forests in ravines; 570–950 m.

Vernacular names. Da-guo-an-xi-xiang (Hwang, 1980), Zhe-jiang-an-xi-xiang (Hwang, 1983).

Styrax macrocarpus, occurring in mountainous regions between 570 and 950 m elevation, has been collected only rarely. This species is easily distinguished from sympatric species of *Styrax* by its much shorter petioles (less than 1(–2.5) mm long); solitary, lateral, and larger (2.3–3.2 cm long) flowers that open before the leaves on shoots of the previous year; and a larger (1.0–2.5 cm wide) fruit, with a pericarp (1–)1.5–3 mm thick that is densely appressed-pubescent inside with long simple or 2-armed white trichomes.

Hwang (1983) described *Styrax zhejiangensis* from a single fruiting specimen collected in Jiande Xian, Zhejiang Province. Although she considered a possible relationship of *S. zhejiangensis* with *S. macrocarpus* based on their common solitary, laterally produced flowers, Hwang (1983) felt that the combination of a smaller, pyriform (vs. ovoid) fruit, broadly elliptic to ovate-oblong (vs. elliptic to obovate-elliptic) leaves, and sparsely stellate-pubescent (vs. glabrous) seeds was sufficient justification for the recognition of a new species. There is, however, ample evidence for a close affinity between the two taxa, so much so that we regard the two as conspecific. In addition to their solitary, laterally produced flowers, *S. macrocarpus* and *S. zhejiangensis* share many other features such as the two most proximal leaves on each shoot subopposite to opposite; the petiole very short or absent; the leaves with a similar number of secondary veins and an entire or indistinctly toothed margin; the calyx adaxially glabrous, abaxially gray stellate-tomentose, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry, margins with 4 to 6 broadly deltoid teeth, subglabrous on both sides; the fruiting calyx patelliform, not appressed to the fruit; the fruit ovoid to pyriform with the apex rounded or apiculate, a smooth gray to brown stellate-tomentose surface, and an inner fruit wall densely appressed-pubescent with long simple or 2-armed white trichomes; and seeds ellipsoid to ovoid-ellipsoid, with an irregularly rugose testa.

Furthermore, characters that reportedly distinguish *Styrax zhejiangensis* from *S. macrocarpus* are unreliable or do not otherwise serve to delimit the two taxa. According to the protologues of the species, *S. zhejiangensis* tends to have wider leaves with reticulate tertiary veins and a smaller, pyriform fruit, whereas *S. macrocarpus* tends to have narrower leaves with subparallel tertiary veins and a larger, ovoid fruit. We regard the tertiary veins of *S. zhejiangensis* as subparallel rather than reticulate and the fruit shape of *S. macrocarpus* (i.e., specimens outside of Zhejiang Province) as encompassing both ovoid and pyriform variants, as was also observed by Hwang (1987). Hwang (1987) described *S. macrocarpus* as a tree (6–9 m tall) with glabrous seeds, and *S. zhejiangensis* as a shrub (less than 2 m tall) with pubescent seeds. Our examination of more collections than were available to Hwang (1983, 1987), however, has revealed several specimens of *S. macrocarpus* that exhibit a shrub habit with intermediate height (ca. 4 m; e.g., *X. Q. Liu 28884* and *G. L. Shi 14815*). The number of stellate trichomes distributed on the surface of the seeds of *S. zhejiangensis* varies from several to dozens, even on those from the same plant. High infraspecific seed pubescence variation is present in two other species in this revision (*S. odoratissimus* and *S. tonkinensis*), so this character by itself cannot be used to justify the recognition of *S. zhejiangensis.*

Most collections of *Styrax macrocarpus* are from Mang-shan, Yizhang Xian, southern Hunan Province, where the type collection was made. All other collections were made far from the type locality except one specimen from adjacent Ruyuan Xian, northern Guangdong Province (*Z. L. Chen 30610*). This species exhibits a discontinuous distribution between Fengkai Xian, western Guangdong Province (*G. L. Shi 14815* and *Exp. Guangdong 5185*), Jiande Xian, Zhejiang Province (*Y. Y. Ho 29344*), and the region of the type locality. This discontinuity may be an artifact of human-induced extirpation between the known localities, rather than the species' original distribution, because the original vegetation of the whole region encompassing the range of *S. macrocarpus* has been heavily modified by human disturbance.

Additional specimens examined. CHINA. **Guangdong:** Fengkai Xian, Qi-xing-xiang, *Exp. Guangdong 5185* (IBSC); Hei-shi-ding, *G. L. Shi 14815* (IBSC); Ruyuan Yaozu Zizhixian, Tian-men-zhang, *Z. L. Chen 30610* (IBSC). **Hunan:** Yizhang Xian, Mang-shan, *collector unknown* (PE); Mang-shan, Shui-kou-miao, *S. Q. Chen 2889* (AAU, BR, IBK, IBSC, KUN, PE); Mang-shan, *S. Q. Chen 5408* (IBSC), *M. X. Huang 112743* (IBSC); Mang-shan, Yang-gong-dong, *P. H. Liang 85107* (IBK, IBSC); Mang-shan, *X. Q. Liu 28884* (IBK, IBSC, PE), *Zhong-nan-lin-shi-xi-dui 137* (IBSC).

9. Styrax obassia Siebold & Zucc., Fl. Jap. 1: 93. 1839. TYPE: Japan. *I. Keiske 287* (lectotype, designated here, L [accession no. 908241–452] not seen; digital image of lectotype!).

Shrubs or trees to 15 m tall. Young twigs brown stellate-pubescent; older twigs dark purple, glabrescent. Petiole of larger leaves 10–15(–20) mm long, dilated at base and covering the bud. Two most proximal leaves on each shoot subopposite to opposite, smaller than distal leaves, with petioles not dilated at base or covering the bud. Lamina 5–17 × 4–15 cm, chartaceous, broadly elliptic, broadly obovate, or suborbicular; apex abruptly caudate-acuminate; base subrounded to broadly cuneate; adaxially glabrous except for sparse gray pubescence on major veins, abaxially gray-white stellate-tomentose; margin subentire or remotely apiculate-dentate; secondary veins 5 to 8(to 10) on each side of midvein, tertiary veins ± parallel and perpendicular to the secondary nerves, abaxially prominent. Fertile shoots 14–26 cm long, 1- to 3-leaved. Inflorescences arising from shoots of the current growing season, usually pseudoterminal, occasionally also lateral; lateral inflorescences usually consisting of a single flower; pseudoterminal racemes 10–18 cm long, 10- to 18(to 23)-flowered, rachis glabrous or nearly so. Pedicel 4–6(–10) mm long, white stellate-tomentose, sometimes with larger scattered brownish stellate trichomes; bracteoles 3–5 mm long, linear, positioned at the base or middle part of pedicel, sometimes those toward the base of the inflorescence leaf-like. Flowers 1.2–2 cm long. Calyx 5–6 × 4–5 mm, campanulate; adaxially glabrous; abaxially white stellate-tomentose throughout, often also with various amounts of larger yellow or brownish stiff stellate trichomes especially proximally; margin with 5 or 6 lanceolate to narrowly deltoid, irregularly distributed teeth, contiguous. Corolla 1.0–1.5 cm long, white or rarely pink, tube 4–5 mm long, glabrous, lobes 5(6), 13–16 × 4–6 mm, elliptic, apex acute, white stellate-tomentose on both sides. Stamens 10(12); filaments 6–8 mm long, straight, of equal width throughout, subglabrous or glabrous; anthers 4–5 mm long, equal to filament in width or narrower; connective glabrous. Style proximally stellate-pubescent, otherwise glabrous; stigma 0.1–0.3 mm wide, punctiform. Fruit 1.4–2.0 × 0.7–1.2 cm, ovoid to subovoid, apex rounded or apiculate, dehiscent by 2 valves; pericarp dry, 0.2–0.5 mm thick, outside coarsely and irregularly rugose, white or yellow-brown stellate-tomentose, inside glabrous. Seeds dark brown, ellipsoid, smooth, glabrous.

Illustrations. Siebold & Zucc., Fl. Jap. 1: t. 46. 1835; Gard. Chron. ser. 3, 16: 513. 1888, 34: 507. 1897; Hook. f., Bot. Mag. 115: t. 7039. 1889; Dippel, Handb. Laubholzkunde 1: fig. 205. 1889; Nakai, Sylv. Korea 13: t. 13. 1923; Nakai, Trees Shrubs Japan ed. 2: fig. 157. 1927; Anonymous, Ic. Cormophyt. Sin. 3: 338, fig. 4629. 1974; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1601, fig. 796. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 85, pl. 28 (1–5). 1987; X. M. Liu in X. H. Qian, Fl. Anhui 4: 64, fig. 1766. 1991; S. Y. Wang in B. Z. Ding, Fl. Henan 3: 229, fig. 1774. 1997; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 197, fig. 197 (1–5). 2000.

Phenology. Flowering: May–July. Fruiting: June–November.

Distribution. China (Anhui, Hubei, Hunan, Jiangsu, Jiangxi, Liaoning, Shandong, and Zhejiang), Japan (Hokkaido and Honshu), North Korea, and South Korea (Cheju, Kangwon, Kyonggi, North Chungchong, North Kyongsang, Seoul City, and South Kyongsang); Figure 8.

Habitat. In mesic, open mixed forests on mountain slopes, and in deciduous forests in ravines; 9–1400 m.

Vernacular names. Lao-dan-pi (China, Shandong; *Shandong Wild Pl. Exp. [1959] 89*), Lao-kai-pi (Anonymous, 1974), Oho-ba zisja (Japan; Siebold, 1835–1841), Sei ton kwa (Japan; Siebold, 1835–1841), Shan-zhen-zi (China, Shandong; Hwang & Qi, 1985), Shu-ling-hua (China, Anhui; *Exp. Anhui 219*), Yu-ling-hua (Hwang, 1987; Anonymous, 1974), Yun-jin-du-juan (China, Zhejiang; *Y. Y. Ho 23309*).

Styrax obassia occurs at the extreme northern edge of the range of *Styrax* in Asia, extending from the island of Hokkaido (northern Japan) through North and South Korea to southeastern China. *Styrax obassia* is the only species of *Styrax* that occurs as far north as Hokkaido and Liaoning Province, northeastern China. It appears to be a relatively common component of wet temperate forests in Japan. The dilated petiole base covering the bud separates *S. obassia* from most other species of *Styrax* except *S. shiraianus,* which is distinguished from *S. obassia* by its shorter shoots (4–8 cm) and inflorescences (2–3 cm), much shorter pedicels (less than 1 mm), and generally narrower leaves (to 9.5 cm) with more robust teeth. These species range farther north than any other species of *Styrax* in Asia except *S. japonicus,* suggesting that the dilated petiole base is an adaptation to temperate conditions in lieu of bud scales. Besides the dilated petiole base, *S. obassia* differs from other sympatric species by its larger flowers with glabrous filaments and styles (cf. *S. odoratissimus*) and shorter pedicels and longer inflorescences (cf. *S. japonicus*). See also *S. hemsleyanus* for additional comments.

This wide-ranging species is not extremely variable morphologically, and no unusual specimens were encountered in this revision. This could explain the highly constant treatment regarding this species since its description in 1839.

No specimens were cited in the protologue of *Styrax obassia.* New species in volume 1 of *Flora Japonica* were described by J. G. Zuccarini based on data supplied by von Siebold. The only material that we have seen from the von Siebold herbarium consists of on-line images of two L collections from a database of the von Siebold collections maintained by the National Herbarium Nederland (<http://www.nationaalherbarium.nl>). One of these collections (L accession number 950161–812) bears the stamp "Herbarium Ch. D'Alleizette" and a typeset (not handwritten) label that contains a reference to K. I. Maximovicz, who collected in Japan between about 1860 and 1866, long after von Siebold was there (from 1823 to 1830). The label also bears an indication that this specimen was designated for exchange. D'Alleizette was a plant collector residing in Bordeaux, France, and apparently never collected in Japan. Based on these data, we conclude that this specimen was not part of von Siebold and Zuccarini's original material. The other collection (*I. Keiske 287,* L accession number 908241-452) bears labels that are consistent in handwriting and format with most others in von Siebold's herbarium. Keiske was one of von Siebold's collaborators while von Siebold was in Japan. Although only a single leaf constitutes this specimen, it is clearly recognizable as that of *S. obassia* on the basis of, among other features, the overall obovate-orbicular shape and a coarsely dentate margin with the teeth most prominent apically. On this basis, we have lectotypified the name *S. obassia* on the L specimen of *I. Keiske 287.*

The specific epithet "*obassia*" is derived from the common name for the species in Japanese. Because the epithet is a noun in apposition, it should not be modified to "*obassis*" (see Greuter et al., 2000: Article 23.5), as was done by Hwang and Grimes (1996).

Selected specimens examined. CHINA. **Anhui:** Jinzhai Xian, Bai-ma-zhai, Xi-da-wa, *K. Yao 8928* (A, CAS, K, MO); Yuexi Xian, *E China Work Station 7007* (IBSC). **Hubei:** Luotian Xian, *G. Hei 1251* (PE). **Hunan:** Hengshan Xian, Heng-shan, *S. Q. Chen 3431* (IBSC). **Jiangsu:** *collector unknown 2337* (BR). **Jiangxi:** Wuyuan Xian, *R. C. Ching 3253* (A, E, IBSC, K, PE, UC); Xiushui Xian, Mofu-shan, Tian-yu-tang, *Y. K. Hsiung 5891* (PE[2]). **Liaoning:** Dandong Shi, An-dong, Zhen-jiang-shan, *G. Sato 5250* (PE); Fengcheng Shi, Feng-huang-shan, *Z. Wang 1611* (PE). **Shandong:** Pingyi Xian, Meng-shan, *T. Y. Zhou 6389* (PE); Qingdao Shi, Lao-shan, *F. N. Meyer 275* (A, DS, UC); Yantai Shi, Kun-yu-shan, *Shandong Wild Pl. Exp. 89* (PE). **Zhejiang:** Anji Xian, Tian-mu-shan, *Y. Y. Ho 22113* (IBSC, PE); Lin'an Shi, Da-ming-shan, *Y. Y. Ho 23309* (IBSC, MO, PE); Tiantai Xian, *G. R. Chen 2442* (KUN, PE); Zhuji Shi, *Y. Y. Ho 24026* (IBSC, MO). JAPAN. **Hokkaido:** Haku-unloke, *collector unknown* (K), in 1887 (A); Sapporo, Yezo, 1903, *S. Arimoto s.n.* (GH, MO); Hakodate, 1861, *K. I. Maximovicz s.n.* (BM); Shirileshi, Okushiri, 1890, *K. Miyabe & E. Tokubuchi s.n.* (GH); Furano City, Yamabe, *K. Sohma & M. Takahashi 535* (A, MO). **Honshu:** Aomori Pref., Shimokita-gun, Kawauchi-cho, *K. Deguchi 5737* (MO); Fukui Pref., Nanjo-gun, Imajo-cho, N slope of Yashaga-ike, *G. Murata & H. Nishimura 5663* (A, AAU, KYO, L, PE, TI); Gifu Pref., Ohno-gun, Takane-mura, Dohgo-gawa, *H. Kanai & H. Ohashi 731182* (BM, BR, E, K, L, UC); Gumma Pref., Tano-gun, Uenomura, Narahara, betw. Akegasawa & Shionosawa, *J. Murata 1769* (A); Hyogo Pref., Tabu-gun, Oya-cho, Ikada, Tentaki, *G. Murata 1030* (A, AAU, C, E, L, MO, UC); Ishikawa Pref., Shiramine-mura, Akatani, Akatani-rindo, *S. Tsugaru et al. 22237* (KYO); Iwate Pref., Morioka, Mt. Iwayama, *H. Muroi 5028* (A); Kyoto Pref., Kitakuwata-gun, Miyama-cho, Ashiu, from Sugou to Kadzura-goya, *M. Ito et al. 1293* (TI); Miyagi Pref., Mono-gun, Kitakami-machi, Yoogai, S side of Okinakura-yama, *D. E. Boufford & E. W. Wood 25412* (A, CAS, E, MO); Nagano Pref., Suwa-gun, Fujimi-cho, Hanaba, Shiraya-zawa, *T. Shimizu 22540* (AAU); Nara Pref., Mt. Kurokami-yama, *H. Muroi 6962* (A); Niigata Pref., Minami-uwonuma, Mikuni, *Y. Ikegami 2628* (A); Saitama Pref., Chichibu-gun, Kamiizumi-mura, Inamura, *J. Murata et al. 1790* (AAU[2], PE); Shiga Pref., Ika-gun, Kinomoto-cho, Harikawa, *G. Murata & S. Kitamura 3362* (AAU, C, E, K, L, UC); Shimane Pref., Lishi-gun, Tonbara-cho, Mt. Oyorogi, *K. Mimoro & S. Thugaru 3195* (A, MO); Tochigi Pref., Nikko, 1864, *S. Tschonoski s.n.* (A, BM, C, K); Tokyo Pref., Nishitama-gun, Mt. Mitake-Nanayo Fall, *S. Kobayashi 1055* (CAS); Yamagata Pref., Nishi-murayama-gun, Nishikawa-machi, upper Mazawa River, *S. Tsugaru & T. Takahashi 6607* (MO). NORTH KOREA. **Locality unknown:** 1963, *collector unknown* (IBSC); Wolgoic Jongsan, 1914, *R. G. Mills s.n.* (PE). SOUTH KOREA. **Cheju:** Halla-san, *T. Taquet 3036* (A, C, E). **Kangwon:** Kongo-san, *E. H. Wilson 10422* (BM, K). **Kyonggi:** near Duigen, *E. H. Wilson 8467* (A). **North Chungchong:** Hwanghak-san, 33 mi. SE of Taejon, *Chung In Cho 8276* (E). **North Kyongsang:** Port Chusan, *C. Wilford 934* (A, K). **Seoul City:** Tobong-san, *R. Moran 5209* (BM, BR, E, GH, L, MO, UC). **South Kyongsang:** S'onch'ong Dist., slopes of Chiri-san, Chiri-san Natl. Park, *F. Kirkham & Boyce KFBX86* (K).

10. Styrax odoratissimus Champ. ex Benth., Hooker's J. Bot. Kew. Gard. Misc. 4: 304. 1852 [as *S.* "*odoratissimum*"]. TYPE: China. Hong Kong: ravines of Mt. Victoria, *J. G. Champion 138* (holotype, K!; isotypes, E!, K[3]!).

Styrax prunifolius Perkins, Bot. Jahrb. Syst. 31: 486. 1902. TYPE: China. Province unknown: Pokfolanz [from Perkins, 1907], *Hillebrand s.n.* (holotype, B destroyed).

Styrax veitchiorum Hemsl. & E. H. Wilson, Bull. Misc. Inform. Kew 1906: 161. 1906 [as *S.* "*Veitchiorum*"]. TYPE: China. Hubei: Fang Xian, 2100–2400 m [protologue], June 1907, *E. H. Wilson 2015* (holotype, K not seen; isotypes, A[2]!, IBSC!).

Trees to 10 m tall. Young twigs sparsely short-yellow-brown stellate-pubescent; older twigs purplish or dark brown, glabrescent. Petiole 5–12 mm long. Two most proximal leaves on each shoot alternate. Lamina 4–15 × 2–8 cm, chartaceous to thick-chartaceous, ovate, ovate-elliptic, or elliptic, dull light green to yellow-green at maturity when dry; apex acute to short-acuminate; base broadly cuneate to rounded; adaxially usually glabrous except midvein, abaxially usually glabrous except midvein and axils of secondary veins, sometimes yellow-brown stellate-tomentose or -hirsute but surface remaining visible through the pubescence; margin entire or remotely serrulate apically, secondary veins 6 to 9 on each side of midvein; tertiary veins subparallel, densely, adaxially plane or slightly sunken, abaxially prominent. Fertile shoots 7–15 cm long, 3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- to 2-flowered or racemose, 3–5 cm long, (3- to)5- to 7-flowered; pseudoterminal inflorescences usually racemose or rarely paniculate, 3–8 cm long, 5- to 7(to 11)-flowered, rarely 1-flowered, rachis and branches yellow stellate-tomentose. Pedicel 4–9 mm long, yellow stellate-tomentose; bracteoles 2–4 mm long, subulate, positioned at various places along the pedicel but mostly near the base, more rarely near the middle. Flowers 1–1.5 cm long. Calyx 3–4(–5) × 3–4 mm, cupuliform; adaxially glabrous; abaxially yellow stellate-tomentose, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin truncate, undulate, or irregularly lobed, the teeth minute, not contiguous if present. Corolla 0.6–1.0 cm long, white, tube 3–4 mm long, glabrous, lobes 5(6), 9–11 × 4–6 mm, 1.7–2.2 × as long as wide, elliptic to obovate-elliptic. Stamens 10(12); filaments 1.5–3 mm long, slightly flexuous at middle, proximally broadened, distally attenuate, densely white stellate-pubescent throughout; anthers 4–5 mm long, wider than distal portion of filament; connectives (at least proximally) densely appressed-stellate-pubescent. Style densely white stellate-pubescent nearly throughout, distally thinning; stigma 0.2–0.5 mm wide, punctiform. Fruit 0.8–1.0 × 0.6–0.8 cm, usually subglobose, occasionally ovoid, apex rostrate, rarely merely apiculate, dehiscent; pericarp dry, (0.3–)0.5–1.0 mm thick, outside smooth or slightly rugose, gray-yellow stellate-tomentose, inside sparsely appressed-stellate-pubescent. Seeds brown, ovoid, slightly rugose, usually appressed-stellate-pubescent or lepidote, rarely glabrous.

Illustrations. Miers, Contr. Bot. I: t. 29. 1851–1861; Hu, Bull. Fan Mem. Inst. Biol. 3: pl. 16. 1932; Anonymous, Ic. Cormophyt. Sin. 3: 336, fig. 4626. 1974; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1620, fig. 813. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 101, pl. 34 (1–5). 1987; J. Q. Liu in L. G. Lin, Fl. Fujian. 4: 352, fig. 285. 1989; X. M. Liu in X. H. Qian, Fl. Anhui 4: 67, fig. 1771. 1991; S. Y. Wang in B. Z. Ding, Fl. Henan 3: 231, fig. 1776 (1–2). 1997; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 203, fig. 203 (1–6). 2000.

Phenology. Flowering: March–July, September. Fruiting: March–November.

Distribution. China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hong Kong, Hubei, Hunan, Jiangsu, Jiangxi, Shanxi, Sichuan, Yunnan, and Zhejiang); Figure 9.

Habitat. In relatively mesic, semi-open, broad-leaved forests on mountain slopes, along streams in ravines; 30–2100 m.

Vernacular names. Bai-mu (China, Guangxi; *G. X. Li 54*), Er-huan-dong-gua (China, Hunan; *P. C. Tam 61731*), Fen-fang-an-xi-xiang (Hwang, 1980), Gou-len-cai (China, Guangdong; *K. P. To et al. 12645*), Guang-ye-mo-li-bao (China, Guizhou; *P. C. Tsoong 681*), Hong-la-jiu-shu (China, Guangdong; *W. T. Tsang 20435*), Huang-ye-shu (China, Anhui; *Exp. Anhui 2376*), Ji-gu-duan (China, Jiangxi; *J. Xiong 1860*), Mao-ye-mo-li (China, Zhejiang; *Y. Y. Ho 24610*), Mao-ye-shui-dong-gua (China, Guangxi; *S. Q. Chen 14692*), Niu-zi-shu (China, Jiangxi; *C. M. Hu 5271*), Ru-bai-ye-mo-li (Hwang & Qi, 1985), Shan-long-yan (China, Guangdong; *W. T. Tsang 21712*), Shuang-chi-shan-mo-li (China, Hunan; *Z. H. Shen 1235*), Ye-jin-gu (China, Zhejiang; *Zhejiang Bot. Res. Team 25888*), Ye-ling-li (China, Zhejiang; *Y. Y. Ho 26445*), Yu-xiang-ye-mo-li (China, Shanxi; *T. W. Liu & Z. B. Zeng 1372*), Xiang-ye-ye-mo-li (China, Zhejiang; *Zhejiang Bot. Res. Team 28350*), Yu-xiang-ye-mo-li (Anonymous, 1974).

The Chinese endemic species *Styrax odoratissimus* is one of the most common and widespread species treated in this revision. This species is most abundant in eastern and southeastern China, gradually decreasing in abundance northward and westward.

Styrax odoratissimus exhibits much morphological variation across its range. The lower laminar surface is mostly glabrous, but is sometimes stellate-tomentose or -hirsute, although the surface always remains visible through any pubescence present. In addition, leaf size, inflorescence length, and flower number vary significantly throughout the range of the species. It nonetheless can easily be distinguished from other sympatric species with imbricate corolla aestivation (i.e., *S. hemsleyanus, S. hookeri, S. japonicus, S. macrocarpus, S. supaii,* and

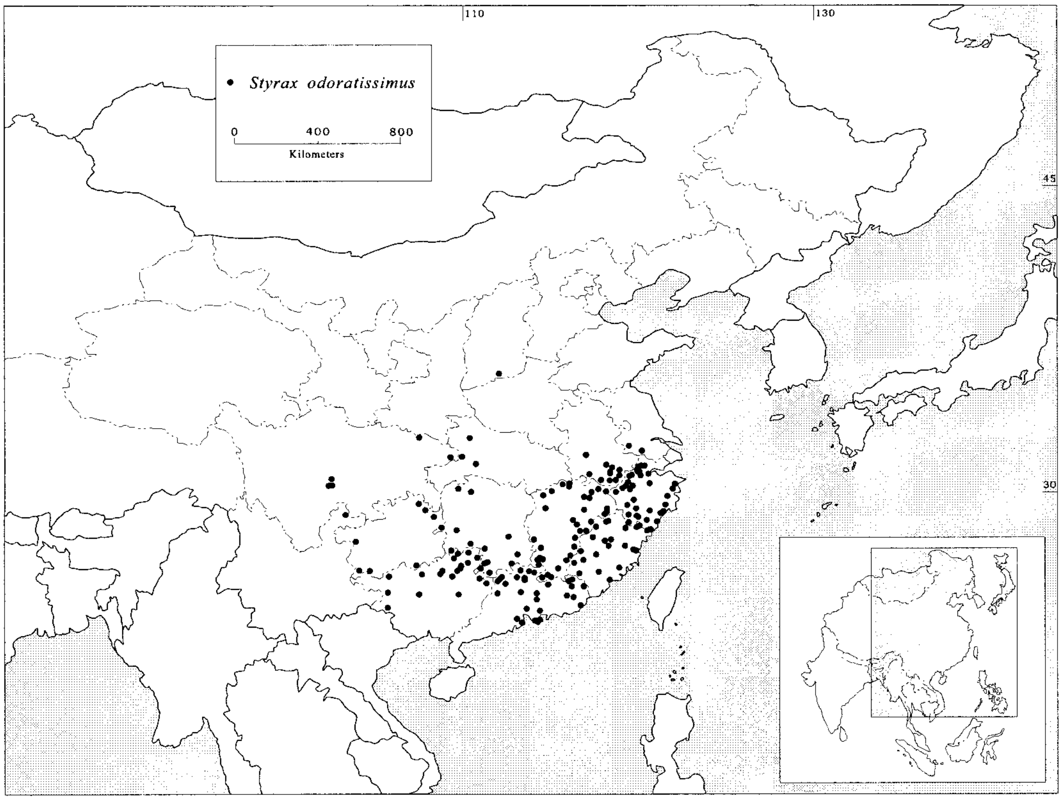

Figure 9. Geographic distribution of *Styrax odoratissimus.*

S. tonkinensis) by the combination of its distinctively flexuous filaments and densely pubescent stamens and styles. Furthermore, the appressed-stellate-pubescent or lepidote seeds often served to distinguish it from other species of *Styrax,* although some glabrous individuals exist. Sterile herbarium specimens can usually be distinguished from other sympatric species by leaves that are yellow-green in the dried state and often slightly scabrous adaxially. Moreover, the petiole and proximal portion of the midvein are both usually red-tinged in the living state. It is unknown whether this feature is restricted to this species within the genus, but it seems at least to distinguish *S. odoratissimus* from sympatric species.

Perkins (1907) considered differences in inflorescence length and the leaf margin sufficient to separate *Styrax veitchiorum* Hemsl. & E. H. Wilson, a species described from flowering material collected in Fang Xian, Hubei Province, China, from *S. odoratissimus.* Subsequently, Rehder (1912) identified fruiting material from the same county (*Wilson 308*) as *S. veitchiorum.* We consider the characters used by Perkins (1907) to separate these two taxa to vary continuously. The fruit of *S. veitchiorum* differs from that of most other fruiting collections of *S. odoratissimus* in its glabrous (vs. pubescent or lepidote) seeds. Glabrous seeds, however, appear sporadically in other individuals of *S. odoratissimus.* Because no other characters are apparent for use in delimiting the two entities, our treatment follows that of Hwang (1987) in placing *S. veitchiorum* as a synonym of *S. odoratissimus.*

Perkins (1902) described *Styrax prunifolius* Perkins based on a specimen from China (*Hillebrand s.n.*) but later (1907) treated this species as a synonym of *S. odoratissimus.* We assume that the holotype of *S. prunifolius* was at B because that is where Perkins conducted her work on *Styrax,* and that this has been destroyed. Having seen no duplicate material of *Hillebrand s.n.,* we here place *S. prunifolius* under *S. odoratissimus* following the precedent set by Perkins (1907), and in considering its similarity to *S. odoratissimus* as inferred from the original description.

Some specimens of *Styrax odoratissimus* collected at the northwestern edge of the species' range, especially on and near Mt. Emei (E-mei-shan in Pinyin) in Sichuan Province, exhibit atypical features (i.e., a more cylindrical fruit, larger leaves, and glabrous seeds; e.g., *China-USSR team 1853*; *Ching & Shun 80*; *H.-C. Chow 7547* and *8016*; *Rev. E. Faber 195*; *W. P. Fang 2462, 7560, 12624,* and *16790*; *X. Y. Huo 5654*; *C. B. Peng 6070*; *S. L. Sun 540*; *T. H. Tu 347* and *407*; *G. H. Yang 55029*). Several of these have been identified as *S. hemsleyanus,* but are easily distinguished from that species by the alternate (vs. subopposite to opposite) arrangement of the two most proximal leaves on each shoot. Furthermore, the fruits available for study from these specimens are rostrate, as in *S. odoratissimus,* and the flower buds (no open flowers are available for study) do not deviate from the range of variation within *S. odoratissimus* as defined here (e.g., the filaments and styles are densely pubescent throughout, the connectives are slightly pubescent, and the filaments are flexuous). The atypical fruits and seeds observed in these specimens are distributed sporadically across the range of *S. odoratissimus,* i.e., in the provinces of Anhui (*C. S. Fan & Y. Y. Li 221*), Guangdong (*H. G. Liu 490* and *P. C. Tam 58332*), Guangxi (*L. X. Chen 500159*), Hunan (*P. H. Liang 83722*), and Yunnan (*B. X. Sun et al. 254*) in addition to Sichuan and Hubei mentioned above, and thus have no apparent taxonomic significance. Thus, we place the Emei specimens under this species, with the caveat that specimens collected at anthesis would be highly desirable for corroboration.

The closest relatives of *Styrax odoratissimus* appear to be several species from the southern part of the range of *Styrax* in Asia. These include *S. buchananii, S. chrysocarpus, S. curvirostratus, S. porterianus,* and *S. subpaniculatus.* The relationships among these species are not well understood, but each shares with *S. odoratissimus* the alternate arrangement of the two most proximal leaves on each shoot; a lower laminar surface that is visible through any pubescence that may be present (vs. a tomentum that obscures the surface); a calyx that is truncate, undulate, or irregularly lobed, the teeth not contiguous if present, and the outer surface within 1 mm of the margin more sparsely pubescent than the rest of the calyx or subglabrous to glabrous, somewhat scarious, and brown when dry, but without scattered orange or brown stiff long stellate pubescence. Differences between *S. odoratissimus* and these species are addressed in respective discussion sections of each species.

Selected specimens examined. CHINA. **Anhui:** Dongzhi Xian, Xiang-ling, *C. M. Tan 971113* (PE); Huangshan Shi, Huang-shan-qu, Huang-shan, *M. J. Wang 3780* (IBSC, PE); Jingde Xian, Ou-yuen, *P. Courtois 25676* (P); Jixi Xian, *Exp. Anhui 1059* (PE); Qimen Xian, Li-xi, Ku-liu-feng, *Y. F. Xiao & W. Z. Xie 152* (IBSC); Qingyang Xian, Jiu-hua-shan, *S. C. Sun 1204* (A); She Xian, Huang-shan, *M. Chen 1061* (IBSC, PE); Shucheng Xian, Wan-fu-shan, *M. P. Deng 11153* (PE); Xiuning Xian, Wu-cheng, *Exp. Anhui 2344* (PE). **Fujian:** Changting Xian, Gui-long-shan, *C. M. Hu 3737* (IBSC, KUN, PE); Chong'an Xian, Xin-chun-xiang, *Exp. Wu-yi-shan 11* (IBSC, PE); Fuding Xian, Tong-mu-xiang, Tong-shan, *P. X. Qiu 1487* (PE[2]); Fuzhou Shi, hillside near University Foo-chow, *T. S. Ging 7524* (A); Guangze Xian, Chu-fu-xiang, Xia-yang-da-dui, *Y. T. Zhang 79025* (IBSC); Gutian Xian, *Y. G. Yan 6215* (KUN); Hua'an Xian, Xin-kou, *P. C. Tsoong 648* (IBSC[2], PE); Liancheng Xian, Zhang-di-jing, 1932, *Y. Ling s.n.* (PE); Minhou Xian, *H. H. Chung 2742* (A, UC); Nanping Shi, Yan-dang-shan, *G. S. He 4256* (MO); Ninghua Xian, Hui-hua, Shui-kou-xiang, *K. M. Wu 60225* (IBSC); Shanghang Xian, Bu-yun, *Exp. Wu-yi-shan 6839* (PE); Sha Xian, Xi-qing, *Pl. Res. Exp. in Fujian 52459* (IBSC); Shouning Xian, *R. C. Ching 2241* (A[2], IBSC, UC); Shunchang Xian, Tian-ping, Hou-shan, *M. S. Li & Z. Y. Li 4584* (PE); Taining Xian, Long-an, Chen-keng, Wu-niu-wan-shan, *M. S. Li & Z. Y. Li 252* (IBSC); Xiamen Shi, Ban-tou Reservoir, *G. L. Cai 38* (IBSC); Yong'an Xian, *D. S. Wang 453* (PE); Yongchun Xian, Fang-guang, *collector unknown 273* (PE); Zhenghe Xian, *H. H. Chung 2615* (A, IBSC, PE, UC). **Guangdong:** Dabu Xian, Tong-gu-shan, *W. T. Tsang 21712* (A[3], BM, IBSC, K, PE[2], UC); Fengshun Xian, Da-tian-xiang, Bei-xi, *X. G. Li 200955* (IBSC, PE); Heping Xian, Li-ming-shan, *G. C. Zhang 256* (IBSC); Huaiji Xian, Hei-chong, Yuan-shan-lin-chang, *Z. Y. Li 1681* (MO); Huiyang Shi, Luo-fu-shan, Hua-sou-tai, *N. K. Chun 41677* (IBK, IBSC, KUN, PE); Jiaoling Xian, Si-hu-xiang, *L. Tang 4630* (IBSC, PE); Lechang Shi, Heo-tse-ling, Da-lang, *Y. Tsiang 1386* (A, IBSC, UC); Liannan Yaozu Zizhixian, Jin-keng-xiang, *P. C. Tam 59535* (PE); Lianshan Zhuangzu Yaozu Zizhixian, He-gang-xiang, Huang-niu-shan, *P. C. Tam 58332* (IBK, IBSC, PE); Lianzhou Shi, Xin-jiu-xiang, *Exp. Nan-ling 272* (IBSC); Longmen Xian, San-jiao-shan, Cong-hua, *W. T. Tsang 20435* (PE); Meizhou Shi, Mei-song-dong, *X. G. Li 202464* (IBK, IBSC, PE); Nanhai Shi, Shih-pi-keng, Hao-shan, *S. S. Sin 9444* (A); Pingyuan Xian, Cha-gan-xiang, Huang-zhu-ping, *L. Tang 4380* (IBSC, PE); Qujiang Xian, Long-tou-shan, *S. P. Ko 50337* (IBK, IBSC, MO, PE); Renhua Xian, Jen-hwa Dist., Shi-bi-xia-cun, Wan-chi-shan, *W. T. Tsang 26345* (A, E, IBSC); Ruyuan Yaozu Zizhixian, Qing-xi-dong, *S. P. Ko 52889* (A, IBK, IBSC); Shantou Shi, Wu-king-fu, 60 mi. W of Swa-tow, *J. M. Gilchrist 79* (IBSC); Shaoguan Shi, *Exp. Guangdong 1244* (IBSC); Shixing Xian, Chang-keng, Che-ba-ling, *C. L. Zhang 56031* (MO); Wuhua Xian, Chang-bu-xiang, Qi-mu-shan, *X. G. Li 201687* (IBK, IBSC, PE); Xinfeng Xian, Ah-p'o-kai-shan, Cha-ping-cun, *Y. W. Taam 721* (A, CAS, K, KYO); Yangshan Xian, Wu-yuan-xiang, *L. Tang 1069* (IBSC, KUN); Yingde Shi, Sha-kou-xiang, Hua-shui-shan, *C. Huang 163471* (IBSC); Zengcheng Shi, Nan-kun-shan, *W. T. Tsang 20301* (PE). **Guangxi:** Bose Shi, Wu-lao-shan, *Exp. S China 2658* (IBSC); Du'an Yaozu Zizhixian, He-jing-xiang, Mao-er-shan, *Exp. Guangxi 455* (IBSC, KUN, PE); Fuchuan Yaozu Zizhixian, Ku-cun, *S. S. Sin 21326* (IBSC); Guilin Shi, Da-jiang-yuan-cun, Jin-gang-shan, *W. T. Tsang 28311* (A, IBSC); Hezhou Shi, Xi-shan-xiang, *H. C. Chen et al. 500072* (IBK, IBSC); Huanjiang Maonanzu Zizhixian, Wu-hua-shan, Jiu-ren, *H. N. Qin 895180* (K); Jingxi Xian, Biao-lin-xiang, Long-yang-shan, *S. P. Ko 55648* (A, IBSC); Jinxiu Yaozu Zizhixian, Niu-xiang-xiang, Da-ling, *D. H. Qin et al. 65266* (PE); Leye Xian, Niu-wei, Ba-wang-shan, *Exp. Hong-shui-he 1085* (KUN);

Lingchuan Xian, Qi-fen-shan, *Z. Z. Chen 53822* (KUN); Lingui Xian, Huang-sha-xiang, *Z. Z. Chen 51016* (IBK, IBSC, KUN, PE); Longsheng Gezu Zizhixian, Da-di-xiang, *Guang-fu Coll. Team 707* (IBK, IBSC, KUN, PE); Quanzhou Xian, Shan-chuan-xiang, Bao-ding-shan, *C. H. Tsoong 83331* (IBK, IBSC, PE); Xing'an Xian, Wu-tong-shan, *T. M. Tsui 250* (A, IBSC, K, PE); Yongfu Xian, He-shun-xiang, *G. X. Li 54* (IBK, IBSC); Ziyuan Xian, Chuen yuen, *T. S. Tsoong 82058* (A, IBK). **Guizhou:** Anlong Xian, Shi-pan-xiang, Shi-hui-dui, *Exp. Guizhou 2924* (PE); Jiangkou Xian, Fan-jing-shan, *Exp. Hunan & Guizhou (1983) 2626* (KUN); Libo Xian, Wei-zi, *X. H. Song 185* (MO); Shuicheng Xian, *P. C. Tsoong 437* (KUN); Wuchuan Xian, Lian-tai-shan, *P. C. Tsoong 681* (KUN, PE[2]); Yinjiang Xian, Qing-du-he, Fan-jing-shan, *Z. S. Zhang et al. 402501* (IBSC). **Hongkong:** N of Shou-son Hill, Hong Kong Island, *B. Bartholomew 1916* (CAS). **Hubei:** Badong Xian, Ge-zi-he, *Z. Y. Wang 618* (PE); Fang Xian, *E. H. Wilson 308* (A, BM, E, K); Yichang Shi, 1888, *A. Henry s.n.* (K). **Hunan:** Cili Xian, Suo-xi-yu Nature Reserve region, *X. Y. Xi et al. 443* (PE); Dao Xian, Niu-tou-jiang, *P. C. Tam 61731* (IBK, IBSC); Hengyang Shi, Li-mu-you, *P. C. Tam 62348* (IBK, IBSC); Jianghua Yaozu Zizhixian, He-luo-kou-xiang, *B. G. Li 5149* (IBSC); Lingling Xian, Yang-ming-shan, Huang-jiang-yuan, *S. Q. Chen 674* (IBK, IBSC); Qianyang Xian, Huai-hua, *X. G. Li 203380* (IBSC); Sangzhi Xian, Bao-mao-xi, *T. R. Cao 90621* (KUN); Tongdao Dongzu Zizhixian, *T. C. Chen 1028* (IBSC); Xinhuang Dongzu Zizhixian, Tian-lei forest farm, *Zhong-nan-lin-shi-xi-dui 163* (IBSC); Xinning Xian, Jin-shi-zhen, Dong-tou-cun, *L. B. Luo 93* (BM, BR, CAS, IBSC, PE); Yizhang Xian, Mang-shan, Jin-quan-xiang, *P. H. Liang 83707* (IBK, IBSC, MO); Zixing Shi, Ping-jiang-xiang, Luo-jia-qiao, *P. H. Liang 86298* (IBSC, MO). **Jiangsu:** Yixing Shi, Long-chi-shan, *S. H. Mao et al. 44* (IBK, KUN, MO, PE). **Jiangxi:** Anyuan Xian, Du-jiang-xiang, *C. M. Hu 2758* (IBK, IBSC, KUN, PE); Boyang Xian, Li-ming-shan, *Q. H. Li & C. Chen 1146* (PE); Chongren Xian, Kou-ling, Tsoong-jen, *Y. Tsiang 10140* (IBSC, UC); Chongyi Xian, Mi-xi, Ji-gong-zui, *M. Q. Nie et al. 8625* (IBK, IBSC, KUN); Dayu Xian, Huang-long, *M. Q. Nie et al. 6700* (IBSC); Dingnan Xian, Da-cha, *J. Xiong 1860* (PE); Dongxiang Xian, *Q. H. Li & C. Chen 1470* (PE); Guangchang Xian, Ping-fang-xiang, *C. M. Hu 5271* (IBSC, PE); Huichang Xian, Fu-cheng-xiang, *C. M. Hu 3342* (IBK[2], IBSC, KUN, PE); Jingdezhen Shi, Fu-liang, Xi-hu-xiang, *Q. H. Li & C. Chen 834* (PE); Jinggangshan Shi, *S. K. Lai et al. 5008* (IBSC); Jiujiang Shi, Lu-shan, Sai-yin, *M. X. Nie 7265* (KUN); Leping Shi, Li-jun-shan, Da-he-shan, *Q. H. Li & C. Chen 1335* (PE); Lichuan Xian, Yan-chuan-qu, Wu-yi-shan, *M. X. Nie & S. S. Lai 2881* (IBSC, KUN[2]); Longnan Xian, Wu-zhi-shan, near Lin-wu-dong-cun, *S. K. Lau 4432* (A, BM); Nanfeng Xian, San-xi-xiang, *X. X. Yang 650492* (IBSC, PE); Nankang Xian, *X. X. Yang 650367* (IBSC); Quannan Xian, Zhu-shan-xiang, Yao-shan, *J. Xiong 723* (PE); Ruijin Shi, Qing-xi-xiang, Lian-tang, *C. M. Hu 4252* (IBSC, KUN[2], PE); Shangrao Shi, Wu-yi-shan, *M. X. Nie & S. S. Lai 4331* (IBSC, KUN); Shangyou Xian, Guang-gu-shan, *M. Q. Nie et al. 8342* (IBK, KUN); Shicheng Xian, Jing-kou-xiang, *C. M. Hu 4585* (KUN, PE); Suichuan Xian, Qi-ling-xiang, *S. K. Lai et al. 235* (PE); Wuning Xian, Yi-shan-gong-she, *S. S. Lai 2464* (KUN, PE); Xiushui Xian, Huang-sha-gang, Xiang-jia-ping, *S. S. Lai 3458* (KUN); Yifeng Xian, Guan-shan, Xi-keng, *S. K. Lai et al. 433* (PE); Yihuang Xian, Bai-zhu-xiang, *X. X. Yang 16820* (IBSC); Zixi Xian, Ma-tou-shan-xiang, Wu-yi-shan, *M. X. Nie & S. S. Lai 3530* (IBSC, KUN). **Shanxi:** Yangcheng Xian, Gan-qi-tong, Shu-pi-gou, *T. W. Liu & Z. F. Zeng 235* (MO). **Sichuan:** Emeishan Shi, E-mei-shan, *W. P. Fang 2462* (A, IBSC, K, PE); Fengjie Xian, Xin-he-xiang, *H. F. Zhou 26228* (KUN); Hongya Xian, Chang-tsun, *T. H. Tu 347* (PE); Wanyuan Shi, *K. L. Chu 1266* (IBSC). **Yunnan:** Yanjin Xian, Cheng-feng-shan, *Exp. NE Yunnan 1163* (KUN). **Zhejiang:** Anji Xian, Long-wang-shan, *W. C. Wang L8532018* (IBSC); Chun'an Xian, Lin-qi-xiang, Xia-keng, *Zhejiang Bot. Res. Team 27581* (MO, PE); Hangzhou Shi, Bei-gao-feng, Ning-ying-shi, *S. Y. Chang 1512* (MO); Jiande Xian, from Jian-de to Shuang-xi-kou, *Y. Y. Ho 29245* (MO); Kaihua Xian, Gu-tian-miao, *J. X. Wang 2099* (PE); Lin'an Shi, Shun-xi, *G. B. Li J8112140* (PE); Lishui Shi, Da-gang-tou, Xiao-jing, *S. Y. Zhang 6054* (KUN, PE); Longquan Shi, Feng-yang-shan, *H. Y. Zou 123* (A); Pingyang Xian, Suan-ke, S of Ping-yung, *R. C. Ching 2080* (A, IBSC, K, UC); Qingtian Xian, Tsimp-tien, *Y. L. Keng 211* (A, PE); Qingyuan Xian, Long-gong, *S. Y. Zhang 3450* (PE); Suichang Xian, Qiu-jia-ping, *R. C. Ching 1622* (A, UC); Taishun Xian, Jin-fen, Liao-yan, *S. Y. Chang 8514* (MO); Tiantai Xian, Tian-tai-shan, *R. C. Ching 1434* (A, IBSC); Wencheng Xian, Da-jun, Jing-ning, *S. Y. Chang 5178* (MO); Wuyi Xian, Xi-lian-xiang, *R. J. Jin et al. J8311012* (IBSC); Xianju Xian, *S. Y. Chang 7772* (MO); Yunhe Xian, Chen-chiong, 40 mi. S of Sia-chu, *R. C. Ching 1809* (A, E, IBSC, UC); Zhuji Shi, Wu-qian, *X. B. Li et al. J8212029* (PE).

11. Styrax porterianus G. Don, Gen. Hist. 4: 5. 1838 [as *S.* "*Porterianum*"]. *Styrax serrulatus* var. *rugosus* Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 249. 1932. TYPE: Malaysia. Pulau Pinang: Pinang, *Wall. Cat. No. 4401* (*G. Porter s.n.*) (holotype, BM!; isotypes, K[3]!).

Styrax floribundus Griff., Not. Pl. Asiat. 4: 287. 1854 [as *S.* "*floribunda*"]. TYPE: Myanmar. Tenasserim: between Kulweng and Mergue, Apr. 1835, *W. Griffith s.n.* (lectotype, designated here, K [loan accession no. H2000/01016-380]!; isotypes, K [loan accession no. H2000/01016-39]!, E!).

Styrax betongensis H. R. Fletcher, Bull. Misc. Inform. Kew 1937: 509. 1938. TYPE: Thailand. Pattani: Betong, 200 m, 6 Aug. 1923, *A. F. G. Kerr 7494* (holotype, K!; isotypes, BM!, E!, K!).

Trees to 20 m tall. Young twigs dull red or gray tomentose; older twigs gray, glabrescent. Petiole 3–7 mm long. Two most proximal leaves on each shoot alternate. Lamina 5–11 × 3–5 cm, membranaceous or thin-chartaceous, ovate- to elliptic-oblong, green to dark green at maturity when dry; apex slightly acuminate; base usually oblique-rounded, rarely oblique-cuneate, short-attenuate; adaxially glabrous except along the major veins; abaxially glabrous or sparsely to densely white stellate-pubescent, pubescence especially prevalent on veins and the most proximal two leaves on each shoot, surface remaining visible through the pubescence; margin entire or usually remotely serrulate; secondary nerves 5 or 6 on each side of midvein; tertiary veins ± parallel and perpendicular to the secondaries, faintly prominent on both sides. Fertile shoots 5–12 cm long, 2- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- to 2-flowered or racemose, 2–3 cm long, 1(to 5)-flowered; pseudoterminal inflorescences racemose, 2–4 cm long, 3- to 5(7)-flowered, rachis red-gray stellate-tomentose. Pedicel 3–10 mm long, densely stellate-pubescent; bracteoles 0.5–2 mm long, linear, positioned at various places along the pedicel but mostly near the base, more rarely near the middle, sometimes those toward the base of the inflorescence leaf-like. Flowers 0.7–1.3 cm long. Calyx 3–4 × 3–4 mm, campanulate; adaxially glabrous or sparsely short-appressed-stellate-pubescent; abaxially gray stellate-tomentose, within 1 mm from the margin more sparsely pubescent, somewhat scarious, brown when dry; margin truncate, undulate, or slightly 5-lobed, the teeth minute and not contiguous. Corolla 0.5–0.9 cm long, white, tube 2–3 mm long, glabrous proximally, lobes 5, 10–11 × 3–4 mm, linear-lanceolate, apex acute-acuminate, adaxially sparsely stellate-pubescent, abaxially densely so. Stamens 10; filaments 3–4 mm long, straight or flexuous at middle, distally attenuate, moderately to densely white stellate-pubescent on both sides, thinning to glabrous distally; anthers 3–4.5 mm long, wider than distal portion of filament; connective glabrous. Style glabrous; stigma 0.4–0.5 mm wide, subcapitate. Fruit 0.9–1.5 × 0.8–1.2 cm, subglobose to globose, apex rounded or short-apiculate, indehiscent; pericarp fleshy, ca. 2 mm thick, outside deeply rugose when dried, gray stellate-tomentose, inside glabrous. Seed brown, ellipsoid to ovoid-ellipsoid, nearly smooth, glabrous.

Illustrations. Miers, Contr. Bot. I: t. 29. 1851–1861; Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 222, fig. 3 (5). 1932 (as *S. serrulatus* var. *rugosus*). F. E. Putz & F. S. P. Ng, Tree Flora of Malaya 3: 265, fig. 1. 1978 (as *S. serrulatus* var. *rugosus*).

Phenology. Flowering: March–May, July. Fruiting: March–May, July, August, November.

Distribution. Malaysia (Kedah, Pahang, Perlis, and Pulau Pinang), Myanmar (Tenasserim), and Thailand (Chumphon, Krabi, Nakhon Si Thammarat, Pattani, Phangnga, Phuket, Satun, Songkhla, Surat Thani, and Trang); Figure 4.

Habitat. In mesic, mixed primary forests; 50–400 m.

Vernacular names. Fa La Mi Bai Leg (Thailand; *S. Phusomsaeng 241*), Kam Yan (Thailand; *A. F. G. Kerr 7494*), Lang Ka Re (Thailand; *A. F. G. Kerr 15300*), Pang Ka Re (Thailand; *A. F. G. Kerr 18505*).

Styrax porterianus is the only species of *Styrax* with imbricate corolla aestivation known from the Malay Peninsula, where it is endemic. *Styrax porterianus* appears to be most closely related to *S. odoratissimus* and *S. subpaniculatus.* All three species share relatively small flowers, a truncate, undulate, or irregularly lobed calyx margin, and an abaxial laminar surface usually visible through any pubescence present. Furthermore, they all occur at relatively low elevations. *Styrax porterianus* is easily distinguished from *S. subpaniculatus* by its shorter raceme and thinner, dry and rigid pericarp, and from *Styrax odoratissimus* by the characters in couplet 20 of the key.

Despite the placement of *Styrax porterianus* into series *Imbricatae* by Perkins (1907), Steenis (1932) considered this species to be a variety of *S. serrulatus* (var. *rugosus* Steenis). Perkins (1907) placed *Styrax serrulatus* in series *Valvatae* based on its valvate corolla aestivation. Steenis's concept of *S. serrulatus,* however, contained both imbricate and valvate types of aestivation based on Perkins's (1907) assertion that this and several other species in series *Valvatae* include individuals that exhibit a mixture of these types, even within the same flower. In contrast, we consider aestivation type to be a reliable taxonomic character with which to distinguish *S. porterianus* from *S. serrulatus.* In several species of series *Cyrta* (those listed by Perkins under series *Valvatae* and several other more recently described species), a subvalvate condition occurs whereby the edges of the corolla lobes are contiguous but oblique in cross section (see Steenis, 1932: fig. 10c). This is qualitatively different, however, from the strictly imbricate corolla aestivation observed in all specimens of *S. porterianus* (see Steenis, 1932: fig. 10d).

Styrax porterianus differs from *S. serrulatus* s. str. in other aspects of both the foliage and fruit, as Steenis recognized. In *S. porterianus,* the margin of the lamina is entire or at most remotely denticulate, whereas that of *S. serrulatus* is distinctly toothed. The fruit of *S. porterianus* has a fleshy pericarp at maturity (Putz & Ng, 1978; unique among species of section *Styrax*) that is rugose and ca. 2 mm thick in the dried state. In contrast, the pericarp of *S. serrulatus* is dry and rigid at maturity, nearly smooth, and less than 1 mm thick. Furthermore, the ranges of these two entities are geographically distinct, with *S. serrulatus* in the Himalayan region and not extending as far south as the Malay Peninsula (P. Fritsch, unpublished data). The sum of these differences warrants the recognition of *S. por-*

terianus at the species level. Fletcher (1938) appears to have understood the significance of these differences as well in describing *S. betongensis* H. R. Fletcher from Thailand, apparently unaware of the earlier name.

We have seen two sheets of W. Griffith's collection of *Styrax floribundus* from K and one from E. None of these display any indication of holotype status. Because Griffith's herbarium was transferred to K, we have chosen a lectotype from among the two K specimens. The two sheets offer little evidence for a decision on proper lectotypification, and we could not locate a literature source with a sample of Griffith's handwriting. On one of the K sheets, however, the locality is spelled as in the protologue ("Mergue"), whereas on the other it is spelled differently ("Mergui"), suggesting that the locality information on the latter was transcribed incorrectly some time after the original collection was made. On this basis, we have designated the sheet with the protologue spelling of the locality as the lectotype.

Additional specimens examined. MALAYSIA. **Kedah:** Jeniang, Kedah, bin Kiah, *Sidek S345* (C, L). **Pahang:** Tembeling, Ulu Sg., NW Tanjong Bungkal, *M. Shah Bin Haji Mohamad Nur & M. Noor MS2027* (C, L). **Perlis:** Kaki bukit, *M. S. Kiah bin Hadji 35302* (BM, K, L). **Pulau Pinang:** Pinang, *collector unknown* (BM), 1890, *collector unknown* (E), *C. Curtis 1538* (BM, L), *M. R. Henderson 18* (L); Pinang Island, 1824, *J. Phillips s.n.* (K); Peuara Bakir, 1896, *collector unknown* (BM); Polo Boelong, *collector unknown 1189* (K). THAILAND. **Chumphon:** Kao Po Ta luang Kaew, Ranong, *C. Niyomdham 339* (L). **Krabi:** Pen, Nong Khon, *B. Sangkhachand 1014* (C, K, L). **Nakhon Si Thammarat:** Tung Song, *N. Rabil Bunnag 92* (BM, K, L); Ban Kram, Nakawn Sritamarat, *A. F. G. Kerr 15300* (E[2], K); Ban Kram, Palatung, *A. F. G. Kerr 15302* (BM). **Phangnga:** Khao Phra Mi, *Flora of Thailand Project 4th Exp. (1972) 30878* (L); Nai chong, *R. Geesink & T. Santisuk 5275* (AAU, C, E, K, L). **Phuket:** Satul, Tung nui, *A. F. G. Kerr 14659* (BM, E, K); Kaokatawam, *A. F. G. Kerr 18505* (BM, E, K); Lanta, *A. F. G. Kerr 18988* (BM, E, K). **Satun:** Tarutao Natl. Park, from Talo Wao to Talo Oo Dang, *G. Congdon 507* (AAU). **Songkhla:** Dist. Haad Yai, Ko Hong Hill, *J. F. Maxwell 85346* (AAU, BM, E, L), *85535* (AAU, E, L); Lansagah Dist., Khao Luang Natl. Park, Gahrome Galls, Nakorns Itammarat, *J. F. Maxwell 85669* (L). **Surat Thani:** Klaung Jan, *A. F. G. Kerr 12519* (BM, E, K). **Trang:** Pen, Khao Chong, *S. Phusomsaeng 241* (AAU, C, E, L[2]).

12. Styrax rugosus Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40(2): 61. 1871 [as *S.* "*rugosum*"]. TYPE: Myanmar. Pegu: hills between Sittang & Salween, 1212 m, *Brandis s.n.* (as *Brandis 936*, Perkins, 1907) (holotype, CAL not seen).

Shrubs or trees to 6 m tall. Young twigs yellow-brown stellate-tomentose; older twigs purplish and glabrescent. Petiole 2–3 mm long. Two most proximal leaves on each shoot alternate, or more often subopposite to opposite. Lamina 3–7 × 2–3 cm on fertile branches, those on sterile branches usually larger, to 9 × 4.5 cm, chartaceous, ovate-oblong, ovate, or elliptic; apex acute or more often acuminate; base rounded to broadly cuneate, often slightly oblique; adaxially rugose and densely covered with simple and 2- or 3-armed to stellate trichomes when young, becoming sparsely pubescent or rarely glabrous; abaxially gray-yellow stellate-tomentose; margin serrate or apically dentate, secondary veins 4 to 7 on each side of midvein, tertiary veins parallel, quaternaries as well as the tertiaries abaxially prominent and raised in young leaves. Fertile shoots (4–)6–10(–12) cm long, 3- to 5-flowered. Inflorescences arising from shoots of the current growing season; lateral inflorescences usually 1- or 2-flowered; pseudoterminal inflorescences racemose, 2–4(–6) cm long, 3- to 6-flowered, rachis yellow stellate-tomentose, also intermixed with stalked trichomes; bracteoles 4–12 mm long, linear, positioned at various places along the pedicel or at the base of the calyx, sometimes those toward the base of the inflorescence leaf-like, margin conspicuously serrate. Pedicel 3–4 mm long, stellate-tomentose. Flowers 1.4–1.6 cm long. Calyx 4.5–5 × 3.5–5 mm, cupuliform; adaxially sparsely appressed-pubescent with short white 2- or 3-armed or stellate trichomes; abaxially yellow stellate-tomentose throughout, often also with various amounts of larger scattered dark yellow or orange stiff stellate trichomes, especially proximally; margin distinctly dentate, the teeth usually contiguous or separated by a shallow concave portion; teeth 2–3 mm long, lanceolate to subulate, apex acuminate, densely stellate-pubescent on both sides. Corolla 1.0–1.2 cm long, white, tube 4–5 mm long, glabrous proximally, lobes 5, 5–10 × 4–5 mm, elliptic to obovate, adaxially subglabrous, abaxially densely pale yellow stellate-pubescent. Stamens 10; filaments 7–8 mm long, straight, of equal width throughout, densely white stellate-villous proximally, trichomes up to 0.5 mm long, becoming glabrous distally; anthers ca. 5 mm long, wider than distal portion of filament; connectives glabrous. Style glabrous or sparsely white stellate-villous; stigma 0.2–0.4 mm wide, punctiform. Fruit 0.7–0.9 × 0.5–0.6 cm, ovoid, apex rounded or apiculate, dehiscent; pericarp dry, 0.2–0.3 mm thick, outside irregularly longitudinally striate throughout, yellow-brown stellate-tomentose, inside glabrous or sparsely downy-pubescent. Seeds brown, ovoid, smooth, glabrous.

Illustrations. C. Y. Wu, Fl. Yunnan. 3: 426, pl. 121 (1–5). 1983; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1605, fig. 800. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 85, pl. 28 (7–12). 1987; W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 894, pl. 471 (1–6). 1990; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 198, fig. 198 (8–14). 2000.

Phenology. Flowering: March–July. Fruiting: April, July, August, October, November.

Distribution. China (Yunnan), Myanmar (Mandalay Division and Shan State), and Thailand (Chiang Mai, Loei, and Mae Hong Son); Figure 5.

Habitat. In relatively sunny, mixed forests on mountain slopes; 700–1650(–2300) m.

Vernacular names. Zhou-ye-an-xi-xiang (Hwang, 1980), Zhou-ye-ye-mo-li (Anonymous, 1974).

Styrax rugosus occurs primarily in open forests at middle elevations in northwestern Thailand, central and southern Myanmar, and southern Yunnan Province, China. Numerous specimens are available from throughout most of the geographic range of this species, especially at the extreme northern (Jingdong Yizu Zizhixian, Yunnan Province) and southern (Chiang Mai Province, Thailand) edges. In addition to its close morphological similarity to *S. limprichtii* (see discussion under that species), *S. rugosus* is also sympatric with three other imbricate-flowered *Styrax* species in southern Yunnan Province (*S. hookeri, S. japonicus,* and *S. tonkinensis*), from which it is easily separated by the prominently long calyx teeth and rugose leaves. The longer pedicels and glabrous abaxial leaf surfaces of *S. japonicus,* the larger fruit of *S. hookeri,* and the longer petioles and tuberculate seeds of *S. tonkinensis* also can be used to distinguish these species from *S. rugosus.*

Additional specimens examined. CHINA. **Yunnan:** Jingdong Yizu Zizhixian, Cai-sheng-miao, *China-USSR team 18* (IBSC, PE); Chuing-tung, Cheng-nan, *M. K. Li 346* (IBK, IBSC, KUN); Xin-min, *H. Peng 445* (KUN); Cheng-xi, *H. Peng 1851* (KUN); near Jiu-tsun, Meng-kuho, *Y. Tsiang 12348* (IBSC, KUN, PE); Huang-cao-ling, *Z. H. Yang 101327* (KUN); *Z. H. Yang 101681* (KUN[2]); Menghai Xian, *K. L. Le 235* (KUN); Fo-hai, *C. W. Wang 74113* (A, IBSC, KUN, PE), *77088* (A, PE); Nan-chiao, *C. W. Wang 75068* (A, KUN, PE), *75198* (A, IBSC, KUN, PE); Mojiang Hanizu Zizhixian, betw. Mo-jiang & Pu-er, near Jiang-xi-zhai, *China-USSR team 217* (PE). MYANMAR. **Mandalay Division:** 1978, *M. Togashi s.n.* (TI); Maymyo, *Buchanan 25* (E); Maymyo, *C. E. Parkinson 680* (K). **Shan State:** Mt. Mo-la-hein, *F. G. Dickason 8750* (A, E, L); Laungyi, *A. Khalil DI189* (A); Paugmi State, near Leja, *W. A. Robertson 152* (K). **Locality unknown:** *C. B. Collett 800* (K); Thaymyo, *F. G. Dickason 6008* (A). THAILAND. **Chiang Mai:** forest station at Ban Bo Luang, *C. F. van Beusekom & C. Phengkhlai 1078, 1082* (AAU, C, E, K, L); Doi Intanon, *Danish Exp. (1958/1959) 3295* (C, K); Bo Luang, *Flora of Thailand Project Second Exp. (1968) 1913* (AAU, C, L); Doi Angka, Dci Pa Maun, *H. B. G. Garrett 376* (E, K, L); Chiang Dao Dist., Doi Sahm Meun Range, Doi Chiam, *A. Griffith 2* (CAS, L); Me Jun, *A. F. G. Kerr 6201* (BM, K), *6201A* (BM, E, K); from Sop Aep to Pha Mawn (Ban Yang), *G. Murata et al. T15602* (L); Mae Sanam, *C. Phengklai et al. 4150* (C, K, L). **Loei:** Jam yai, *collector unknown DI189* (A); Phukrading, *T. Smitinand 328* (A). **Mae Hong Son:** Jawm Tong, Mae Soi Ridge, Mae Soi Subdist., Awp Luang Natl. Park, near Ban Bah Gluay (Mong Village), *J. F. Maxwell 91535* (AAU, E, P, CAS), *93944* (CAS, L). **Locality unknown:** Bo Luang, *R. Geesink et al. 5776* (AAU, C, E), *T5776* (L), *A. F. G. Kerr 4201A* (K), *8855* (BM, K); Hoi, Pu Jang, *A. F. G. Kerr 8855A* (E, K).

13. Styrax shiraianus Makino, Bot. Mag. (Tokyo) 12: 50. 1898 [as *S.* "*Shiraiana*"]. *Strigilia shiraiana* (Makino) Nakai, Trees Shrubs Japan 1: 256. 1922. TYPE: Japan. Honshu: Shizuoka Pref., Sugura, Araizawa in Abe-gori, *Herb. Sc. Coll. Imp. Univ. Tokyo s.n.* (lectotype, designated here, TI!).

Styrax shiraianus var. *discolor* Nakai, J. Jap. Bot. 14: 631. 1938. TYPE: Japan. Kyushu: Kumamoto Pref., Higo Province, Itukimura, May 1908 (fl) and Aug. 1908 (fr), *T. Nakazima s.n.* (type material, TI missing).

Trees to 8 m tall. Young twigs purple-gray, yellow or brown stellate-tomentose; older twigs gray, glabrescent. Petiole of larger leaves 8–15 mm long, dilated at base and covering the bud. Two most proximal leaves on each shoot subopposite to opposite, smaller, with petioles not dilated at base or covering the bud. Lamina 8–10 × 7–9.5 cm, chartaceous, broadly obovate or rhomboid-orbicular; apex rounded or short-caudate; base cuneate or cuneate-rounded; adaxially deep green, with scattered simple or 2- or 3-armed to stellate trichomes, especially prevalent proximally, glabrescent; abaxially pale green to pale white, sparsely stellate-pubescent, glabrescent except in the axils of the midrib and secondary veins; margin proximally glandular-serrulate, distally irregularly grossly dentate; secondary veins 4 to 6 on each side of midvein; tertiary veins parallel, abaxially prominent. Fertile shoots 4–8 cm long, 2- to 4-leaved. Inflorescences arising from shoots of the current growing season; lateral racemes usually 1-flowered; pseudoterminal inflorescences racemose, 2–3 cm long, 3- to 11-flowered, distally congested, rachis yellow stellate-tomentose. Pedicel < 1 mm long, densely white and brown stellate-villous; bracteoles ca. 6 mm long, linear or setaceous, positioned at the base of pedicel, often those toward the base of the inflorescence leaf-like. Flowers 1.5–2 cm long. Calyx campanulate, 4–6.5 × 4–6 mm; adaxially densely appressed-pubescent with 2- or 3-armed or stellate

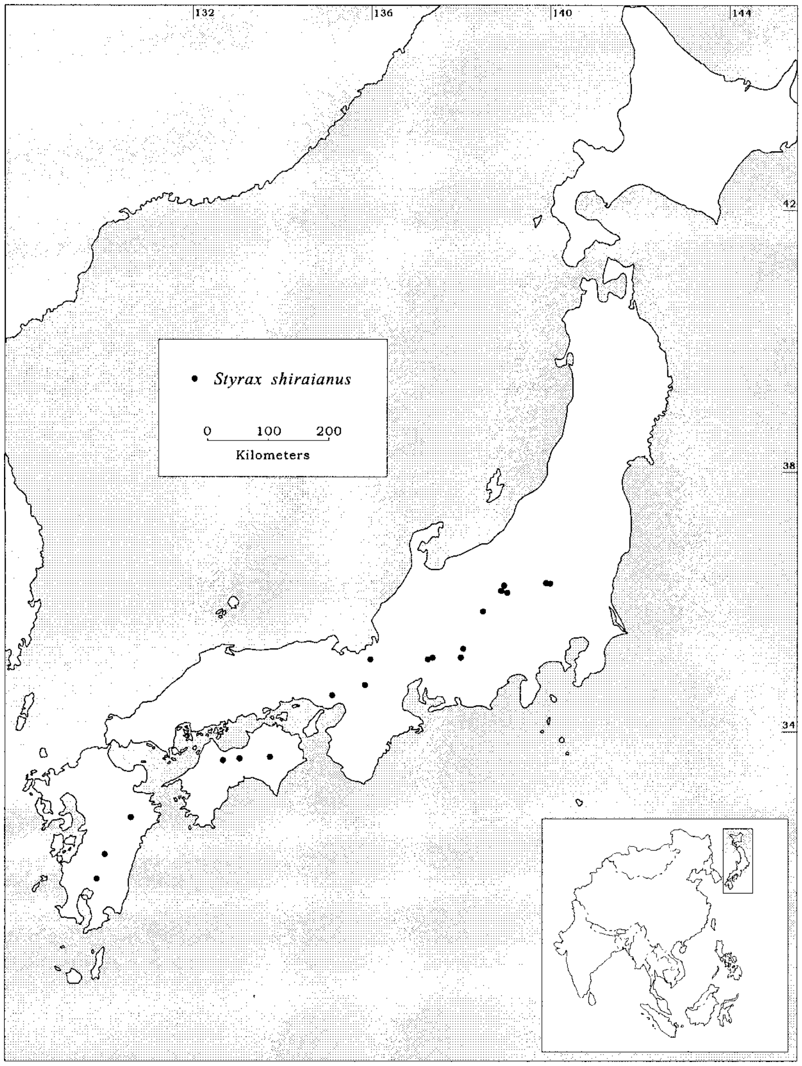

Figure 10. Geographic distribution of *Styrax shiraianus*.

trichomes; abaxially stellate-tomentose, often also with various amounts of larger yellow or brownish stiff stellate trichomes, especially proximally, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin 5- to 8-toothed, teeth 1.5–2 mm long, deltoid, contiguous, apex acute. Corolla 1.0–1.5 cm long, white, tube 10–12 mm long, proximally glabrous, distally pubescent, lobes 5, 6–8 × 2.5–3 mm, ovate, apex acute, stellate-tomentose on both sides. Stamens 10; filaments 3–4 mm long, straight, of equal width throughout, sparsely stellate-pubescent; anthers 2–3 mm long, wider than distal portion of filament; connective glabrous; style proximally stellate-pilose, distally glabrous; stigma 0.4–0.6 mm wide, punctiform. Fruit 0.8–1.0 × 0.6–0.8 cm, ellipsoid to subglobose, apex rounded or apiculate, dehiscent by 2 or 3 valves from apex; pericarp dry, 0.3–0.7 mm thick, outside smooth, white stellate-tomentose, inside sparsely pubescent. Seeds brown, ellipsoid, smooth, glabrous.

Illustrations. Perkins in Engl., Pflanzenr. IV. 241 (Heft 30): 71, fig. 9. 1907; Nakai, Trees Shrubs Japan 1: 256, fig. 141. 1922 (as *Strigilia shiraiana*); Perkins, Übers. Gatt. Styrac.: fig. 9. 1928.

Phenology. Flowering: May, June. Fruiting: July–November.

Distribution. Japan (Honshu, Kyushu, and Shikoku); Figure 10.

Habitat. In open deciduous forests; 600–1500 m.

Vernacular names. Ko-hakuunboku (Japan; 1901, *T. Makino s.n.*), Uraziro-kohakuunboku (Japan; Nakai, 1938).

Styrax shiraianus is endemic to Japan (but see below), occurring on the islands of Honshu, Shikoku, and Kyushu. It appears to be a rare species, relatively little material being available for study. This species is easily distinguished from other species of *Styrax* series *Cyrta* by the racemes with distally congested flowers, long (10–12 mm) corolla tube, and very short pedicel (less than 1 mm). When only sterile specimens are available, the only other taxon with which *S. shiraianus* might possibly be confused is *S. obassia.* Both species have petioles that are dilated at the base and cover the bud, unlike all other species of *Styrax,* in which the bud is exposed. Sterile material of *S. shiraianus* can be distinguished from that of *S. obassia* by its smaller leaves that are abaxially glabrous or nearly so (vs. densely gray-white stellate-pubescent) and irregularly grossly deltoid-dentate (vs. subentire or remotely apiculate-dentate) leaf margins.

Apparently based on an erroneous observation of valvate corolla aestivation in *Styrax shiraianus,* Nakai (1922) transferred this species to *Strigilia* Cav., a genus described by Cavanilles (1789) and taken up by Miers (1859) to accommodate many South American species of *Styrax.* Later Nakai (1938) transferred it back to *Styrax.*

Styrax shiraianus has been reported from South Korea by Nakai (1938) on the basis of two collections from "Tiisan" (Chiisan) Mountain (*S. Okamoto s.n.* from "Zennan" (North Cholla) Province and *Tei-daigen s.n.* from "Keinan" (South Kyongsang) Province). Subsequently, the species was listed in three references on the Korean flora (T. B. Lee, 1989; W. T. Lee, 1996; Y. N. Lee, 1996), but locality or source information was not specified in any of these works. Nakai worked at TI until 1943, and from this we assume that the Korean material of *S. shiraianus* is stored at TI. We have not seen any material of *S. shiraianus,* however, from Korea among our loans from TI or other herbaria. Furthermore, we have not observed any photographs of living plants of *S. shiraianus* from Korea. The *Flora of Korea* (Y. N. Lee, 1996) contains color photographs of nearly all Korean species, including *S. japonicus* and *S. obassia,* but a photograph of *S. shiraianus* is notably lacking. No specimens of *Styrax* at SNU in Seoul, South Korea, have been identified as *S. shiraianus* (C.-W. Park, pers. comm.). We cannot be certain, therefore, that the Korean specimens cited by Nakai are not merely misidentified individuals of, e.g., *S. obassia.*

Four collections were cited in the protologue of *Styrax shiraianus*: Aug. 8, 1884, *T. Makino s.n.*; Aug. 1885, *T. Makino s.n., K. Watanabe s.n.*; and *Herb. Sc. Coll. Imp. Univ. Tokyo s.n.* The Makino herbarium (MAK) houses none of these specimens (M. Wakabayashi, pers. comm.), and TI has only the last of these (one sheet). Therefore, we have chosen to lectotypify on the only sheet of the syntypes known to exist among these herbaria. The TI herbarium does not have type material of *S. shiraianus* var. *discolor* (H. Ohba, pers. comm.).

Additional specimens examined. JAPAN. **Honshu:** Gifu Pref., Gifu-ken, Nakatugawa-shi, near Okunodaira, S foot of Mt. Ena, *K. Hidehiko 14* (KYO); Mino, *K. Shiota 2771, 5846, 6525, 7198, 9048* (A); Hyogo Pref., Mt. Setsuhiko, *H. Muroi 38* (A); Nagano Pref., Shinano, Ogawa, 1905, *J. G. Jack s.n.* (A, GH); Shinano, Ihida-shi, Mt. Surikogi Ohdaira, 1961, *F. Miyoshi s.n.* (A); Shinano, Nishichikuma-gun, Ohtaki-mura, *M. Mizushima 2379* (A); Kodzuke, Agatsuma-gun, Sawada-mura, Shima hot well, *M. Mizushima 2958* (A); Nishichikuma-gun, Okuwa-mura, Mt. Atera-yama, *G. Murata & H. Nishimura 906* (AAU, C, E, K, L, TI, UC); Shinano, *E. H. Wilson 7012* (A, BM, GH, K); Okayama Pref., Okayama-ken, Ushiroyama aidagun, 1951, *K. Uno s.n.* (A); Shiga Pref., Shiga-gun, Sgiga-cho, Yakumogahara in Hirasan Mts., *G. Murata 55807* (A, KYO); Tochigi Pref., Nikko, 1901, *collector unknown* (A), 1914, *collector unknown* (E), 1915, *collector unknown* (K), *T. Makino s.n.* (A, TI), *105785, 121299* (CAS), *105786* (A), 1904, *N. Mochizuki s.n.* (A), 1920, *H. Takeda s.n.* (BM), *E. H. Wilson 7710* (A); Nikko-shi, Mt. Nakimushi-yama, *Y. Tateishi 10287* (A). **Kyushu:** Kumamoto Pref., Mt. Ichibusa, Higo, 1908, *collector unknown* (E), 1947, *E. E. Harmsen s.n.* (L), 1910, *N. Mochizuki s.n.* (E), 1917, *Tashiro s.n.* (A); Sobosan, *Père U. J. Faurie 3272* (P); Kagoshima Pref., Mt. Kirishima, 1938, *T. Naito s.n.* (A). **Shikoku:** Tokushima Pref., Mt. Tsurugi, *M. Hiroe 13411* (C, UC); Ehimi Pref., Kamiukena-gun, Omogokei, 1940, *G. Murata s.n.* (A); Kochi Pref., Iyo sikoku, Yogo Ikkaku, *I. Yogo 9510* (A).

14. Styrax subpaniculatus Jungh. & de Vriese, in de Vriese, Pl. Nov. Ind. Bat. 9. 1845. *Styrax serrulatus* var. *mollissimus* Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 250. 1932. TYPE: Indonesia. Sumatra: province unknown, Tobing Dist., Battalands, 900 m, 1860–1862 (Steenis, 1932), *F. W. Junghuhn s.n.* (holotype, L [accession no. 90631-105]!; isotype, L [accession no. 908239-1494]!).

Styrax subdenticulatus Miq., Fl. Ned. Ind., Eerste Bijv. 474. 1860 [as *S.* "*subdenticulatum*"]. TYPE: Indonesia. Sumatra: province unknown, western Sumatra, Battang Baroes ["near Batang-barus"; protologue], 1856 (Steenis, 1932), *J. E. Teysmann 965HB* (holotype, U not seen; digital image of holotype!; isotype, BO not seen).

Styrax oliganthes Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 241. 1932. TYPE: Indonesia. Sumatra: Sumatera Barat, E coast, Manindjau, Kp. Silajang, 500 m, 7 July 1922, *Forest Research Institution b.b. 3965* (holotype, BO!; isotype, L!).

Trees to 33 m tall. Young twigs yellow-brown stellate-tomentose, terete; older twigs dark brown, glabrescent. Petiole 3–9 mm long. Two most proximal leaves on each shoot alternate. Lamina of fertile shoots 4–8.5 × 2–5 cm, those of sterile shoots 14.5 × 7.5 cm, membranaceous to thick-chartaceous, ovate, ovate-oblong, elliptic, or lanceolate; apex acuminate to caudate; base subrounded or broadly cuneate, slightly attenuate, sometimes oblique; adaxially subglabrous except on the midrib and the primary nerves, glabrescent; abaxially nearly glabrous to stellate-pubescent or -tomentose, the surface usually remaining visible through the pubescence; margin entire or indistinctly toothed, occasionally revolute; secondary veins 6 to 8 on each side of midvein; tertiary veins ± parallel and perpendicular to the secondaries. Fertile shoots (12–)15–21 cm long, (1- to)3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- or 2-flowered or racemose, 3–8 cm long, (1- to)5- to 13-flowered; pseudoterminal inflorescences racemose or paniculate, 7–17 cm long, 9- to 20(to 23)-flowered, lateral branches 2 to 7, sometimes with 2 to 3 additional racemes from base of inflorescence, rachis and branches yellow-brown tomentose. Pedicel 4–6.5 mm long, stellate-tomentose; bracteoles 1–3 mm long, subulate or linear, mostly positioned at the base of the pedicel. Flowers 0.9–1.2 cm long. Calyx 3–4 × 3–4 mm, campanulate; adaxially glabrous or finely short-appressed-stellate-pubescent; abaxially yellow tomentose, arms of trichomes < 0.2 mm long, densely gray-white stellate-pubescent throughout; margin truncate, undulate, or irregularly lobed, the teeth minute, not contiguous if present. Corolla 0.5–0.8 cm long, white, tube 2.5–3 mm long, glabrous proximally; lobes 5, 7–9 × 2.5–3 mm, 2.3–2.8× as long as wide, oblong-elliptic, apex obtuse or acute, tomentose on both sides. Stamens 10; filaments 2.5–3 mm long, slightly flexuous at middle or occasionally straight, distally attenuate, densely white stellate-pubescent; anthers 3–4 mm long, equal to filament in width or narrower; connectives glabrous. Style glabrous; stigma 0.3–0.5 mm wide, punctiform. Fruit 0.7–1.0 × 0.6–0.8 cm, obovoid or globose, apex rounded or subacute, rarely also apiculate, indehiscent; pericarp dry, 0.2–0.5 mm thick, outside smooth, gray tomentose, inside downy-pubescent. Seed brown, ovoid, nearly smooth to irregularly rugose, glabrous.

Illustrations. Jungh. & de Vriese, in de Vriese, Pl. Nov. Ind. Bat.: pl. 3, 1–12. 1845; Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 222, fig. 3 (3). 1932 (as *S. oliganthes*); ibid.: 242, fig. 9. 1932 (as *S. oliganthes*).

Phenology. Flowering: February–April, October. Fruiting: May–August, October.

Distribution. Indonesia (Sumatra); Figure 4.

Habitat. In mesic, mixed primary forests, and in montane rain forests; 100–1600 m.

Vernacular names. Kajoe lomlang kajoe (*R. S. Boeea 9285*), kajoe komajan (*J. E. Teysmann 965HB*), or kajoe keminjan (Perkins, 1907 ex F. A. W. Miquel).

Styrax subpaniculatus is the only species of *Styrax* with imbricate corolla aestivation known from the island of Sumatra, Indonesia, where it is endemic. Steenis (1932) considered this species to be a variety of *S. serrulatus* (var. *mollissimus* Steenis), a species placed by Perkins (1907) in series *Valvatae* on the basis of its valvate corolla aestivation. Using the same reasoning as that outlined in the discussion of *S. porterianus,* we consider *S. subpaniculatus* a species distinct from *S. serrulatus.* The consistently imbricate corolla aestivation in *S. subpaniculatus* sharply delimits this species from *S. serrulatus,* which in our view possesses a subvalvate type of corolla aestivation. *Styrax serrulatus* is geographically distinct from *S. subpaniculatus,* occurring in the Himalayas and vicinity but not extending as far south as the Malay Peninsula or Sumatra. *Styrax subpaniculatus* can also be distinguished from *S. serrulatus* by its usually pubescent (vs. glabrous or nearly so) abaxial leaf surfaces and the truncate or undulate (vs. distinctly toothed) calyx margin.

Styrax porterianus has many features in common with *S. subpaniculatus,* but has shorter (2–4 vs. 7–17 cm long), strictly racemose (vs. often paniculate) inflorescences, and a fruit with a fleshy (vs. dry and rigid) pericarp that is deeply rugose (vs. smooth) in the dry state. In addition, the ranges of *S. subpaniculatus* and *S. porterianus* are completely nonoverlapping, the latter being restricted to the Malay Peninsula. *Styrax subpaniculatus* is also similar to *S. buchananii* and *S. odoratissimus* but distinguishable from both by its glabrous connectives and styles. In addition, the larger flowers (1.3–1.6 vs. 0.9–1.2 cm long) and longer anthers (6–7 vs. 3–4 mm) are useful characters to distinguish *S. buchananii* from *S. subpaniculatus,* whereas the wider petals (4–6 vs. 2.5–3 mm) and usually appressed-stellate-pubescent or lepidote (vs. glabrous) seeds readily distinguish *S. odoratissimus* from *S. subpaniculatus.*

Steenis (1932) described *Styrax oliganthes* based on a single fruiting collection from western Sumatra. Although hesitant to describe this species as new from only fruiting material, Steenis felt that the combination of densely pubescent abaxial leaf surfaces and apparent lack of any brown leaf pubescence (i.e., only white trichomes) provided sufficient justification for the recognition of a new species. Steenis postulated *Styrax benzoides* Craib and *S. tonkinensis* as close relatives of *S. oliganthes,* with *S. benzoides* distinguishable by its indehiscent fruit and *S. tonkinensis* by its tuberculate seeds. We agree that neither species could possibly be conspecific with *S. oliganthes*: besides its smooth seeds, *S. oliganthes* differs from *S. tonkinensis* in its truncate or undulate (vs. distinctly dentate) calyx margin and rounded (vs. rostrate) fruit apex. *Styrax benzoides* has the depressed-globose seeds of series *Benzoin* (see Fritsch, 1999); those of *Styrax oliganthes* are ellipsoid, clearly establishing its inclusion in series *Cyrta.*

Steenis did not consider a possible relationship of *Styrax oliganthes* with *S. subpaniculatus.* Nonetheless, there is ample evidence of affinity between these two entities. Both can reach a height of 30 m or more, which is uncommonly tall for species of *Styrax*; the leaves are of the same general dimensions, with equivalent numbers of secondary veins on each side of the midvein and an entire or indistinctly toothed margin; the fruiting calyx margins are truncate or undulate; the fruit is indehiscent, ± subglobose to slightly obovoid, smooth, and of similar general dimensions and color; the seeds are glabrous; finally, the locality of *S. oliganthes* is well-embedded within the general range of *S. subpaniculatus,* both being restricted to Sumatra.

Furthermore, characters that reportedly distinguish *Styrax oliganthes* from *S. subpaniculatus* are not reliable or otherwise do not serve to delimit the two taxa. The densely pubescent abaxial leaf surfaces in *S. oliganthes* differ from all collections of *S. subpaniculatus* known, but the degree of pubescence in *S. subpaniculatus* varies continuously from nearly none to nearly covering the entire surface. Variation in the amount of infraspecific abaxial leaf pubescence is common in species of *Styrax,* including several in this revision (e.g., *S. hemsleyanus, S. hookeri*). Steenis stated that there are only white trichomes on the abaxial leaf surface of *S. oliganthes,* but upon inspection at 64× magnification we observe scattered yellow, orange, and even brown stellate trichomes. The inflorescences of *S. oliganthes* are reportedly few-flowered, unlike the many-flowered condition of the pseudoterminal inflorescences of *S. subpaniculatus.* Only infructescences, however, are known in *S. oliganthes.* Typically, more flowers than fruits are borne on each reproductive structure in *Styrax,* and thus it is often difficult to infer the number of original flowers, or the structure and length of an inflorescence, from fruiting material. Furthermore, as in *S. subpaniculatus,* several pseudoterminal infructescences on the holotype of *S. oliganthes* are branched.

We examined several other features not mentioned by Steenis (1932) in considering the separation of the two species. The arms of the trichomes on the leaves abaxially average ca. 0.1 mm long in *S. oliganthes* versus those on most specimens of *S. subpaniculatus* (averaging ca. 0.4 mm long), but close inspection of all collections of *S. subpaniculatus* available to us indicates that trichome length is a continuously variable character. The leaves are thick-chartaceous in *S. oliganthes* whereas in most specimens of *S. subpaniculatus* they are membranaceous, but one specimen in bud (*Boeea 8857*) has leaves that are nearly as thick as *S. oliganthes* and several more have leaves that are notably thicker than usual. The seeds of *S. oliganthes* are irregularly rugose whereas those in *S. subpaniculatus* are smooth, but many species of *Styrax* exhibit infraspecific variation for this character (e.g., *S. japonicus*). Ultimately, we can detect no distinctive characters upon which to base the separation of *S. oliganthes* from *S. subpaniculatus.*

The only reference made to collections of *Styrax subdenticulatus* in the protologue is indicated with "(T.)," an abbreviation for J. E. Teysmann. According to Steenis (1932), Teysmann made three collections of *Styrax* from the type locality cited in the protologue. Two of these are identified by Steenis as *S. paralleloneurus* (*J. E. Teysmann 963* and *966*), and the third is specified by Steenis as the type of *S. subdenticulatus* (as "*Teysmann 965HB* [B, U])" (B in this case is BO, Herbarium of the Botanic Gardens, Buitenzorg, Java). Miquel's herbarium was U, but no indication of type status or any other annotation of Miquel exists on the U specimen of this collection. Although we have not seen the collections of *S. paralleloneurus* made by Teysmann from the type locality of *S. subdenticulatus,* the two species are easily distinguishable with vegetative characters. For example, the leaf surfaces of *S. subdenticulatus* are visible through the pubescence, whereas those of *S. paralleloneurus* are not. Thus, a mistake in identification of these specimens by Steenis is extremely unlikely. On this basis, we feel confident that the *Teysmann 965HB* specimen at U is the holotype of *S. subdenticulatus* (and thus there is no need to lectotypify in this case).

Additional specimens examined. INDONESIA. SUMATRA. **Aceh:** Saurauja, Blangkedjeren, *A. H. G. Alston 14716* (BM, L); Gajolanden, Goempang to Koengke, *C. G. G. J. Van Steenis 9802* (A, K, L); Gunung Leuser Natl.

Park, from Kutacane to Belangkejeren, Kulam, near Agusan, pass betw. Alas & Palok, *T. C. Whitmore TCW3348* (L); Gunung Leuser Nature Reserve, Gunung Mamas, 6 km SW from the mouth of Lau Ketambe, *W. J. J. O. de Wilde & B. E. E. de Wilde 15756* (BO, L); Gunung Leuser Nature Reserve, upper Mamas River Valley, ca. 15 km W Kutacane, *W. J. J. O. de Wilde & B. E. E. de Wilde 18342* (K, L). **Bengkulu:** G. Kaba, near Aer Angat, hot springs, *H. O. Forbes 2866* (BM, GH, L). **Sumatera Barat:** Ayer mancior, *O. Beccari 699* (BM, L); Pinang-Pinang plot, Ulu Gadut, *M. Hotta 26604* (BO); Pesisir Selatan, 12 km W of Muarasako, *Y. Laumonier YL5961* (K, L); Pajakumbuh, Mt. Sago, *P. Maradjo 87* (L), *W. Meijer 3175* (BO); Pajakumbuh, N slope of Mt. Sago, *W. Meijer 3186* (BM, L). **Sumatera Selatan:** Res. Palembang, Pasemah Lands, near Paoe, *H. O. Forbes 2335* (BM, GH, L[2]). **Sumatera Utara:** Tapanoeli, Kampoeng Sitoemba, *Forest Research Institution b.b. 5225* (L); Tapiannodi, Angkola & Sipirok, near Kampoeng Battang-Kola, *Forest Research Institution b.b. 5249* (L); Kampoeng Petjeren, *Forest Research Institution b.b. 6854* (L); Asahan, Pargambiran, *H. H. Bartlett 8077* (K, L); Kaban Djahe, *A. H. Batten-Pool 5* (L); Adian Rindang, Asahan, vicinity of Hoeta Tomoean Dolok, *R. S. Boeea 8857* (A, K, L, UC); Asahan (NE of Tomoean Dolok & W of Salabat), *R. S. Boeea 9285* (A, K, L, UC); S Tongkoh, Berastagi, Karoland, *J. Dransfield 3418* (L); NW Sibolangit, bank of the Betimoes, *J. A. Lörzing 5641* (L); Sibolangit, *J. A. Lörzing 14096* (K, L); Bandarbaru, near Sibolangit, *J. A. Lörzing 14129* (L); E Mt. Sibajak, *J. A. Lörzing 15167* (BO, K, L); Gunung Leuser Natural Park, Sekundur Forest Reserve, upper Besitang River area, *W. J. J. O. de Wilde & B. E. E. de Wilde 21156* (L). **Locality unknown:** Sumatra, *Ajoeb 728* (L); Sumatra, *H. O. Forbes 2835* (BM), *7866* (L); Karo Uplands, near Lake Laut Kawar & Kampoeng Sigarang, *Forest Research Institution b.b. 8618* (L); Sumatra, Langsdin, 1913, *J. C. v. der Meer Mohr s.n.* (L); Sumatra, E Batavae, 1857, *W. H. de Vriese s.n.* (L[6]); E coast of Sumatra, *H. S. Yates 1411* (BM, L, UC), *1467* (A, BM, IBSC, UC).

15. Styrax supaii Chun & F. Chun, Sunyatsenia 3: 34. 1935 [as *S.* "*Supaii*"]. TYPE: China. Guangdong: Ruyuan Yaozu Zizhixian, Chutsien Dun [Qi-xian-gou], 9 May 1934, *S. P. Kwok 80419* (lectotype, designated here, IBSC!; isotypes, A!, IBSC!).

Shrubs to 2 m tall or trees to 6 m tall. Young twigs brown or dark brown, densely stellate-pubescent; older twigs dark purple, glabrescent. Petiole 2–5 mm long. Two most proximal leaves on each shoot subopposite or opposite. Lamina 4–8 × 2–5 mm, chartaceous to thick-chartaceous, rarely membranaceous, ovate to obovate; base rounded to broadly cuneate; adaxially with a few simple or 2- or 3-armed to stellate trichomes when young, glabrescent; abaxially sparsely stellate-pubescent, glabrescent; margin coarsely serrate, deeply 3- to 5-dentate or lobed apically, lobes serrate-triangular or lanceolate, often remotely apiculate-serrate along the whole margin, up to 0.5 mm long; secondary veins 3 to 5 on each side of midvein; tertiary veins reticulate, adaxially plane, abaxially raised. Fertile shoots 2–5 cm long, 2- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- or 2-flowered; pseudoterminal inflorescences 2–3 cm long, 2- or 3-flowered, rachis and pedicel sparsely short-stellate-pubescent, with additional long simple or 2-armed trichomes. Pedicel 10–15 mm long; bracteoles 3–4 mm long, linear or subulate, positioned at the base or middle part of pedicel. Flowers 1.5–1.8 cm long. Calyx 5–6 (excluding teeth) × 4–5 mm, obconical; adaxially sparsely appressed-pubescent with long simple trichomes; abaxially with numerous simple or 2-armed trichomes ca. 1–1.5 mm long, stellate tomentum only sparsely distributed near the base, otherwise absent; margin distinctly dentate, the teeth 4–5 mm long, narrowly lanceolate or deltoid, unequal, contiguous. Corolla 0.9–1.3 cm long, white, tube ca. 3 mm, glabrous, lobes 5, 14–15 × 4–5 mm, lance-elliptic, adaxially sparsely pubescent with white 2- or 3-armed to stellate trichomes along the costae or distally, otherwise glabrous, abaxially densely stellate-pubescent. Stamens 10, conspicuously alternately unequal in length; filaments 4–5 mm long, straight, proximally broadened and white stellate-villous, distally attenuate and glabrous; anthers 4–6 mm long; connectives glabrous. Style glabrous; stigma 0.2–0.4 mm wide, punctiform. Fruit 1.0–1.5 × 0.7–0.9(–1.3) cm, ovoid or ellipsoid, apex apiculate to short-rostrate, dehiscent; pericarp dry, 0.3–0.6 mm thick, outside longitudinally striate and rugose, rarely smooth, densely white stellate-villous, inside glabrous. Seeds brown, ovoid, smooth, glabrous.

Illustrations. Chun & F. Chun, Sunyatsenia 3: pl. 3. 1935; Hu & Chun, Ic. Pl. Sin. 5: pl. 248. 1937; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1617, fig. 810. 1985; S. M. Hwang in F. H. Chen, Fl. Guangdong 1: 388, fig. 421. 1987; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 96, pl. 32 (1–7). 1987; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 201, fig. 201 (1–7). 2000.

Phenology. Flowering: May, June. Fruiting: June–November.

Distribution. China (Guangdong and Hunan); Figure 5.

Habitat. In mixed woods or near roadsides, and usually in relatively dry, disturbed habitats; 310–900 m.

Vernacular name. Lie-ye-an-xi-xiang (Hwang, 1980).

Styrax supaii is known only from the mountainous regions of Yizhang Xian, Hunan Province, and Ruyuan Yaozu Zizhixian, Guangdong Province, China. Based on the few specimens available for study, we believe this taxon must be a rare component of the vegetation. This distinctive species is easily identified by its long calyx teeth (4–5 mm) and a calyx covered with long simple trichomes (averaging 1.5 mm long), stellate calyx trichomes being absent nearly throughout. It also can easily be distinguished from sympatric species by its coarsely serrate to deeply 3- to 5-dentate or lobed leaves apically, and stamens alternately differing in length by 1–2 mm.

Additional specimens examined. CHINA. **Guangdong:** Ruyuan Yaozu Zizhixian, Daikiu [Da-qiao-qu, Hou-zhi-e], 1933 [5 June 1934; protologue], *S. P. Ko 52797* (IBK, IBSC[2], PE). **Hunan:** Yizhang Xian, Mang-shan, Rong-jia-dong, *S. Q. Chen 3552* (IBK, IBSC); Mang-shan, *B. G. Li 86* (IBSC); Dong-shan-keng, Mang-shan, *P. H. Liang 85344* (IBK, IBSC); Rong-jia-dong, *Q. Lin 167* (IBSC); Mang-shan, *Zhong-nan-lin-shi-xi-dui 94* (IBSC).

16. Styrax tonkinensis (Pierre) Craib ex Hartwich, Apotheker-Zeitung 28: 698. 1913. *Anthostyrax tonkinensis* Pierre, Fl. Forest. Cochinch. 4: t. 260. 1892 [as *A.* "*Tonkinense*"]. TYPE: Vietnam. Province unknown: Tu Phap, 12 May 1887, *B. Balansa 4332* (lectotype, designated by Svengsuksa & Vidal (1992), P not seen; isotype, P!).

Styrax hypoglaucus Perkins, Bot. Jahrb. Syst. 31: 486. 1902. TYPE: China. Yunnan: Simao Shi, eastern mountains, 1600 m, *A. Henry 12006* (lectotype, designated here, K!; isotypes, A!, E!, IBSC!, MO!, PE!).

Styrax subniveus Merr. & Chun, Sunyatsenia. 1: 78. 1930. TYPE: China. Guangdong: Lechang Shi, 24 May 1929, *C. L. Tso 20732* (holotype, IBSC!; isotype, PE!).

Trees to 30 m tall. Young twigs gray-brown stellate-tomentose, older twigs dark brown, glabrescent. Petiole 8–12(–15) mm long. Two most proximal leaves on each shoot alternate. Lamina 5–18 × 4–10 cm, chartaceous to thick chartaceous, elliptic to ovate; apex short-acuminate; base rounded to cuneate; adaxially glabrous except the major veins when young, glabrescent; abaxially gray or white stellate-tomentose, arms of trichomes very short, uniform, surface completely concealed by the tomentum; margin entire or apically 2- to 3-crenately toothed on young leaves; secondary veins 5 or 6 on each side of midvein; tertiary veins subparallel, adaxially plane or slightly sunken, abaxially prominent. Fertile shoots (7–)10–25 cm long, 3- or 4-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- or 2-flowered or racemose, 3–5 cm long, 1- to 7-flowered; pseudoterminal inflorescences racemose or paniculate, (5–)7–20 cm long, (6- to)8- to 18(to 23)-flowered, lateral branches 2 to 5, sometimes with 2 or 3 lateral racemes from base of inflorescence, rachis and branches yellow-brown stellate-tomentose. Pedicel 5–10 mm long, yellow-brown stellate-tomentose; bracteoles 3–5 mm long, subulate or linear, positioned at the middle of pedicel or base of calyx. Flowers 1.2–1.5(–1.7) cm long. Calyx 3–4 × 2.5–3 mm, cupuliform; adaxially appressed-pubescent with white 2- or 3-armed or stellate trichomes; abaxially densely gray-white stellate-pubescent throughout; margin distinctly dentate, glandular-dotted, the teeth 0.3–0.7(–1.2) mm long, narrow-deltoid, usually contiguous or rarely separated by a shallow concave portion, unevenly distributed. Corolla 0.8–1.1(–1.3) cm long, white, tube 3–4 mm long, glabrous proximally, lobes 5, 10–15 × 3–4 mm, lance-ovate or oblong-elliptic, white stellate-tomentose on both sides. Stamens 10; filaments ca. 4 mm long, straight, of equal width throughout, moderately to densely white stellate-villous throughout, sometimes thinning apically; anthers ca. 5 mm long, as wide as filament; connective glabrous or short-stellate-pubescent. Style glabrous; stigma 0.2–0.5 mm wide, punctiform. Fruit 0.8–1.2 × 0.7–1.1 cm, subglobose, apex rostrate, irregularly dehiscent by 3 valves from apex; pericarp dry, 0.8–1.1 mm thick, outside nearly smooth, gray stellate-tomentose, inside sparsely downy-stellate-pubescent. Seeds brown or dark brown, ovoid, densely tuberculate, sometimes the tubercles arranged in stellate formations.

Illustrations. Pierre, Fl. Forest. Cochinch. 4: t. 260. 1892; Anonymous, Ic. Cormophyt. Sin. 3: 338, fig. 4630. 1974 (as *S. hypoglaucus*); C. Y. Wu, Fl. Yunnan. 3: 424, pl. 120 (1–6). 1983; L. Yang in Y. K. Li, Fl. Guizhou. 2: 548, fig. 234 (5–7). 1984; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1603, fig. 798. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 85, pl. 28 (8–13). 1987; J. Q. Liu in L. G. Lin, Fl. Fujian. 4: 357, fig. 290. 1989; W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 892, pl. 470 (1–6). 1990; B. Svengsuksa & J. E. Vidal, Flore du Cambodge du Laos et du Viêtnam 26: 169, pl. 30, 4–7. 1992; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 197, fig. 197 (8–13). 2000.

Phenology. Flowering: April–July, September, November, December. Fruiting: January, February, April–December.

Distribution. China (Fujian, Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Yunnan, and Zhejiang), Laos (Houa Phan, Luang Prapang, Phongsali, and Xieng Khouang), and Vietnam (Bac Can, Cao Bang, Ha Tay, Lai Chau, Lao Cai, Ninh Binh,

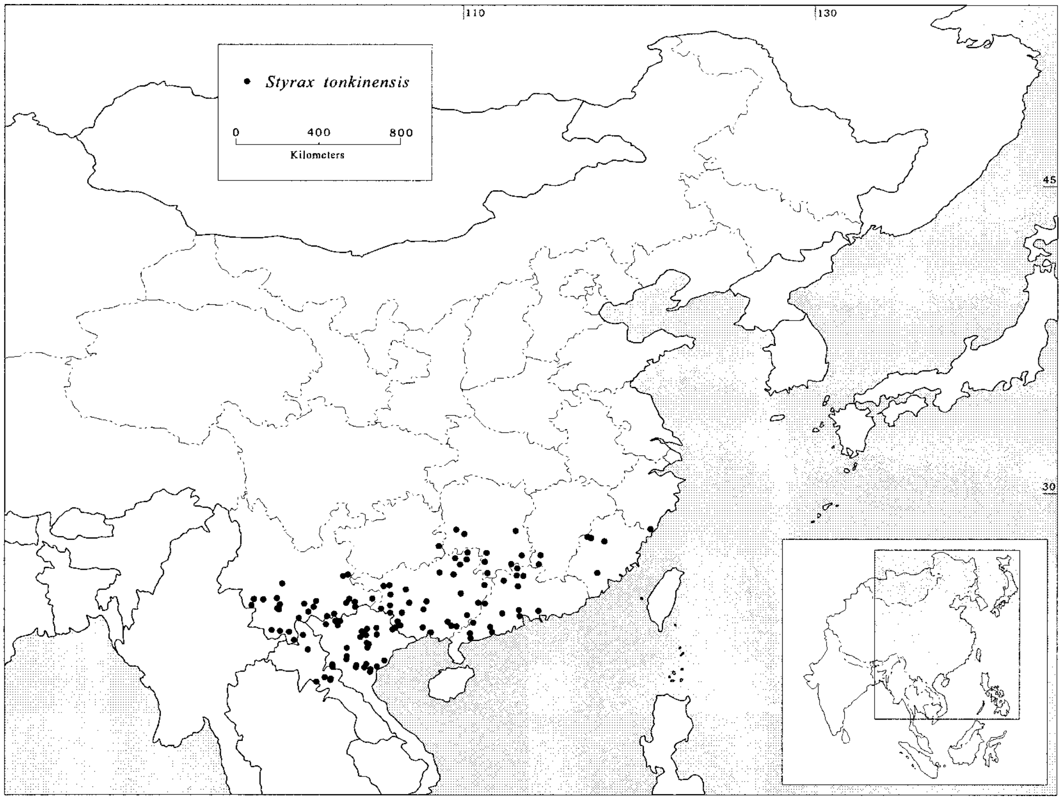

Figure 11. Geographic distribution of *Styrax tonkinensis.*

Phu Tho, Son La, Thanh Hoa, Tuyen Quang, and Yen Bai); Figure 11.

Habitat. In open forests on mountain slopes, and along edges of mixed forests in relatively disturbed sites; 30–2400 m.

Vernacular names. Ba-fan-long (China, Yunnan; *W. X. Liu 694*), Bai-bei-an-xi-xiang (China, Guangdong; *Exp. Guangdong 587*), Bai-bei-mu, Bai-hua-mu (China, Guangxi; *S. Q. Zhong A63811*), Bai-hua-lang (China, Guangxi; *Y. X. Lin 16575*), Bai-hua-lang-shu (China, Guangdong; *W. T. Tsang 25866*), Bai-hua-shu (China, Yunnan; *W. X. Liu 566*), Bai-hua-shu-guo (China, Yunnan; *Exp. Wen-shan 259*), Bai-hua-zhan (China, Guangdong; *K. P. To et al. 12025*), Bai-mai-an-xi-xiang (Hwang, 1987), Bai-ye-an-xi-xiang (China, Guangdong; *Exp. Guangdong 70*), Bai-ye-ye-mo-li (China, Hunan; *Q. Z. Lin 514*), Da-qing-shan-an-xi-xiang (China, Guangxi; Hwang, 1987), Dian-gui-mo-li-hua (China, Guizhou; *P. C. Tsoong 1094*), Dian-gui-ye-mo-li (Hwang & Qi, 1985), Dou-zha-shu (China, Yunnan; *P. Y. Mao 2468*), Ge-jian-ge (China, Guangxi; *Y. K. Li P1122*), Jie-yong (China, Yunnan; *P. Y. Mao 2779*), Jing-guo (China, Guangxi; *Y. K. Li P901*), Mei-lu-zai (China, Guangxi; *Exp. Guangxi 3468*), Niu-you-shu (China, Yunnan; *P. Y. Mao 2941*), Qing-shan-an-xi-xiang (China, Guangxi; *H. N. Qin 245*), Shi-chi-yang (China, Guangxi; *F. H. Xie et al. 3727*), Tai-guo-an-xi-xiang (Hwang, 1987), Xiao-jie-yong (China, Yunnan; *K. M. Feng 5149*), Yue-nan-an-xi-xiang (Anonymous, 1974).

Styrax tonkinensis is a relatively common component of primary and secondary forests and disturbed sites across southern China and the northern regions of Laos and Vietnam. The gray to white stellate-tomentose abaxial surface of the lamina (often nearly glaucous in appearance) appears to be a constant character in *S. tonkinensis,* and serves to distinguish it from most other sympatric species of the imbricate members of series *Cyrta.* Three species occurring within the range of *S. tonkinensis* have at least some individuals with a stellate-tomentose abaxial laminar surface (*S. hookeri, S. limprichtii,* and *S. rugosus*). *Styrax limprichtii* and *S. rugosus* differ from *S. tonkinensis* by their smooth and glabrous (vs. tuberculate) seeds, leaves with shorter petioles and more prominent teeth, a calyx with scattered orange or brown stiff stellate pubescence, and a fruit with a rounded or apiculate (vs. rostrate) apex and a longitudinally striate (vs.

smooth or irregularly rugose) pericarp. *Styrax hookeri* differs by its truncate, undulate, or irregularly lobed calyx with the teeth not contiguous if present, and the outer surface of the calyx within 1 mm of the margin more sparsely pubescent than the rest of the calyx and somewhat scarious.

Styrax tonkinensis was described first as *Anthostyrax tonkinensis* Pierre from specimens collected in Vietnam (*B. Balansa 4332* and *4358*). Perkins (1902) may well have overlooked this taxon, because *S. macrothyrsus* Perkins was published from one of the type collections of *Anthostyrax tonkinensis* (*B. Balansa 4332*), and no reference was made to *Anthostyrax* Pierre in Perkins's 1907 monograph. Realizing Perkins's error, Hartwich (1913) made the transfer to *Styrax*. Perkins (1902) described *S. hypoglaucus* Perkins from a specimen collected from Simao Shi, Yunnan Province, China (*Henry 12006*). *Styrax hypoglaucus* supposedly differs from *S. tonkinensis* by its 6- to 10-flowered racemose or sparsely branched inflorescences 5–6 cm long (vs. multi-flowered paniculate inflorescences 17–18 cm long; Perkins, 1902, 1907). Merrill and Chun (1930) described *S. subniveus* Merr. & Chun based on a specimen collected from Lechang Shi, Guangdong Province (*C. L. Tso 20732*). They considered this species to be allied to *S. hypoglaucus* and *S. tonkinensis.* According to their protologue, *S. subniveus* has racemose or narrowly paniculate inflorescences 3–8 cm long with few to many flowers.

We agree with Hwang (1980) that both of these species are synonyms of *Styrax tonkinensis.* The constancy of such features as the entire or weakly toothed leaves that are densely pubescent abaxially, relatively small flowers, dentate calyx, glabrous style, rostrate fruit, and especially the tuberculate seeds (which occur nowhere else in the genus) all serve to delimit this species. As in *S. odoratissimus,* inflorescence length and flower number per inflorescence exhibit notable variation in *S. tonkinensis.* This is reflected in the key to species, in which *S. tonkinensis* falls out twice because of the variation in these characters.

Suvatti (1978) cited *Styrax tonkinensis* from eastern Thailand, but we have not seen any specimens of this taxon from that country. *Styrax tonkinensis* was introduced to the island of Java after World War II for reforestation purposes (Backer & van den Brink, 1965).

The holotype of *Styrax hypoglaucus* at B is presumably destroyed. Perkins may have only seen the specimen at B because none of the other sheets of *A. Henry 12006* that we have examined possess Perkins's annotation label. No herbaria are cited in either Perkins (1902) or Perkins (1907) to establish whether Perkins examined additional material. We have chosen the K specimen of *A. Henry 10644* as the lectotype because Kew was the location of Henry's headquarters.

Selected specimens examined. CHINA. **Fujian:** Hua'an Xian, Xin-kou, *P. C. Tsoong 635* (IBSC, PE); Jianning Xian, Wu-yi-shan, from Hong-du to Pi-keng, *H. Y. Zou 20266* (MO); Taining Xian, Xin-qiao-xiang, *G. D. Ye 2137* (IBSC). **Guangdong:** Fengkai Xian, Yu-lao-xiang, Huang-gang-shan, *C. Huang 164273* (IBSC, KUN); Gaozhou Shi, Fen-zhi-ling, *Y. Tsiang 2262* (IBK, IBSC, KUN, PE); Guangzhou Shi, *H. G. Yip 364* (A, BM, L); Huiyang Shi, San-keng-shi-tou-cun, Lian-hua-shan, *W. T. Tsang 25866* (A, CAS, E, IBSC); Huizhou Shi, Luo-fu-shan, *N. K. Chun 41251* (IBK); Lechang Shi, Yang-guo-tian, Zhong-shan, *S. P. Ko 54545* (IBK, IBSC, KUN, PE); Maoming Shi, Da-po-qu, Ge-chang-xiang, *L. Tang 2413* (IBSC, KUN, PE); Qujiang Xian, Lung-t'au-shan, near Iu, *K. P. To et al. 12267* (UC); Ruyuan Yaozu Zizhixian, Tian-jing-shan, *H. G. Liu 488* (IBSC, MO); Xinyi Xian, Ba-yi, *Exp. Guangdong 587* (IBSC); Yangchun Shi, He-tang-xiang, *C. Wang 41987* (IBK, IBSC, KUN); Yangjiang Shi, San-tang-xiang, Long-gao-shan, *C. Wang 41442* (IBK, IBSC[2], MO); Yangshan Xian, Wu-yuan-xiang, *L. Tang 1082* (IBSC, KUN); Yingde Shi, Sha-kou-xiang, Hua-shui-shan, *P. H. Liang 84294* (IBK, IBSC); Zhaoqing Shi, Ding-hu-shan, *G. L. Shi 13948* (IBSC). **Guangxi:** Bama Yaozu Zizhixian, Ling-lu-xiang, *Y. K. Li P1122* (IBK, IBSC, PE); Bobai Xian, Song-shan-xiang, *Y. X. Lin 16575* (IBSC, PE); Bose Shi, Ba-ko-shan, *R. C. Ching 7398* (A, IBSC, PE, UC); Cangwu Xian, Tong-luo-shan, *S. Q. Chen 10192* (IBK, IBSC); Daxin Xian, *H. N. Qin 245* (PE); Debao Xian, Huang-lian-shan, *C. C. Chang 13769* (IBK, IBSC); Hezhou Shi, Li-song-xiang, *H. C. Chen et al. 500132* (IBK, IBSC); Jingxi Xian, *Z. J. Li 1458* (IBK); Jinxiu Yaozu Zizhixian, Yao-shan, Tseung-yuen, *C. Wang 39419* (A, CAS, IBSC, L); Lingchuan Xian, Gong-ping-qu, *F. H. Xie et al. 3183* (IBK); Lingshan Xian, Yan-dun-xiang, *C. F. Liang 33787* (IBK); Lingyun Xian, Yu-hong-xiang, Lao-shan, *X. Q. Liu 28504* (IBK, IBSC, KUN, PE); Longlin Gezu Zizhixian, Ling-wan Dist., *S. K. Lau 28504* (A); Longsheng Gezu Zizhixian, Da-di-xiang, *Guang-fu Coll. Team 306* (IBK, IBSC, MO, PE); Longzhou Xian, Da-qing-shan, *C. C. Chang 11921* (IBSC, KUN); Nanning Shi, *R. C. Ching 7957* (A, IBSC, PE); Ningming Xian, Shang-si-xiang, *C. C. Chang 13025* (IBSC, KUN); Pingguo Xian, Na-lu-xiang, *Y. K. Li P901* (IBK, IBSC, PE); Pingxiang Shi, *Guangxi Institute of Botany 2* (IBK); Pubei Xian, Long-men-xiang, *W. C. Chen 61* (IBSC); Qinzhou Shi, San-wan-da-shan, *S. Q. Chen 4141* (IBSC); Rongshui Miaozu Zizhixian, Ping-shi-xiang, Jiu-wan-da-shan, *S. Q. Chen 16565* (IBK, IBSC, KUN, PE); Rong Xian, Ta-tseh-tsuen, *A. N. Steward & H. C. Cheo 1085* (A, BM); Shanglin Xian, Ta-ming-shan, *S. S. Sin 25360* (IBSC); Shangsi Xian, Deng-long-cun, Shi-wan-da-shan, *W. T. Tsang 24105* (A, IBSC, MO); Tianlin Xian, Mao-bi-liang, *Z. T. Li 600853* (IBK, IBSC, KUN, PE); Xing'an Xian, Liang-jin-kuang-xiang, Mao-er-shan, *Z. Z. Chen 51517* (IBSC, KUN); Yongfu Xian, Sheng-li-xiang, *J. F. Qin 700397* (IBK); Ziyuan Xian, Qi-gu-shan, *Z. Z. Chen 51906* (IBK). **Guizhou:** Xia-jiang, *P. C. Tsoong 1094* (PE[2]). **Hunan:** Dao Xian, *P. C. Tam 63707* (IBK); Dongkou Xian, Xue-feng-shan-qu, Ba-qu, Shui-wei, *C. T. Lee 2472* (IBSC, PE[2]); Hengshan Xian, Heng-shan, *C. J. Qi S8* (IBSC); Jianghua Yaozu Zizhixian, An-ning, *Hunan Forest Institute 6214*

(IBSC); Qianyang Xian, *C. T. Lee 2279* (IBSC); Shuangpai Xian, *Q. Z. Lin 341* (IBSC); Yizhang Xian, Mang-shan, *Q. Z. Lin 514* (IBSC); Zixing Shi, Ping-jiang-xiang, *P. H. Liang 86286* (IBSC, MO). **Jiangxi:** Dayu Xian, Zuo-bo-xiang, *M. Q. Nie et al. 9637* (IBK, IBSC, KUN); Shangyou Xian, from Sheng-shui to Xi-long, *Exp. Jiangxi 718* (PE). **Yunnan:** Cangyuan Wazu Zizhixian, Ban-hong-xiang, *Y. H. Li 11725* (IBSC, KUN); Funing Xian, Jar-gei, *C. W. Wang 89220* (IBSC, KUN, PE); Gengma Daizu Wazu Zizhixian, Xi-shan, *China-USSR team 5610* (IBSC, PE); Hekou Yaozu Zizhixian, Wu-tai-shan, *W. X. Liu 566* (IBSC, KUN, PE); Jianshui Xian, *H. T. Tsai 53147* (IBSC, KUN, PE); Jingdong Yizu Zizhixian, Wen-po-xiang, *Q. A. Wu 9040* (KUN); Jinggu Daizu Yizu Zizhixian, Weng-lang, *F. Konta & H. Takahashi CH3721* (KUN); Jinghong Shi, *C. W. Wang 73643* (A, KUN). Jinping Miaozu Yaozu Daizu Zizhixian, Yong-ping-xiang, *China-USSR team 1510* (IBSC, PE); Lüchun Xian, Fen-shui-ling, Lei-bo Valley, *D. D. Tao 164* (IBSC, KUN); Luoping Xian, Ba-da-he-qu, Beng-shan, *H. Sun 518* (KUN); Malipo Xian, Tung-ting, *K. M. Feng 13452* (A, KUN, PE); Menghai Xian, Fo-hai, *C. W. Wang 74118* (A, IBSC, KUN, PE[2]); Mengla Xian, Luo-shan, *S. K. Wu et al. 289* (KUN); Pingbian Miaozu Zizhixian, Liang-zi-xiang, San-cha-he, *P. Y. Mao 4083* (IBSC, KUN, PE); Pu'er Hanizu Yizu Zizhixian, Maretee, *A. Henry 13693* (A, E, K); Shizong Xian, *S. C. Ho 85251* (IBSC); Shuangjiang Lahuzu Wazu Bulangzu Daizu Zizhixian, Bang-tuo, *J. S. Xing 1082* (IBSC, KUN, PE); Simao Shi, Yi-xiang-qu, *P. Y. Mao 6173* (IBSC, KUN, PE); Wenshan Xian, Lao-jun-shan, *K. M. Feng 22614* (IBSC, KUN); Xichou Xian, Lian-hua-tang, Jin-ping-shan, *S. Z. Wang 889* (KUN); Yanshan Xian, Pie-shih-eih, *C. W. Wang 84747* (KUN, PE); Yuanjiang Hanizu Yizu Daizu Zizhixian, Xi-gui-he, *G. D. Tao 38695* (KUN); Yuanyang Xian, Fen-shui-ling, *S. C. Ho 85159* (IBSC). **Zhejiang:** Longquan Shi, Feng-yang-shan, *H. Y. Zou 454* (A). LAOS. **Houa Phan:** Tasseng de Samneua Muong de Samneua, *M. Borel 7* (P, UC). **Luang Prapang:** NE de Muong Ngoi, Louang Prabang, *E. Poilane 20726* (P). **Phongsali:** *E. Poilane 26003*. **Xieng Khouang:** km 226, betw. Vinh & Tranninh, *E. Poilane 16779* (P). VIETNAM. **Bac Can:** Dac Kiet, *E. Poilane 1831* (A, P). **Cao Bang:** Nangoa, 1997, *U. Kurosu s.n.* (CAS). **Ha Tay:** Da Chong, *P. A. Pételot 5755* (A, P). **Lai Chau:** betw. Tsinh Ho & Chinh Nua N of Lai Chau, *E. Poilane 25690* (P). **Lao Cai:** Chapa, *P. A. Pételot 3259* (CAS, P, UC). **Ninh Binh:** Phu Kho, Trung Giap, *F. Fleury 469* (P). **Phu Tho:** Phu Ho, *P. A. Pételot 1033* (P, UC). **Son La:** Pha Din, 1995, *U. Kurosu & S. Aoki s.n.* (CAS). **Thanh Hoa:** from Hoa Binh to Chobo, *E. Poilane 13018* (A, P). **Tuyen Quang:** Nui La, Ha Tuyen, *F. Fleury 37970* (P). **Yen Bai:** Bao Ha, *E. Poilane 25294* (P).

17. Styrax wilsonii Rehder, in Sarg., Pl. Wilson. 1: 293. 1912 [as *S.* "*Wilsonii*"]. TYPE: China. Sichuan: Baoxing Xian, Mu-pin, 1300–1700 m, June 1908, *E. H. Wilson 884* (lectotype, designated here, A [accession no. 18452]!; isotypes, A[3]!, BM!, E!, K[2]!).

Shrubs to 2 m tall. Young twigs densely ferrugineous stellate-pubescent. Older twigs dark brown, glabrescent. Petiole < 2 mm long. Two most proximal leaves on each shoot opposite to subopposite. Lamina 1–2.5(–4) × 0.7–2(–2.5) cm, chartaceous, obovate, rhomboid, or rarely elliptic-ovate; apex acute to short-acuminate; base cuneate; adaxially sparsely stellate-pubescent along the major veins, otherwise glabrous; abaxially finely gray-white stellate-tomentose, also with scattered yellow-brown or dark brown short stellate trichomes on major veins and the two most proximal leaves on each shoot; margin coarsely serrate or apically 2- to 4-dentate; secondary veins 4 to 6 on each side of midvein, adaxially slightly sunken, abaxially prominent; tertiary veins inconspicuous, plane or slightly sunken adaxially, faintly prominent abaxially. Fertile shoots 1–2.5 cm long, 2- to 4-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences usually 1-flowered; pseudoterminal racemes 1–2 cm long, 3- to 5-flowered, rachis yellow stellate-tomentose. Pedicel 2–3 mm long, yellow or brown stellate-tomentose; bracteoles 0.5–1 mm long, subulate or linear, usually positioned at the middle of pedicel, sometimes those toward the base of the inflorescence leaf-like. Flowers 0.9–1.1(–1.3) cm long. Calyx 2–3 × 3–3.5 mm, cupuliform; adaxially sparsely white appressed-pubescent with 2- to 3-armed or stellate trichomes; abaxially gray-white stellate-tomentose throughout, often also with larger scattered orange or brown stiff stellate trichomes, especially proximally; margin distinctly dentate, the teeth narrow-deltoid, unevenly distributed, usually contiguous or rarely separated by a shallow concave portion. Corolla 0.6–0.8(–1.0) cm long, white, tube ca. 3 mm long, glabrous, lobes 5(6), 6–7 × 3.5–4 mm, narrowly oblong, adaxially sparsely pubescent except at the apex, abaxially pale yellow stellate-tomentose. Stamens 10(12); filaments 4.5–5 mm long, straight, distally slightly attenuate, ventrally white stellate-pubescent, becoming glabrous distally; anthers ca. 3 mm long, wider than distal portion of filament; connective glabrous. Style glabrous; stigma ca. 0.2 mm wide, punctiform. Fruit 0.5–0.6 × 0.4–0.5 cm, subglobose, apex rounded or apiculate, dehiscent; pericarp dry, 0.2–0.3 mm thick, outside longitudinally striate, gray tomentose, inside glabrous. Seeds brown, ovoid to globose, smooth, glabrous.

Illustrations. Prain, Bot. Mag. 148: t. 8444. 1912; F. T. Tai & T. C. Pan in W. P. Fang, Fl. Sichuan. 1: 420, fig. 162. 1981; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 87, pl. 29 (1–6). 1987; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 198, fig. 198 (1–7). 2000.

Phenology. Flowering: May, June, September. Fruiting: April, September.

Distribution. China (Sichuan); Figure 2.

Habitat. In relatively sunny, open forests on mountain slopes; 700–1500 m.

Vernacular names. Ai-mo-li (Hwang, 1987), Xiao-ye-an-xi-xiang (Hwang, 1980), Xiao-ye-yemo-li (Anonymous, 1974).

Styrax wilsonii is known only from middle (1000–1700 m) elevations of Baoxing Xian, Sichuan Province, China. It is similar to the more widespread *S. limprichtii* in its shrub habit, scattered to dense orange or brown stiff stellate trichomes on the calyx, globose fruit with longitudinally striate pericarp, and flowering time usually before the full expansion of the leaves, such that we initially considered whether the two species might be best treated as varieties of a single species. *Styrax wilsonii* can be readily separated from *S. limprichtii,* however, by its smaller leaves, flowers, and fruit. In addition, the abaxial laminar surface of *S. wilsonii* possesses a tomentum of uniform height, whereas that of *S. limprichtii* possesses a layer of longer trichomes in addition to the white base tomentum, or is glabrous or nearly so. The apparent disjunction between these two species is likely to be real rather than an artifact of inadequate collecting because numerous collections of other species of *Styrax* have been made in the intervening areas of Sichuan Province. The morphological differences together with the discontinuous distribution provide sufficient evidence for treating *S. limprichtii* and *S. wilsonii* as separate species.

We have seen four sheets from A of *Styrax wilsonii* labeled as *E. H. Wilson 884.* Two of these indicate a collection date of June 1908, one a collection date of September 1908, and one a collection date of October 1910. The protologue indicates that *E. H. Wilson 884* is the type, but does not indicate a date of collection; thus, these sheets must be regarded as syntypes. We have chosen the June 1908 sheet with accession number 18452 as the lectotype because it possesses the best flowering material for examination. Furthermore, on the other June 1908 sheet (accession number 18453) is written "isotype" (with handwriting unknown but probably not Rehder's). Thus, alternatively designating 18453 as the lectotype would cause undue confusion.

Additional specimens examined. CHINA. **Sichuan:** Baoxing Xian, *C. Pei 8120* (PE), *T. P. Soong 9476* (IBSC, PE), *39476* (KUN), *T. T. Yü 1903* (IBSC, PE); Liang-hekou, *X. B. Zhang & Y. X. Ren 4507* (PE); Wu-long, *X. B. Zhang & Y. X. Ren 4534* (PE); Ming-ling-xiang, Zhuang-zi-he-ba, *X. B. Zhang & Y. X. Ren 4640* (PE); Yan-bicun, *X. B. Zhang & Y. X. Ren 4957, 4982* (PE).

Excluded Name

Styrax bashanensis S. Z. Qu & K. Y. Wang, Bull. Bot. Res., Harbin 9(1): 27. 1989. TYPE: China. Shaanxi: Zhenping Xian, 1190 m, 28 May 1976, *K. Y. Wang 548* (holotype, NWFC lost).

We have located no authentic material referable to this name; the type is missing at NWFC. The description is consistent with the characters exhibited by some specimens of *S. hookeri* distributed near the periphery of this species' range (e.g., *X. H. Song 272* and *907, C. Wang 41180*; narrowly lance-elliptic, subcoriaceous leaves and/or relatively small fruits ca. 7 mm wide) where Wang's collection is located. There is sufficient uncertainty in the nature of these characters, however, to preclude the placement of this name in synonymy.

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Appendix 1. List of species.

1. *Styrax buchananii* W. W. Sm.
2. *Styrax chrysocarpus* H. L. Li
3. *Styrax curvirostratus* (B. Svengsuksa) Y. L. Huang & P. W. Fritsch
4. *Styrax hemsleyanus* Diels
5. *Styrax hookeri* C. B. Clarke
6. *Styrax japonicus* Siebold & Zucc.
7. *Styrax limprichtii* Lingelsh. & Borza
8. *Styrax macrocarpus* W. C. Cheng
9. *Styrax obassia* Siebold & Zucc.
10. *Styrax odoratissimus* Champ. ex Benth.
11. *Styrax porterianus* G. Don
12. *Styrax rugosus* Kurz
13. *Styrax shiraianus* Makino
14. *Styrax subpaniculatus* Jungh. & de Vriese
15. *Styrax supaii* Chun & F. Chun
16. *Styrax tonkinensis* (Pierre) Craib ex Hartwich
17. *Styrax wilsonii* Rehder

Appendix 2. Index to exsiccatae.

All specimens examined by the authors are listed alphabetically by collector, followed by collection numbers (and herbarium if anonymous). Numbers in parentheses correspond to those in the numerical list of species. If more than two persons participated in the collection, only the first collector listed on the label is cited.

236 Team 641 (10); 1251 (10); 1449 (10); 1944 (5). 713 Team 520 (5).

Ajoeb 728 (14). T. Akagi in 1985 (6). A. Aldridge in 1891 (6). C. d'Alleizette in 1908 (6); s.n. (4); s.n. (9). A. H. G. Alston 14716 (14). T. Amano 6962 (6). S. Amino et al. 192 (6). H. Ando in 1965 (6); in 1967 (6). Anonymous 3a (9) (IBSC); 3d (9) (IBSC); 1–32 (5) (KUN); 53 (16) (PE); 66 (4) (PE); 7824-70 (10) (PE); 86 (10) (IBK); 87 (6) (PE); 96 (6) (BM); 101 (6) (BM); 124 (16) (PE); 144 (16) (PE); 184 (5) (KUN); 186 (10) (PE); DI189 (12) (A); 195 (5) (KUN); 201 (6) (IBSC); 240 (6) (PE); 250 (9) (PE); 252 (6) (E); 265 (9) (PE); 273 (10) (PE); 279 (6) (C); 284 (9) (PE); 294 (10) (PE); L297 (6) (PE); 334 (6) (PE); 345a (6) (PE); 400 (10) (BM); 490 (6) (KUN); 522 (6) (KUN); 74-522 (6) (IBSC); 528 (6) (PE); 550 (10) (PE); H.III589 (5) (BM); 784 (5) (KUN); D941 (6) (PE); 1160 (6) (PE); 1189 (11) (K); 1326 (16) (IBK); 1344 (5) (E); 1369 (10) (PE); 1662 (5) (E); 1681 (16) (IBK); 1768 (10) (PE); H1795 (4) (A); 83-2052 (10) (PE); 2110 (16) (PE); 2160 (6) (BM, E); 2161 (6) (E); 2162 (6) (E); 2163 (6) (E); 2337 (9) (BR); 2346 (4) (A); 2705 (6) (KUN); 2742 (6) (PE); 3544 (6) (PE); 3584 (6) (PE); 3746 (1) (K); 4499 (16)

(IBK); 5093 (6) (IBSC); 6061 (9) (A); 6473 (16) (IBSC); 7047 (16) (IBSC); 10153 (6) (PE); 11840 (9) (A, MO); 12835 (9) (MO); 27495 (6) (PE); 31010 (9) (IBSC); 40225 (16) (P); 69965 (6) (IBK); 84100 (10) (KUN); 90244 (16) (IBSC); L8515037 (10) (PE); 8521239 (10) (PE). S. Arimoto in 1903 (9). L. Averyanov et al. VH4544 (3).

B. Balansa 4332 (16); 4339 (16); 4358 (16); 4365 (16); 12587 (16). S. Y. Bao 1 (7); 4 (5); 169 (6); 175 (6); 217 (6); 391 (5). S. P. Barchet in 1906 (10). B. Bartholomew 1916 (10). H. H. Bartlett 8077 (14). A. H. Batten-Pool 5 (14). R. K. Beattie & Y. Kurihara 10753 (6); 10814 (6). O. Beccari 699 (14). Beijing Youth Team (Guizhou, 1986) 54 (6). C. F. van Beusekom & C. Phengkhlai 1078 (12); 1082 (12). E. Beyer & Cowley 96 (9). J. Bisset 4605 (9). C. Bock & A. von Rosthorn 2423 (6). E. M. Bodinier in 1902 (6); s.n. (6); 1099 (10); 2221 (6). R. S. Boeea 8857 (14); 9285 (14). P. H. F. Bon 338 (10). A. Borel 8 (16); n8 (16). M. Borel 1 (16); 2 (16); 3 (16); 7 (16); 8 (16); 13 (16); 16 (16); 17 (16). D. E. Boufford & B. Bartholomew 24085 (6); 24853 (6). D. E. Boufford & E. W. Wood 25412 (9). D. E. Boufford et al. 25729 (6); 25808 (6); 26287 (6). F. S. A. Bourne in 1897 (6). H. S. Bowes 3199 (5). P. W. Bristol & P. W. Meyer 131 (9). W. P. Brooks 511 (9); 52511 (9). E. M. Buchanan 21 (1); 25 (12); 51 (1).

G. L. Cai 38 (10); 464 (6). K. H. Cai 850 (16); 1089 (16). T. R. Cao 90621 (10). Z. Y. Cao 191 (6). W. R. Carles 29 (6); 90 (6). J. Cavalerie 997 (6); 1062 (6); 3319 (6); 4526 (6); 8190 (6). C. H. Cave in 1912 (5); in 1913 (5); in 1917 (5); in 1919 (5); in 1922 (5). J. G. Champion 138 (10). D. Champluvier 5481 (6). T. R. Chand 1846 (5); 7065 (5); 7586 (5); C. C. Chang 602 (16); 11921 (16); 13025 (16); 13769 (16); 13901 (16); 13910 (16). C. E. Chang 2950 (6); 5547 (6); 6279 (6); 9719 (6); 15576 (6). H. T. Chang 3181 (6). J. H. Chang 19216 (16). R. E. Chang 4906 (6). S. Y. Chang 1512 (10); 1740 (6); 3319 (6); 5178 (10); 5822 (10); 6258 (10); 7772 (10); 8514 (10). Y. L. Chang 2512 (9). B. Y. Chen 2949 (10). C. Chen 1520 (10). G. R. Chen 2368 (10); 2442 (9). H. C. Chen et al. 500072 (10); 500132 (16); 500159 (10). L. X. Chen 500132 (16); 500159 (16). M. Chen 1061 (10); 1176 (10). S. Chen 519 (9). S. Q. Chen 674 (10); 2889 (8); 3431 (9); 3552 (15); 3573 (10); 4141 (16); 4875 (16); 5408 (8); 5649 (10); 10192 (16); 12850 (16); 13215 (16); 14263 (6); 14376 (5); 14420 (16); 14442 (6); 14692 (10); 14709 (6); 15240 (6); 15255 (16); 15281 (16); 15364 (6); 15367 (6); 15908 (6); 16408 (6); 16565 (16). S. Y. Chen 5649 (10). T. C. Chen 410 (6); 414 (10); 885 (16); 886 (6); 1028 (10). W. C. Chen 61 (16). Y. Chen & B. Bai 562 (5). Z. L. Chen 30585 (16); 30601 (10); 30603 (16); 30605 (10); 30610 (8); 30613 (10); 30614 (10). Z. Z. Chen 50892 (10); 50893 (10); 50983 (6); 50995 (10); 51016 (10); 51055 (6); 51074 (6); 51257 (6); 51517 (16); P51517 (16); 51906 (16); 52034 (6); 52458 (6); 52659 (10); 53822 (10). W. Cheng 103 (10). W. C. Cheng in 1937 (8); s.n. (8); 2926 (6); 3732 (10); 4588 (10); 6198 (5); 6332 (5); 6540 (5); 10388 (6); 10441 (4); 10638 (4); 11008 (4); 11022 (4). W. C. Cheng & C. T. Hwa 559 (6); 662 (6); 975 (6). X. Cheng et al. 1385 (16). Y. Q. Cheng 170066 (10); 170129 (10); 170262 (10); 170294 (10). H. C. Cheo & W. F. Wilson 229 (10). K. H. Cheo C302 (10). A. J. B. Chevalier 38674 (3); 41007 (16). C. C. Chi 5256 (10). C.-Y. Chiao 1634 (5); 2715 (6); 2800 (6); 2848 (6). C. P. Chien 623 (16). Chin & Shun 80 (4); 137 (4). China-USSR team 18 (12); 46 (16); 217 (12); 346 (6); 431 (6); 832 (6); 1510 (16); 1713 (10); 1853 (10); 1870 (16); 1876 (16); 2256 (5); 3070 (16); 3726 (16); 5570 (5); 5610 (16); 5958 (16); 6268 (5); 8531 (4); 9559 (16); 9688 (16); 185312 (10). China-Vietnam Exp. s.n. (16). Ching & Shun 80 (10). R. C. Ching 137 (4); 1415 (10); 1434 (10); 1622 (10); 1809 (10); 2080 (10); 2241 (10); 2911 (10); 3253 (9); 3273 (6); 4699 (10); 4825 (6); 5966 (6); 7096 (16); 7160 (6); 7398 (16); 7652 (16); 7957 (16); 8415 (16); 20264 (7); 20267 (7); 21670 (7); 22139 (7); 22316 (5); 22621 (5); 22673 (5); 24523 (7); 24887 (7). R. C. Ching & C. L. Tso 407 (10); 485 (10). L. H. Chiu 50078 (16). C. H. Chow 11767 (4). H.-C. Chow 832 (6); 7547 (10); 8016 (10). K. L. Chu 1266 (10); 2179 (6); 2963 (5). T. S. Chu 60946 (10). D. C. Chun 414 (10); 885 (16); 886 (6). N. K. Chun 41130 (16); 41251 (16); 41677 (10); 41913 (10). W.-Y. Chun 3699 (6); 3707 (6); 3708 (6); 4081 (6); 4159 (6); 4165 (6); 4990 (10); 5079 (10); 6051 (10); 7369 (16); 9744 (10); 9808 (10); 10623 (10). Chung In Cho 8276 (9). H. H. Chung 1345 (10); 1867 (10); 2615 (10); 2667 (10); 2742 (10); 2867 (10); 3438 (10); 7003 (10); 8455 (10). Z. S. Chung 81981 (10). Chungtien-Lijiang-Dali Exp. 1446 (5). C. B. Clarke 728B (5); 26889B (5); 27995B (5); 34944D (5); 43631A (5). Coll. Team for Oil Pl. 650302 (7); 650303 (7). C. B. Collett 800 (12). G. Congdon 507 (11). J. T. Conover 1171 (6). P. Courtois 25676 (10); 28596 (10); 36304 (6). J. M. Cowan s.n. (5). Cultuurtuin van Technische Gewassen in 1936 (6). C. Curtis 1538 (11).

L. Y. Dai & C. H. Qian 616 (6); 771 (6); 1484 (6); 1622 (6). T. L. Dai 1296 (4); 1511 (4); 1609 (4); 1689 (4); 100551 (4); 103315 (6); 105634 (4). J. M. Dalziel in 1906 (6). Danish Exp. (1958/1959) 3295 (12). K. Deguchi 4819 (6); 5737 (9). K. Deguchi & S. Tsugaru 3819 (6). J. M. Delavay in 1883 (7); 1017 (7); 2536 (7); 2782 (7); 2936 (7); 4354 (7); 4394 (7). R. P. Delavay s.n. (7). C. Y. Deng 2018 (6); 2505 (6). M. B. Deng 4134 (9); 4223 (9); 4263 (9); 4768 (10); 4803 (10); 11153 (10). M. P. Deng & K. Yao 79022 (6). X. F. Deng 4 (5); 791361 (5). P. Di 60022 (7). F. G. Dickason 6008 (12); 8750 (12). M. Dickins in 1877 (6). X. Y. Dong & Y. L. Xiong 93565 (10). P. H. Dorsett & W. J. Morse 719 (6). J. Dransfield 3418 (14). F. Ducloux 689 (6); 2291 (6); 2716 (6); 2717 (6); 4626 (5); 4627 (7); 4951 (5). S. T. Dunn 2897C (10).

E China Work Station 6855 (6); 7007 (9). Y. Z. E 77 (16). G. E. Edaño 79248 (6). H. J. Elwes & K. Watanabe in 1904 (6). Y. Endo in 1983 (6). Rev. Père J. H. Esquirol 408 (6). Exp. Anhui 59 (9); 219 (9); 359 (9); 423 (9); 1059 (10); 2344 (10); 2376 (10). Exp. An-shun 70 (6); 660 (6); 890 (5); 1353 (6). Exp. Bi-jie 358 (6); 847 (5); 1491 (6). Exp. Da-yao-shan 11118 (16); 11557 (16); 14243 (10). Exp. E-shan 88155 (5); 88441 (6). Exp. Fan-jin-shan & Feng-huang-shan 31159 (6); 32467 (6); 400532 (6); 400566 (6); 400838 (6); 400911 (6); 401959 (6); 402061 (6); 402110 (4); 402476 (10). Exp. Gao-li-gong-shan (1997) 9518 (5). Exp. Guangdong 70 (16); 144 (16); 249 (6); 445 (16); 587 (16); 1244 (10); 1265 (6); 5185 (8). Exp. Guangxi 455 (10); 627 (6); 3468 (16); 3627 (16). Exp. Guizhou 2924 (10); 3034 (10); 4042 (6); 4481 (6); 4737 (5); 4809 (6); 6836 (5); 7361 (6). Exp. Hainan 711 (6). Exp. Henan 714 (6); 868 (6); 945 (6); 1254 (6); 1405 (6); 1511 (4); 1905 (6); 2188 (6). Exp. Hokkaido EHOK105 (9). Exp. Hong-shui-he 89-999 (10); 1085 (10); 89-1109 (6); 2065 (6); 2336 (6); 2356 (5); 2943 (6). Exp. Hubei 14022 (6). Exp. Hunan 281 (6); 614 (6). Exp. Hunan & Guizhou 2626 (10); 3279 (6); 3802 (6). Exp. Jiangxi. 377 (6); 718 (16); 1411 (6); 1652 (6). Exp. Jin-fo-shan 477 (6); 1205 (6). Exp. Li-bo 1115 (6); 1188 (6); 2240 (6); 2248 (6). Exp. Long-sheng 55 (16); 151 (6). Exp. Lü-chun 43 (16); 803 (6); 866 (16); 902 (16); 1194 (16). Exp. N Guizhou 373 (6); 549 (6); 1360 (6); 1588 (6); 2046 (6). Exp. Nan-ling 55 (10); 272 (10); 560 (10). Exp. NE

Yunnan 137 (5); 309 (5); 568 (5); 905 (6); 1161 (4); 1163 (10). Exp. NW Yunnan 4010 (7); 6389 (7). Exp. Qinghai & Xizang 20 (7); 517 (7); 638 (7); 692 (7); 74-4029 (5); 6603 (5); 7245 (5); 9653 (5); 11362 (7). Exp. Qing-ling (No. 3 Team) 968 (4). Exp. S China 1996 (16); 2658 (10). Exp. S Guizhou 205 (5); 958 (6); 1104 (6); 1274 (6); 1590 (6); 1753 (6); 2008 (6); 2102 (6); 2182 (6); 2745 (6); 2902 (6); 3615 (6). Exp. Sang-zi 737 (4). Exp. SE Guizhou 50113 (6); 50609 (6); 50741 (6); 50915 (6); 50919 (6); 51245 (6). Exp. Sichuan & Guizhou 123 (6); 192 (6); 415 (6); 1774 (6); 1860 (6). Exp. SW China (Guizhou, Sichuan, Yunnan) in 1965 (7); 200 (7). Exp. W Hunan 81 (10); 495 (6); 1087 (6). Exp. Wen-shan 65-138 (16); 60243 (16); 60259 (16); 68275 (16). Exp. Wu-ling-shan 40 (6); 224 (6); 616 (6); 697 (6); 772 (6); 912 (6); 1989 (6); 2345 (6); 2598 (6). Exp. Wu-yi-shan 11 (10); 160 (10); 80-261 (6); 80-472 (6); 912 (6); 932 (6); 1624 (6); 1812 (6); 2409 (10); 6839 (10); 400668 (6); 400829 (6); 400912 (6); 401195 (10); 401260 (6). Exp. Yu-xi 2351 (5); 2373 (5); 2992 (6); 3055 (6); 3067 (6); 89480 (6). Exp. Zhan-jiang 2909 (16); 3648 (16). Exp. Zi-yun-shan 272 (6); 412 (6); 910 (6); 932 (6).

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