STYRAX IN CULTIVATION:

EVALUATION OF AN UNDERREPRESENTED ORNAMENTAL GENUS

by

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ABSTRACT

Styrax (Styracaceae) is a genus consisting of approximately 130 species of woody, dicotyledonous, often resinous trees and shrubs with a wide distribution spanning temperate and tropical regions of the Americas, the Mediterranean, and East and Southeast Asia. The taxonomy of the group is historically confused, with numerous published names, arguably with little justification. Recent revisions of the North American distribution and imbricate group of the East Asian component have largely alleviated this problem, though the valvate group of the latter as well as the Neotropical species of the genus are yet to be treated. Several species, primarily of East Asian origin, have been grown and appreciated as ornamentals but make up only a minute fraction of those known and described in the literature. Anatomical variation between species includes ploidy level as well as differences in the shape of the petiole vasculature and several characteristics associated with both the axial and radial systems of the secondary xylem.

Surveys of public garden collections reveal that *Styrax japonicus*, *Styrax obassia*, *Styrax americanus*, and *Styrax grandifolius* are by far the most commonly cultivated and accessioned species. Several other ornamental species such as *Styrax officinalis, Styrax hemsleyanus*, and *Styrax wilsonii* are also somewhat represented though rare, and certainly worthy of greater use. The ornamental potential of the group is vast and largely underutilized and should be seriously considered for further representation in botanical garden collections.

The exact chromosome number of *Styrax japonicus* could not be determined due to the small size of the chromosomes, but results strongly support a diploid in addition to pentaploid and hexaploid levels to the species. Examination of petiole anatomy revealed significant variability in the shape of the vasculature and number of accompanying bundles within plants of the same species, suggesting the petiole is of limited use as an identification characteristic. Examination of transverse sections of wood anatomy of several species of *Styrax* sect. *Styrax* ser. *Cyrta* suggested possible differences between species not found in the literature, though all results should be taken as tentative due to the limited sample size and lack of analysis of longitudinal sections.

Chapter 1

GENUS DESCRIPTION

Introduction

Styrax Linnaeus is a genus consisting of approximately 130 species of both deciduous and evergreen woody, often resinous, trees and shrubs with a wide distribution spanning East and Southeast Asia, the Americas, and the Mediterranean. A few species have been important economically as sources for the balsam resin benzoin and some are grown as ornamentals, though a large proportion of the group is virtually to completely unknown in cultivation. It is the type and overwhelmingly largest genus of the Styracaceae (Styrax Family, Storax Family), comprising approximately 75% of the species subsumed within the family.

Taxonomic History of Styracaceae

The Styracaceae consists of plants generally characterized by 4-5- merous flowers with a calyx at least partially fused to the ovary, a white to pink corolla tube, an androecium of 8-10 connate stamens appearing somewhat monadelphous, and a gynoecium of a single stigma-style and 3-5 locular ovary exhibiting axial or parietal placentation. Taxa exhibiting 6-merous flowers or with a stamen number equal to twice the number of corolla lobes are also known, though rare relative to the rest of the family. The fruit produced is typically described as a berry, drupe, or capsule, and may be woody, fleshy, or dry, and sometimes winged. Since *Styrax* is such a large genus in relation to the family, the diversity represented across the genus *Styrax* is often nearly equally to that represented across the family. For example, of the uncommon conditions in Styracaceae described above, species of *Styrax* exhibit all save for a winged fruit.

In comparison to *Styrax*, all other genera in the family are relatively small. *Alniphyllum* Matsumura, *Bruinismia* Boerlage & Koorders, *Changiostyrax* C.T. Chen, *Halesia* J. Ellis ex Linnaeus, *Huodendron* Rehder, *Melliodendron* Handel-Mazzetti, *Parastyrax* W.W. Smith, *Pterostyrax* Siebold & Zuccarini, *Rehderodendron* Hu, and *Sinojackia* Hu contain fewer than ten species each, with both *Melliodendron* and *Changiostyrax* currently described as monospecific genera. With the exception of *Halesia* and *Styrax*, these are all Old World genera more or less endemic to East and/or Southeast Asia. Following the transposition of *Afrostyrax* to Huaceae (to be subsequently described) the Styracaceae are completely absent from Africa.

Historic taxonomic systems such as Bentham & Hooker (1873) included three additional genera: *Symplocos* Jacquin, a large widespread mainly tropical group, *Lissocarpa* Bentham, a small Neotropical genus, and *Diclidanthera* Martius, a New World group named for its 2-valvate dehiscent anthers (Don 1838). Modern systems (Hutchinson 1959, Cronquist 1981, Thorne 2000) treat the first two genera as belonging to monotypic families (Symplocaceae and Lissocarpaceae), and the latter as a member of the Polygalaceae, a widespread family absent from only New Zealand, Polynesia, and the Arctic (Cronquist 1981).

Perkins (1907) completed the first thorough treatment of the family, including *Alniphyllum*, *Bruinismia*, *Halesia*, *Pamphilia* Martius, *Pterostyrax,* and *Styrax.* (*Melliodendron, Parastyrax, Rehderodendron,* and *Sinojackia* were not to be discovered and described until the 1920s-1930s). Since this period, the treatment of the family has been relatively consistent save for the addition and later removal of *Afrostyrax* Perkins & Gilg, addition and acceptance of *Changiostyrax* C.T. Chen, proposal of *Neostyrax* (Clarke) G.S. Phan, and consideration of *Pamphilia* as synonymous with *Styrax*.

Afrostyrax is a tropical African genus first described and placed within the Styracaceae by Perkins (1909), apparently on the basis of similar seed structure and stellate pubescence (Baas 1972). As briefly mentioned by Raven & Axelrod (1974), the placement of *Afrostyrax* in this family vs. the small tropical African family Huaceae A. Chevalier was debated through the mid-1900s. Hutchinson (1959) includes it with the Styracaceae. The argument was largely concluded by Baas (1972), who completed a through anatomical study of *Afrostyrax* and *Hua* Pierre ex De Wild., citing 11 morphological or anatomical differences between those two taxa and the Styracaceae, including the presence as opposed to absence of stipules, a choripetalous as opposed to sympetalous corolla, complex vs. simple petiole vasculature, simple as opposed to generally scalariform vessel perforations, and banded as opposed to diffuse xylem parenchyma. These characteristics suggested a closer affinity of *Afrostyrax* to *Hua* and thus Huaceae rather than the Styracaceae, accepted by the majority of recent systems (Cronquist 1981, Thorne 2000).

Changiostyrax is an East Asian genus described relatively recently (Chen 1995), resulting from elevation of one species of *Sinojackia* (*Sinojackia dolichocarpa* C.J.Qi) to the generic level following observations of significant variation in several vegetative and reproductive characteristics (Chen 1995), supported by molecular analysis (Yao et al. 2007). Conversely, *Neostyrax* (Clarke) G.S. Fan resulted from the elevation of one species of *Bruinsmia* (*Bruinsmia polysperma* Clarke) to generic level based on numerical, cluster statistic based taxonomic analysis of the family (Fan 1996), with the elevation resulting from an indurate endocarp in that species as opposed to the soft endocarp characteristic of *Bruinsmia* (Fritsch et al. 2001). The genus *Neostyrax* has largely been ignored in the subsequent literature.

Pamphilia, a Neotropical genus, is now considered synonymous with *Styrax* based on its close similarity to Neotropical species of that genus. Earlier authors primarily recognized the androecium consisting of five stamens as opposed to the typical ten of *Styrax* as grounds for separation (Wallnöfer 1997).

Unique Characteristics of *Styrax*

The dichotomous key present in Hwang & Grimes (1996) suggests *Styrax* can typically be separated from other genera of the family by examination of the gynoecium. The ovary of *Styrax* is interpreted as superior on the basis of fusion to the calyx tube, a characteristic which separates it from all genera save for *Alniphyllum* and *Bruinsmia*. These two genera have a 5 or 6-locular ovary, whereas that of *Styrax* is only 3-locular (eventually fusing to 1-locular as the flower ages). Fritsch (1999) instead focuses on the attachment of the stamen tube high as opposed to low on the corolla, bitegmic as opposed to unitegmic ovules, and a thick rather than thin seed coat. Gonsoulin (1974) suggested *Alniphyllum* and *Pterostyrax* were the closest relatives to *Styrax*, but phylogenetic analysis of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA) as well as chloroplast DNA restriction sites of genes trnK, rpoC1, and rpoC2 suggests instead *Huodendron* is likely the closest relative (Fritsch 2001).

Distribution

The largest centers for the genus occur in East and Southeast Asia (49 taxa) and the Neotropics (74 taxa). A smaller distribution is located in North America (9 taxa). The genus is also represented in the Mediterranean and Middle East, though limited to only one species: *Styrax officinalis* Linnaeus. Prevalence across these ranges varies from species to species. Taking the East Asian component as an example, *Styrax japonicus* Siebold & Zuccarini is common and widespread across its range, whereas *Styrax wilsonii* Rehder is an infrequent endemic and *Styrax litseoides* J.E.Vidal is rare and considered vulnerable.

The absence of *Styrax* from Africa suggests the genus dispersed prior to the separation of the African and South American continents, and that the Neotropical component of the genus likely originated in the Northern Hemisphere before migrating from North to South America (Fritsch 1999). One species, *Styrax tonkinensis*, has naturalized in French Guinea (Pinyopusarerk 1994).

As for the purposes of this study, the term "Neotropics" should be taken to include everything south of the range of the Flora of North America Project, and thus the entirety of Mexico and South America. Though this includes much of subtropical Mexico and South America and is thus a wider definition of the Neotropics than generally accepted, it avoids double counting of many Mexican species that bridge the gap between the subtropical and tropical regions. Those seeking more information on this Mesoamerican component should consult Fritsch (1997).

Morphology

Habit

Styrax typically takes the form of a small to medium sized tree or large shrub, with intermediate forms abundant in those species which rarely develop a strong central leader. Despite their multi-stemmed nature, most species of *Styrax* do not tend to sucker profusely from roots (one exception is *Styrax grandifolius*), though prolifically seeding species such as *Styrax japonicus* may have a somewhat clonal appearance due to an abundance of small seedlings in the immediate proximity of the parent plant.

Leaves

The leaves of *Styrax* are borne in an alternate arrangement, though the lowest pair on each branch is often opposite or subopposite, an important diagnostic characteristic in several species. The leaf typical of the genus possesses a lamina with an acute to acuminate apex, cuneate to broadly cuneate base, and entire to serrulate margin. The petiole is relatively short in length and concave to round in cross section. Leaf buds are typically small, white in color, and superposed. In two species, the petiole dilates towards the base of the pulvinus to form a sheath enclosing the following year's bud. Leaf size is highly dependent on species and environmental conditions, ranging from as little as 1 × 0.7 cm to as much as 15 × 20 cm. Leaves borne on sterile shoots are typically larger than those of fertile shoots (Huang et al. 2003). Leaves range from pale to lustrous green in color, papery to leathery in texture, and may be sparsely to densely stellate pubescent depending on species. Tertiary venation is reticulate or subparallel, and in several species prominent abaxially.

Trichomes are present on the lamina and petiole of many species, and can be stellate, peltate, or both (Schadel & Dickison 1979).

Stems

Branchlets may be densely to sparsely pubescent depending on species. Older twigs of some species possess bark exfoliating in long strips. The main stem usually retains a smooth bark for a time though will develop longitudinal fissures with age, sometimes turning orange in color, an effect that adds to the ornament of the genus in the landscape (Dirr 1978).

Flowers

Flowers are typically small, white or more rarely pink in color, and can range from campanulate to reflexed in shape. They are perfect, 5-merous, and consist of a calyx tube with five deltoid teeth, a corolla tube with five lobes typically fused towards the basal end of the corolla, an androecium of ten epipetalous stamens with prominent yellow anthers, and a gynoecium consisting of a 3-locular ovary (1-locular with age) and single stigma-style. The flowers are not generally known for their fragrance. When a fragrance is present, it tends to range from mildly spicy to slightly disagreeable (*Styrax officinalis* is a notable exception). Flowers are borne on pseudoterminal racemes or panicles, in many species reduced and accompanied by a proliferation of smaller axillary, cluster-like racemes or panicles. The flowers typically open in late spring on many of the temperate species, though some species flower more sporadically.

Fruit

Fruits are generally more or less globose to ellipsoid in shape and green in color, though they may appear silvery-grey or brownish from a distance depending on the color and degree of pubescence. The fruit has historically proven difficult to categorize. Taking two North American species for example (*Styrax americanus* Lamarck and *Styrax grandifolius* Aiton), some authors have treated it as a drupe (Bailey 1924), others as a capsule (Radford et al. 1968), and others not assigning a specific type (Fernald 1950). These treatments are in direct conflict, as by definition a capsule dehisces whereas a drupe does not. Observations of the fruiting stage of the plant lifecycle reveal the fruit most closely resembles a drupe during the summer months, owing to the green fleshy layer surrounding the seed. However, by early fall, this fleshy layer has dried leaving only a papery brownish-grey sheath encasing the seed. The sheath then dehisces, generally by 2-3 apical valves to release the large seed (sometimes two seeds) contained within. Current treatments typically refer to the fruit as a capsule (Fritsch 2009). Fruits of some species are truly indehiscent however, generally producing a dry and nutlike fruit though a few produce a true, wet drupe (Huang et al. 2003).

Anatomy

Petiole Vasculature

The vascular system consists primarily of an arc or crescent shaped vascular strand in the center to upper center of the petiole, often accompanied by additional strands towards the distal end of the petiole and base of the lamina. Crystals are often observed in close proximity to these vascular bundles. Schadel & Dickison (1979) suggested there were differences between species based on the pattern of the vasculature at the distal portion of the petiole. Their studies of the family revealed six different configurations of the vasculature in this region: an arc with invaginated ends (1), an arc with invaginated ends accompanied by two dorsal cortical bundles (2), a medullated cylinder (3), a medullated cylinder accompanied by two dorsal cortical bundles (4), a medullated cylinder accompanied by medullary vascular tissue and two dorsal cortical bundles (5), and a dissected cylinder of collateral bundles with numerous medullary bundles and two smaller dorsal dissected cylinders. Again the diversity represented by the Styracaceae is nearly equal to that represented by *Styrax*, as all but the sixth condition (exclusive to *Parastyrax lacei* W.W.Smith) are recorded in various species of *Styrax*.

Howard (1979) encouraged use of petiole cross sections as a field characteristic for sterile material, arguing that examination of freehand sections with a hand lens was a relatively quick method, often sufficient for identification of an unknown specimen to family, genus, or in some cases species level. If the patterns observed by Schadel & Dickison (1974) prove consistent over a large enough sample size, the characteristic would likely prove useful for the identification of sterile material to the species level even though the petioles of many species of Styrax are short in length and small in cross section.

Wood

Wood of stems of the Styracaceae has been described by Metcalfe & Chalk (1950) and studied by Dickison & Phend (1985). Styrax possesses a greater tendency towards the diffuse porous as opposed to ring porous condition. Vessels (pores) are small to medium sized and borne either solitary or in multiples. Perforations of perforation plates are typically scalariform or opposite, though alternate in some species of Styrax (Styrax platanifolius, Styrax redivivus). Ray parenchyma cells are uniseriate or multiseriate, the latter generally 2-4 cells in width. Axial parenchyma cells are abundant, and can occur in uniseriate or more rarely, multiseriate lines. Prismatic calcium oxalate crystals tend to appear more frequently, particularly in the parenchyma of tropical species, than in other genera of the family. Wood also contains fiber-tracheids. Those species occurring furthest from the equator tend to exhibit a greater frequency of vessels (pores) and multiseriate rays (Dickison & Phend 1985).

As examination of wood anatomy typically necessitates fixation, staining, and sectioning with a microtome, histological characteristics of wood are unlikely to show promise for field identification. However, differences such as pore location, pore frequency, and frequency and width of uniseriate and multiseriate rays are easily discernible in cross section, and worth investigation as to their taxonomic significance.

Chromosome Numbers

As is the case with many woody plants, chromosomes of Styrax are small and difficult to count using traditional light microscopy techniques. Known counts are listed in Table 1, though in many cases it is unclear as to the exact methodology in which these counts were determined. Gonsoulin (1974) determined numbers for Styrax americanus and Styrax grandifolius by smearing pollen mother cells, though many attempts were necessary to produce a satisfactory preparation and theorized meiosis in Styrax takes place during a very narrow time frame. Flow cytometry, a laser based technology used commonly for chromosomal analysis, is likely a superior method for further cytogenetic work with the genus.

Table 1 Species of *Styrax* with known chromosome numbers

Species	**Count**	**Source**
S. aureus	*2n=2x=16*	Morawetz 1991
S. americanus	*2n=2x=16*	Gonsoulin 1974
S. ferrugineus	*2n=2x=16*	Morawetz 1991
S. grandifolius	*2n=4x=32*	Gonsoulin 1974
S. hookeri	*2n=2x=16*	Mehra & Bawa 1969
S. hookeri	*2n=4x=32*	Moore 1973
S. japonicus	*2n=2x=16*	Yamikazi 1993
S. japonicus	*2n=5x=40*	Baranec & Murin 2003
S. japonicus var. *tomentosus*	*2n=6x=48*	Shiuchi & Fujita 2006
S. japonicus	*2n=5x?>40*	Manshard 1936
S. maninul	*2n=2x=16*	Morawetz 1991
S. martii	*2n=2x=16*	Morawetz 1991
S. obassia	*2n=2x=16*	Manshard 1936
S. pedicellatum	*2n=2x=16*	Morawetz 1991
S. redivivus	*2n=2x=16*	Copeland 1938
S. serrulatus	*2n=2x=16*	Mehra & Bawa 1969

The base number for *Styrax* appears to be 8 (*2n=2x=16*). Tetraploidy is known from at least one species, *Styrax grandifolius* Aiton (*2n=4x=32*). One report notes tetraploidy for *Styrax hookeri* (Moore 1973) though its subsequent omission from many thorough literature reviews of the group could indicate this is believed to be erroneous. Pentaploidy has been historically reported for *Styrax japonicus*, most citing Manshard's (1932) report of *2n>40*, though Baranec & Murin (2003) report *2n=40* for a plant of North Korean origin. Additionally, hexaploidy has been recently published in *Styrax japonicus* var. *tomentosus* (*2n=48*), a synonym of *Styrax japonicus* per Huang et al. (2003). *Styrax japonicus* also has a published count of *2n=16*, implying that multiple ploidy levels exist over the range of the species. Such a condition is not unheard of in widespread, temperate woody plants, with *Fraxinus americana* Linnaeus (*x=23, 46, 69*) and *Acer rubrum* Linnaeus (*x=ca. 39, 52*) two examples from the North American Flora (Radford et al. 1968). *Styrax japonicus* is the only species of the Styracaceae known to possess this characteristic unless the count of *2n=48* for *Styrax hookeri* is indeed valid.

Hybridization is known or suspected in two occurrences: between *Styrax japonicus* and *Styrax hemsleyanus*, (*Styrax* 'Wespalaar'), and an unnamed hybrid of *Styrax obassia* x *Styrax hemsleyanus* at the Atlanta Botanical Garden. This latter hybrid could imply a chromosome number of *2n=2x=16* for *Styrax hemsleyanus*, though this may not be certain as plants of different ploidy levels are also known to produce viable crosses.

Interestingly, flow cytometry of the group has been attempted once on various cultivars of *Styrax japonicus*, and no significant differences between ploidy levels were ascertained (Tom Ranney, pers. comm.). Though the specific list of cultivars sampled (save for 'Emerald Pagoda') is not currently available, these results suggest that the cultivated component likely does not represent the full the germplasm of the species, though whether the diploid, pentaploid, hexaploid, or another unknown level is dominant in cultivation remains unknown.

Nomenclature and Taxonomic History

Early Treatments and Synonymous Genera

The taxonomic history of *Styrax* is somewhat complex, with a large number of species recognized (ca. 400), many arguably with tenuous justification (Gonsoulin 1974). Recent treatments (Hwang & Grimes 1996, Huang et al. 2003, Fritsch 1997, Fritsch 1999) have largely alleviated this problem, though treatments of the

Neotropical component and of the East Asian taxa exhibiting valvate corolla aestivation (an artificial characteristic) are still forthcoming.

The genus *Styrax* was first described by Linnaeus (1753), with the Mediterranean *Styrax officinalis* Linnaeus as the type. Many species were described thereafter, though until the early 20th century the current concept of *Styrax* was interpreted as five separate genera: *Cyrta* Loureiro, *Foveolaria* Ruiz & Pavon, *Pamphilia*, *Strigilia* Cavanilles, and *Styrax*.

First described was *Strigilia* (Cavanilles 1789), even then considered very similar to *Styrax* but was thought to differ significantly on the basis of the sessile anthers (as opposed to free at apex), which additionally were finely denticulate, inspiring the name for the genus from *strigilus* meaning a comb (Don 1938). Soon thereafter was *Cyrta*, (Loureiro 1790), including three species distributed in tropical China to Laos and Vietnam, thought significant from *Styrax* on the basis of a thicker corolla with stronger tendency towards valvate aestivation (Miers 1858). *Foveolaria* was soon described in the New World (Ruiz & Pavon 1798) as four species with a more adherent, monadelphous nature to the stamens as compared to *Styrax* (Lindley & Moore 1866). Perkins (1907), upon completion of the first detailed monograph of the family, would consider all these genera save for *Pamphilia* as synonymous with *Styrax*.

Gonsoulin (1974) lists two additional synonyms: *Epigenia* Velloso which was made synonymous with *Styrax* only two years after its description, and *Adnaria* Rafinesque, which apparently resulted from a misidentification of *Styrax americanus*. Illegitimate names more rarely seen in the literature include *Benzoin* Hayne, resulting from an unfounded elevation of *Styrax benzoin* Dryander to generic level on the basis of variation in fruit variety (Hayne 1829), *Tremanthus* Persoon, which refers to *Strigilia*, and *Darlingtonia* Torrey, which was first erroneously assigned to *Styrax redivivus*, then conserved for a genus of pitcher plants in the northwestern United States (Gonsoulin 1974).

Series and Sections

Historically, *Styrax* was divided into two sections: section *Styrax* (or section *Eustyrax* Perkins) and section *Foveolaria* Perkins. Variation in number of ovules per ovary served as the basis for separation, with the former containing 16-24, and the latter only with 3-5 (Perkins 1907). Section *Eustyrax* was further divided into two series, series *Imbricatae* Perkins and series *Valvatae* Perkins, on the basis of corolla lobe aestivation. However, this division poses problems as several species, particularly those within series *Valvatae* Perkins, vary greatly in regards to this trait to the extent that often separate flower buds from the same plant will be polymorphic in regards to the imbricate vs. valvate condition (Fritsch 1999).

As Perkins (1907) treated *Pamphilia* as a separate genus from *Styrax*, those six species were not assigned into either section. Wallnöfer (1997) did not consider *Pamphilia* distinct from *Styrax* at the generic level, but did recognize them at the sectional level, placing them within section *Pamphilia* Wallnöfer This section was further divided into series *Pamphilia* Wallnöfer, containing the four species found in Brazil and Colombia with leaves stellate pubescent abaxially, and series *Andinae* Wallnöfer, two species in the Peruvian Andes with leaves glabrous abaxially.

In order to better divide the genus with less emphasis on polymorphic traits, Fritch (1999) proposed two new sections: section *Styrax* P.W.Fritsch and section *Valvatae* P.W.Fritsch, the former containing by and large the deciduous species of the genus found in North America, East Asia, and the Mediterranean and the latter containing the evergreen component located in East to Southeast Asia and South America. Section *Styrax* is broken into two series: series *Styrax* P.W.Fritsch and series *Cyrta* P.W.Fritsch. Series *Styrax* contains the species with entire margins and strictly terminal inflorescences, whereas series *Cyrta* contains those with glandular denticulate to glandular serrate margins and axillary in addition to terminal inflorescences. Series *Cyrta* accounts for roughly 90% of section Styrax, as series *Styrax* consists only of three species: two in the Southwestern United States, and a close relative in the Mediterranean. Section *Valvatae* is also broken into two series: series *Valvatae* P.W.Fritsch consisting of the Neotropical plants with fruits containing a juicy mesocarp, and endocarp adherent to ellipsoid seeds possessing a non-crackled seed coat, whereas series *Benzoin* P.W.Fritsch is comprised of the East and Southeast Asian species with a dry mesocarp, and endocarp not adherent to the depressed-globose seeds with a crackled coat. Fritsch (2001) does not recognize section *Pamphilia*, arguing those species are sufficiently similar to series *Valvatae* to not warrant division at the section level.

Gender

The appropriate gender for *Styrax* has long been a source of debate. Linnaeus treated the genus as neuter during his initial transcription whereas later botanists such as Rehder and Bean preferred use of the feminine gender. Recent treatments seem to have settled on use of the masculine. Nicolson and Steyskal (1976) conducted a thorough evaluation of the issue, presenting the arguments for treating the genus as such: neuter appears justified as it follows the initial publication by Linnaeus, though his writing of the genus as neuter was likely in error, while those treating *Styrax* as feminine follow the Greek and Roman tradition of treating trees as female. The general historic pattern however, evident in Greek and Latin dictionaries, seems to be in treating *Styrax* as masculine, which Nicolson and Steyskal conclude as the most appropriate gender for the species (1976).

Etymology

The name *Styrax* is often considered a Greek word derived from the Arabic *assitirax*, indicating the sweet-smelling resin historically harvested from several species (in this case primarily *Styrax officinalis* Linnaeus). Nicholson & Steyskal (1976) argue the opposite: the term *astirak* is adopted from *styrax* and thus a Greek word introduced into Arabic as opposed to an Arabic word introduced into Greek.

Conservation Concerns

The majority of Styrax species of conservation concern are members of the Neotropical or Southeast Asian components to the genus, which is somewhat problematic as the taxonomy for these species is significantly less clear. IUCN (International Union for Conservation of Nature) lists eleven *Styrax* taxa on their Red List of Threatened Species: *Styrax argyrophyllus* Perkins, *Styrax crotonoides* C.B.Clarke, *Styrax ferax* J.F.Macbride, *Styrax foveolaria* Perkins, *Styrax fraserensis* Putzeys & Ng, *Styrax litseoides* J.E.Vidal, *Styrax mathewsii* Perkins, *Styrax peruvianus* Zahlbruckner, *Styrax portoricensis* Krug & Urban, *Styrax socialis* J.F.Macbride, and *Styrax tafelbergensis* Maguire (Table 2). The majority of the species are considered vulnerable due to their limited distribution, which in many cases is restricted only to the type locality. IUCN notes the rankings of *Styrax* are in need of updating, which is evident as only five of the eleven names appear to be currently accepted following modern monographs: *Styrax crotonoides* C.B. Clarke, *Styrax foveolaria* Perkins, *Styrax litseoides* J.E. Vidal, *Styrax peruvianus* Zahlbruckner, and *Styrax portoricensis* Krug & Urban.

Table 2 Species of Styrax on International Union for Conservation of Nature (IUCN) Red List. * indicates a taxon currently considered synonymous with species of greater distribution.

Species	**Category**	**Range**	**Habitat**	**Threats**
**S. argyrophyllus* Perkins	Vulnerable	Peru	Submontane shrubland	Limited distribution
S. crotonoides C.B.Clarke	Vulnerable	Malaysia, Singapore	Lowland rainforest, swamp & disturbed forest	Forest conversion
**S. ferax* J.F.Macbride	Vulnerable	Peru	Lowland forest	Limited distribution
S. foveolaria Perkins	Vulnerable	Peru	Not listed	Limited distribution
**S. fraserensis* Putzeys & Ng	Vulnerable	Malaysia	Not listed	Limited distribution, tourism
S. litseoides J.E.Vidal	Vulnerable	Vietnam	Not listed	Limited distribution
**S. mathewsii* Perkins	Vulnerable	Peru	Submontane shrubland	Limited distribution
S. peruvianus Zahlbruckner	Vulnerable	Peru	Submontane shrubland	Limited distribution
S. portoricensis Krug & Urban	Critically Endangered	Puerto Rico	Upper montane forest	Limited distribution (only four individuals known)
**S. socialis* J.F.Macbride	Vulnerable	Peru	Shrubland	Limited distribution
**S. tafelbergensis* Maguire	Vulnerable	Suriname	Creek forest	Limited distribution

Styrax tafelbergensis was considered endemic to Tafelberg (Suriname), though is now considered a synonym of *Styrax pohlii* A. de Candolle, a more common species spanning Brazil and Bolivia (Jorgensen et al. 2013).

Styrax argyrophyllus and *Styrax mathewsii* are both listed as synonyms of *Styrax cordatus* (Ruiz & Pavon) A. de Candolle per Jørgensen & León-Yanez (1999), though *Styrax cordatus* would later be considered a synonym of *Styrax pavonii* A. de Candolle per Hokche et al. 2008. Fritsch (1997) also seemed hesitant to accept *Styrax cordatus*, suggesting it was a synonym of *Styrax ovatus* (Ruiz & Pavon) A. de Candolle, another species considered synonymous with *Styrax pavonii* per Hokche et al. 2008. *Styrax pavonii* is a species spanning Colombia, Peru, and Venezuela, suggesting that though the Peruvian populations of the species represented by *Styrax argyrophyllus* and *Styrax mathewsii* may be at risk, the species at a whole is probably more secure. Similarly, two other Peruvian taxa listed as threatened, *Styrax ferax* and *Styrax socialis*, are now considered synonyms of *Styrax pentlandius* J.Rémy, a species distributed in Colombia and Bolivia and probably better interpreted as a rare Peruvian component of that species.

Styrax fraserensis Putzeys & Ng is a Malaysian species which rarely appears in the literature. In the Addenda to Volume 4-9 of Flora Malesiana, Van Steenis (1982) argues there is little difference between the species and *Styrax crotonoides*, though chooses to maintain it as a lower taxon (*Styrax crotonoides* Clarke ssp. *fraserensis* (Putzeys & Ng) Steenis) based on a fruit which is more ovoid and may possess an apical tip as compared to the straight species. *Styrax crotonoides* has a wider distribution extending into Vietnam so this taxon may better be interpreted as a vulnerable lower taxon as opposed to a vulnerable species. Additional taxonomic work on these taxa should likely be considered a critical prerequisite for any serious conservation studies or efforts.

IUCN does not list any species of North American origin, though all four species in the United States have been ranked by NatureServe, a New World based conservation organization. *Styrax americanus* and *Styrax grandifolius* both receive G5 rankings (secure), *Styrax redivivus* receives a G2G3 ranking (imperiled to vulnerable); *Styrax platanifolius* receives a G3 ranking (vulnerable). Two lower taxa of the latter, ssp. *texanus* and *youngiae* are ranked G3T1 (critically imperiled lower taxa). Specific distribution and conservation issues for these taxa will be discussed in Chapter 2.

Chapter 2

STYRAX IN CULTIVATION

History in Cultivation

Styrax has been cultivated since antiquity, largely for the exudation of the balsamic resin produced by several species. This resin is rarely harvested and utilized today, and the cultivated component to the genus is instead comprised predominantly of ornamentals. Approximately 30 species are currently cultivated as such in botanical gardens worldwide, though fewer than five species are common accessions. In the nursery trade, only two species (*Styrax japonicus* and *Styrax obassia*) are available to any great extent, leaving a vast portion of the genus unrepresented.

Resin

Composition and Uses

Styrax resin is thought to have been traded and utilized since antiquity, evidenced by two apparent references in the Bible: the "stacte" of Exodus 30:34 in reference to *Styrax officinalis* resin, and the "sweet storax" of Ecclesiasticus 24:15 possibly a reference to extract of *Styrax benzoin* Dryander (Woodward 1941). Evidence also exists that it was traded to China in 800 AD, thought similar to frankincense but of higher value (Langenheim 2003).

The most important resin produced by *Styrax* species is referred to as benzoin, most often a product of *Styrax benzoin* or *Styrax tonkinensis* Craib ex Hartwich. Due to its phenolic nature, it is generally classified as a true balsam resin (Langenheim 2003). Though both termed “benzoin”, the resins produced by *Styrax benzoin* and *Styrax tonkinensis* differ in their content, the former predominantly of benzoic acid and its esters, while the latter of cinnamic acid and its derivatives (Langenheim 2003). Thus they are often separated as “Sumatra benzoin” and “Siam benzoin” in regards to the distribution of these two species. As a principal component of Sumatra benzoin is benzoic acid, it has been historically utilized for a wide variety of medical applications, primarily as an analgesic, antiseptic, and expectorant (Hommell 1919). Though today benzoic acid sees greater use as antifungal agent and food preservative, it is primarily a synthetic product (Langenheim 2003). Siam benzoin on the other hand has been more important for flavoring and fragrance, smelling of vanilla (Langenheim 2003).

The other species frequently cited as producing resin is the Old World *Styrax officinalis*. Resin of such is typically referred to as “styrax”, or often “storax”, though the latter term is more often used to refer to exudations of *Liquidambar* or *Altingia*. New World species have been recorded to produce a similar resin called *estoraque*, a term also used for *Liquidambar* exudations (Langenheim 2003). The identity of these two resins is thus often confused, with some (Zeybek 1970) arguing that most to all of the resin referred to as styrax or storax was probably harvested from *Liquidambar* as opposed to *Styrax*.

Regardless, numerous Neotropical and Southeast Asian species are known to produce resin (Table 3), though there have apparently been no attempts to harvest from any of the North American species.

Table 3 Species of *Styrax* historically utilized for production of resin.

Species	**Region**	**Resin Name**	**Source**
S. argenteus	Neotropics	*Estoraque*	Morton 1981
S. aureus	Neotropics		Howes 1949
S. benzoin	East Asia	Sumatra benzoin, gum benjamin	Burkill 1966
S. benzoides	East Asia	Benzoin	Svengsuksa & Vidal 1992
S. camporum	Neotropics	*Estoraque, beijoeiro*	Mors & Rizzini 1966
S. ferrugineus	Neotropics	*Estoraque, beijoeiro*	Mors & Rizzini 1966
S. guyanensis	Neotropics		Schultes & Raffauf 1990
S. officinalis	Europe, Mediterranean, Middle East	Styrax-resin, storax	Zeybek 1970
S. paralleloneurus	East Asia	Benzoin	Langenheim 2003
S. ridleyanus	East Asia		Langenheim 2003
S. sieberi	Neotropics		Howes 1949
S. serrulatus	East Asia		Langenheim 2003
S. subpaniculatus	East Asia		Burkill 1966
S. tonkinensis	East Asia	Siam benzoin	Pinyopusarerk 1994
S. warscewiczii	Central/South America	*Estoraque*	Morton 1981

Exudation Procedure

The resin is produced in the wood and bark of the plant following cambial injury, thus a pathological as opposed to natural resin (Pinyopusarerk 1994). Therefore, those wishing to extract resin must induce its production by wounding the plant. The general tapping procedure involves bruising the bark in a period of sap flow, and returning later to harvest the yellowish-white globular tears from the wound. Subsequent wounds typically produce more resin than the first wound, though repeated tapping of resin will kill the tree (Langenheim 2003). Typically the plant must be seven years of age before resin can be successfully extracted (Howes 1949).

Ornamental

Introduction

At least some component of the genus was known to be in cultivation in the East, though introductions to the West did not begin until the early 1900s. The first introduction was likely that of *Styrax japonicus* to Kew Gardens by Richard Oldham in 1862 (Bean 1980) with *Styrax obassia* following soon thereafter as a result of Charles Maries' 1877-1879 expedition to Japan for James Veitch & Sons Nurseries, then one of the largest in London. The majority of the East Asian species less common in cultivation (primarily of Chinese provenance) can be traced back to E.H. Wilson's expeditions to China in 1907, 1908, and 1910 (Wilson 1913).

Though annotations of Wilson's collections make it clear he and others felt the genus had significant landscape value, all species of *Styrax* remained quite rare in cultivation even in botanical gardens into 1950 (Gall 1962), generally understood as an obscure, rare relative of the more commonly grown *Halesia* (Dirr 1987). Likely as a result of the efforts of the Dr. J.C. Raulston, who performed thorough trials on the group and distributed numerous plants to nurseries and botanical gardens, the genus has become more popular over the last two decades, evidenced by the increasing prominence of the North American native and indigenous species *Styrax americanus* and *Styrax grandifolius* in nursery catalogs and botanical gardens.

Ornamental Characteristics and Value

Styrax species are most often grown for their flowers, ranging from white to pink and campanulate to reflexed. The pure white, weakly campanulate form typical of the commonly grown species (*Styrax japonicus*) likely inspires their common name, snowbell. Though rather small in size (generally 1-2cm), the flowers appear en masse in mid to late spring, either on large, pseudoterminal inflorescences, or in a profusion of smaller axillary clusters, particularly on the underside of the branches. In this case, the plant often has a neatly layered look contrasting the pure white flowers against the green to dark-green foliage. The fragrance of the flowers can be anywhere from pleasant to somewhat disagreeable, varying both between species and various individuals of the same species (as evidenced by more noticeable fragrant cultivars of *Styrax japonicus* such as 'Fragrant Fountain' and to a lesser extent, 'Angyo Dwarf' and 'Snowfall'). The stamens are epipetalous, falling still attached to the corolla tubes, creating a sparse carpet underneath the plant reminiscent of a light dusting of snow. The style and calyx remain attached to the plant, and by mid-summer the green-grey drupe-like capsules (or true drupes in some species) are also of ornament due to their unique appearance. Winter interest is provided both by the neat habit of the plants, as well as the ornamental bark of many species, with older stems often splitting longitudinally to expose orange fissures. The species is best utilized to help extend spring flowering into early summer by providing profuse flowering after the seasons of many spring staples such as *Prunus* spp. and *Magnolia* hybrids have ceased.

Aside from snowbell, another common name for the genus is mock orange (Fernald 1950, Radford et al. 1968), as those members of the genus with a stronger tendency towards a reflexed flower (*Styrax americanus, Styrax officinalis*) do somewhat resemble those of *Citrus sinensis* (Linnaeus) Osbeck, albeit with a much less prominent gynoecium. "Storax" is also in use as a common name (Bailey 1949) particularly for the North American species, though I personally find the name undesirable as it invites confusion regarding resin identity described above.

Propagation

Many species of *Styrax* are known to root readily following treatment with 1000-4000ppm IBA, though prove difficult to overwinter and cuttings should be taken in early spring if possible (Raulston 1992). Seed germination can be troublesome as well, since many species exhibit a double dormancy, increasing production time. Generally, the North American species tend to exhibit a single dormancy whereas East Asian species exhibit a double dormancy (Raulston 1992), though the large number of species not trialed, as well as the absence of information as to Neotropical or Mediterranean species, prevents this from being a rule of thumb. Acid scarification is beneficial (Dirr & Heuser 2006). Tissue culture has been attempted but results did not prove satisfactory as relative to other commercial species (Raulston 1992).

Materials & Methods

In order to determine which *Styrax* species are in cultivation, the collections of botanical gardens were surveyed. The Multisite Search feature available on the website of the Royal Botanic Gardens (RBG) – Edinburgh was used. This search engine surveys plant records from 27 organizations running BG-Base Collections Management Software (20 in United States, 7 in Europe). Unfortunately, none of the six botanical gardens listed by Raulston (1992) as possessing the largest living collections of *Styrax* (Morris Arboretum, Washington Park Arboretum, JC Raulston Arboretum, Berkeley Botanical Garden, Tilden Park, Strybing Arboretum) are included in this multisite search. However, all gardens save for Tilden Park (now generally referred to as the Regional Parks Botanical Garden) make their inventory information available online. The Regional Parks Botanical Garden still has a sizeable collection of *Styrax*, though limited to accessions of *Styrax redivivus* (Joe Dahl, pers.

comm.). Inventory records of the remaining five gardens were examined and all *Styrax* species collected were noted. The collection of the University of Delaware Botanic Gardens was also added due to the convenience of the location.

A second and superior search involved utilization of the PlantSearch feature hosted by Botanical Gardens Conservation International (BGCI). PlantSearch indexes the collections records of far more botanical gardens (924) and is thus both less time consuming and provides more complete information than the previous method described. However, though BGCI provides numbers as to how many accessions exist for each taxa, they do not specify which garden collects taxa even to country level in order to protect threatened or vulnerable taxa from illicit collection. They do allow a feature to contact gardens using BGCI as an intermediary. Upon request, BGCI's database entries for the genus *Styrax* were obtained.

Results from both searches combined with information recorded in Wilson (1913), Spongberg (1976), Bean (1980), Dirr (2009), Raulston (1991, 1992), and Grimshaw & Bayton (2009) was taken to provide a thorough portrait of the genus in cultivation. Names of *Styrax* taxa obtained from the above sources were checked for validity and synonymy using Fritsch (1997, 2004, 2009), Huang et al. (2003), and Hwang & Grimes (1996) as primary references, than standardized to a masculine gender as recommended by Nicolson & Steyskal if necessary (1979). For the one species with named cultivars (*Styrax japonicus*) the listing by Dirr (2009) served as main reference. Species are organized into the two sections and four series as defined by Fritsch (1999).

Species descriptions were prepared for all species found to be currently in cultivation by either RBG Multisite Search or BGCI PlantSearch methods. These descriptions follow Hwang & Grimes (1996), Huang et al. (2003), Fritsch (1997, 2004, 2009), Svengsuksa & Vidal (1992), and Gonsoulin (1974). In all cases where leaf indumentum is described, it is in reference to the underside or abaxial surface of the leaf unless otherwise specified. Additionally, the majority of *Styrax* species often display a characteristic in which the most basal leaf pair on each branchlet is arranged in a subopposite to opposite fashion. This characteristic is not noted in the species descriptions unless the basal leaf pair displays significant morphological variation as compared to other leaves. Species which do not display this characteristic (i.e. leaves always alternate) are noted as such.

Stem wood anatomy and petiole anatomy are based on Dickison & Phend (1985) and Schadel & Dickison (1979) where noted, in other cases from observations to be discussed in greater detail in chapter three. Fourteen of these taxa have been observed as living collections, with another six as herbarium specimens.

Rarity of each taxon as a cultivated plant was determined by the following criteria: taxa collected in fewer than ten gardens were deemed rare, whereas those collected in fewer than five gardens were considered to be very rare.

As many gardens seek to use common names for their records and labeling, in some cases I have suggested a common name for the species based on translation of the specific epithet according to Stearn (1983) in combination with “snowbell”, the most widely cited common name for the genus. These should not be taken as widely spoken or understood common names for the various species as the vast majority of species do not possess English common names due to their rarity in western cultivation.

To judge the ornament of these taxa, various references such as Wilson (1913), Bean (1980), Dirr (2009), Raulston (1992), and Grimshaw & Bayton (2009) were consulted. Frequent visits were made to the University of Delaware Botanic Gardens (Newark, DE), due to the convenience of the location, in order to observe accessioned species at various stages of their life cycle. Additionally, site visits were made to the JC Raulston Arboretum (Raleigh, NC), Arnold Arboretum (Jamaica Plain, MA), and Polly Hill Arboretum (West Tisbury, MA). For those species which could not be observed as living collections, preserved specimens were examined at the Harvard University Herbaria (Cambridge, MA) as well as the Cultivated Herbarium of the Arnold Arboretum. For the sake of convenience in this thesis, when referring to collections these institutions are often abbreviated as follows: Arnold Arboretum (AA), JC Raulston Arboretum (JCR), Polly Hill Arboretum (PHA), University of Delaware Botanic Gardens (UDBG).

Results

Data from BGCI reveals a total of 35 *Styrax* species are currently accessioned in worldwide botanical gardens, though 18 of these are very rare in cultivation, known from fewer than 5 accessions (Table 4). Eleven of the taxa in cultivation are known from only a single collection. The most common species in cultivation are *Styrax japonicus*, *Styrax obassia*, *Styrax americanus*, *Styrax hemsleyanus* Diels, *Styrax odoratissimus* Champion ex Bentham, *Styrax dasyanthus* Perkins, and *Styrax grandifolius*. Separating these data out into region reveals differences between North American and European Collections. Though in both cases, the two most prominent species are *Styrax japonicus* and *Styrax obassia*, in American gardens the next three most prominent are *Styrax americanus*, *Styrax grandifolius*, and *Styrax hemsleyanus*, whereas in European gardens the next three most prominent are *Styrax odoratissimus*, *Styrax hemsleyanus*, and *Styrax americanus*. *Styrax americanus* is thus rarer though not entirely unheard of in European gardens; however the closely related *Styrax grandifolius* is present only in one European garden despite its relative prevalence in those of North America. Conversely, *Styrax odoratissimus* is much rarer in North America, present only in three gardens.

Table 4 Number of Gardens Collecting species of *Styrax*. Based on Botanic Gardens Conservation International (BGCI) PlantSearch.

Taxa	**North American**	**Central/South American**	**European**	**Asian**	**Australian**
S. agrestis	0	0	0	1	0
S. americanus	44	0	11	0	0
S. argenteus	0	1	0	0	0
S. benzoin	0	0	0	3	0
S. calvescens	4	0	1	2	0
S. chinensis	0	0	1	1	0
S. confusus	7	0	1	1	0
S. dasyanthus	7	0	10	0	1
S. faberi	1	0	2	1	1
S. formosanus	6	0	6	0	0
S. glaber	0	1	0	0	0
S. glabrescens	1	1	0	0	0
S. grandifolius	16	0	1	0	0
S. hemsleyanus	11	0	17	0	2
S. hookeri	1	0	0	0	0
S. japonicus	79	0	48	3	3
S. macrocarpus	0	0	0	2	1
S. obassia	53	0	38	2	4
S. odoratissimus	2	0	1	1	0
S. officinalis	10	0	20	0	2
S. platanifolius ssp. mollis	1	0	0	0	0
S. platanifolius ssp. platanifolius	2	0	0	0	0
S. platanifolius ssp. texanus	8	0	0	0	0
S. platanifolius ssp. youngiae	1	0	0	0	0
S. ramirezii	2	0	0	0	0
S. redivivus	10	0	1	0	0
S. serrulatus	1	0	4	0	0
S. shiraianus	0	0	0	0	1
S. suberifolius	1	0	1	3	0
S. supaii	0	0	0	1	0
S. tonkinensis	2	0	0	0	1
S. wilsonii	9	0	1	0	0
S. wuyuanensis	0	0	1	0	0

Members from all four series of *Styrax* per Fritsch (1999) are represented in cultivation, with the largest component that of series *Cyrta*, likely due to the temperate climate most of the series thrives in as well as its size relative to the much smaller series *Styrax*. Far fewer members of section *Valvatae* are in cultivation, those which are generally restricted to tropical or subtropical gardens which provide a more suitable climate.

When examining the data based on the RBG Multisite search (Table 5), the same basic trends occur, with *Styrax japonicus* and *Styrax obassia* by far the most commonly collected species. One notable inconsistency as compared to the BGCI data is the presence of *Styrax shiraianus* in the Western Hemisphere. Though still very rare, it is collected in one North American garden (The Washington Park Arboretum) and one European garden (The Botanic Garden of the University of Copenhagen). This inconsistency is explained by the fact that these two institutions do not currently share their collections data with BGCI.

Table 5 Prevalence of *Styrax* in Cultivation: Number of Gardens Collecting species of *Styrax*. Based on Royal Botanic Gardens (RBG) Multisite Search.

Species	# Gardens Collecting
S. americanus	12
S. calvescens	1
S. confusus	3
S. dasyanthus	4
S. formosanus	3
S. glabrescens	1
S. grandifolius	5
S. hemsleyanus	6
S. japonicus	22
S. obassia	19
S. odoratissimus	2
S. officinalis	6
S. platanifolius ssp. *mollis*	1
S. platanifolius ssp. *texanus*	1
S. ramirezii	2
S. redivivus	4
S. serrulatus	2
S. shiraianus	2
S. suberifolius	1
S. tonkinensis	1
S. wilsonii	4

Descriptions of Cultivated Species

Styrax section *Styrax* P.W.Fritsch

Plants deciduous; bases of young shoots with scattered stalked ferrugineous or rarely fulvous stellate hairs distinct from the rest of the vesture; sides of the corolla convex in bud; corolla lobes membranous; mesocarp dry; endocarp at maturity adherent to the mesocarp, not the seed; seeds ellipsoid; seed coat not crackled. 34 species, southern North America, eastern Mediterranean region, eastern and southeastern Asia (Fritsch 1999).

***Styrax* series *Cyrta* P.W.Fritsch**

> Leaf margins of at least some leaves on sterile shoots (and often of fertile shoots) glandular-denticulate to glandular serrate, rarely also lobed; inflorescences produced laterally (as well as terminally) on at least some shoots (often reduced to 1-2 flowers, the subtending leaves often reduced). 31 species, southern North America, eastern and southeastern Asia (Fritsch 2001). 22 species in cultivation (71% of series): three common, five uncommon, five rare, eight very rare, one historic.

Styrax agrestis (Loureiro) G.Don
Reference: Gen. Hist. iv: 5. 1837.
= *Styrax warburgii* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 27. 1907
= *Styrax ledermannii* Perkins, Gatt. Styracac. 20 (1928), in clavi; Perkins in Notizbl. Bot. Gart. Berlin, x.457
= *Styrax subcrenatus* Handel-Mazzetti, Oesterr. Bot. Z. 80: 342. 1931
= *Styrax rostratus* Hosokawa, Trans. Nat. Hist. Soc. Formosa 28: 65. 1938

Trees to 15 m; branchlets sparsely brownish stellate pubescent to glabrous. Leaves alternate; elliptic, oblong, or elliptic-lanceolate; lamina 5-15 × 3-8 cm (1.7-1.9 × longer than wide), sparsely stellate pubescent, margin entire to irregularly denticulate, apex acute to acuminate and slightly curved, base cuneate to broadly cuneate; 4-7 secondary vein pairs, tertiary veins reticulate and conspicuous; petiole 0.8-1.5 cm, vasculature a medullated cylinder or arc with two invaginated ends accompanied by two dorsal cortical bundles (Schadel & Dickison 1979). Flowers white, 1.5-2.2 cm; pedicel 0.8-1.5 cm; 5-10-flowered terminal racemes, 6-12 cm; calyx 5-toothed, ca. 5 × 7 mm, densely yellow stellate tomentose; corolla lobes 5, lanceolate, ca. 7 × 5 mm, valvate in bud; androecium of cream-colored, inserted stamens; fruit 1.2-3.0 × 0.8-1.6 cm; cylindrical to oblique-ovoid; apex rostrate to shortly pointed; densely brownish stellate tomentose; seeds brown; ellipsoid, rugose or smooth, densely scaly to glabrous; 1-2 per fruit.

Native to Southeast China (tropical to barely subtropical provinces), Indonesia, Laos, Malaysia, New Guinea, Vietnam, Pacific Islands. Dense forests to tropical rainforests. Apparently tolerates a wide variety of habitats. 100-700 m and upwards of 1200 m towards the eastern limits of the range. Flowering March-November.

The species is very rare in cultivation with only one accession known worldwide in an Asian garden. Were it more commonly seen, potential may exist for confusion with *Styrax serrulatus,* though it has a much stronger tendency towards an entire leaf margin and smaller, narrower fruit as compared to the latter species.

Van Steenis (1939) mentions *Styrax warburgii* Perkins as a synonym of *Styrax agrestis,* though this name is conspicuously absent from the Hwang & Grimes treatment (1996). The keying differences in Perkins (1907) between the two taxa are glabrous foliage, 4-5 vein pairs, and a locality of Vietnam (Cochinchina) in *Styrax agrestis,* and pubescent foliage, 7-8 vein pairs, and a locality of Malaysia in *Styrax warburgii*. I am hesitant to offer an opinion on synonymy without examining specimens of both taxa, though it seems a possibility based on Hwang & Grimes' (1996) broader definition of *Styrax agrestis* as compared to Perkins (1907).

The specific epithet *agrestis* is an adjective generally referring to fields or cultivated lands, and the species is given the common name "field storax" by Don. Since its native habitat is currently understood as forests or dense forests, this common name is probably somewhat misleading.

Based on the native habitat of *Styrax agrestis,* it is likely only hardy to USDA Zone 9 and not suitable for landscape use in all but the southernmost areas of North America or Europe. Germplasm from significantly high altitudes could make an interesting specimen to experiment with however; the wide variety of habits the species tolerates possibly indicating suitability for cultivation.

Styrax americanus Lamarck
Reference: Encycl. [J. Lamarck & al.] 1(1): 82. 1783 [2 Dec 1783]
= *Styrax laevis* Walter, Fl. Carol. 140. 1788.
= *Styrax laevigatus* Aiton, Hortus Kew. (W. Aiton) 2: 75. 1789
= *Styrax pulverulentus* Michaux, Fl. Bor.-Amer. (Michaux) 2: 41. 1803
= *Styrax americanus* Lamarck var. *laevis* (Walter) Alph.Wood, Class-book Bot. (ed. 1861). 499. 1861
= *Styrax americanus* Lamarck f. *genuinus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
= *Styrax americanus* Lamarck f. *glaber* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
= *Styrax americanus* Lamarck f. *pulverulentus* (Michaux) Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
= *Styrax americanus* Lamarck var. *pulverulentus* (Michaux) Rehder in L.H.Bailey, Stand. Cycl. Hort. 6: 3280. 1917

American Snowbell. Deciduous shrub to 5m; branchlets sparsely to densely grey stellate pubescent; mature stem light brown, glabrous. Leaves alternate; bright green, elliptic to obovate or nearly ovate; lamina 1.2-10 × 0.6-5.7 cm (ca. 1.8-2.0 times longer than wide), glabrous or sparsely to densely grey stellate pubescent, margin serrate, serrulate, denticulate or entire (at least some leaves serrate or denticulate), apex acute to acuminate, base cuneate, 5-8 secondary vein pairs, tertiary veins reticulate; petiole 2-6 mm, vasculature an arc with two invaginated ends, accompanying bundles present or absent. Flowers white, strongly reflexed (Figure 1), ca. 1.3-2 cm; pedicel 4-10 mm (rarely to 14 mm), (1)2-5-flowered pseudoterminal racemes, 2-3.5 cm, often accompanied by solitary axillary flowers; calyx 5-toothed, 2.5-4 × 2.5-4.5 mm; corolla lobes 5, elliptic to narrowly elliptic, 11-16 mm, imbricate in bud; androecium of 10 exserted stamens; capsule 7-9 × 7-9 mm (wall thickness:

0.3-0.4 mm), globose, grey stellate pubescent, 1 (rarely 2-3) seeds per fruit. *2n=2x=16*.

Wood diffuse porous; rays uniseriate or biseriate, (6)8-13(16) uniseriate rays and <1 biseriate ray per 1.73 mm^2 (7% of rays biseriate), uniseriate ray width ca. (11)12-13(14) µm; biseriate ray width ca. (16)17-21(22) µm. Vessel elements (52)57-85(98) per 1.73 mm^2, ca. (18)19-25(29) × 24-29(32) µm (1.2× wider than long), with a mean of 3.0-3.6(4.0) per multiple; rarely solitary (3% of vessels solitary).

Native to wooded floodplains and swamps of the Southeastern and South-central United states; 0-300 m. Flowering March-June. NatureServe Conservation Status Ranking: G5 (Globally secure).

Figure 1 *Styrax americanus* Lamarck (UD# 96-15*1) exhibiting slightly reflexed flowers. Flowering 4/13/13 at the University of Delaware Botanic Gardens (Newark, DE, USA). Photograph by the Author.

Though far less common in the trade than *Styrax japonicus* or *Styrax obassia*, *Styrax americanus* is still relatively common in cultivation. It is represented in the collections of several gardens, though more frequently those of North America than Europe. The species was introduced to Kew Gardens in 1765 and long cultivated since then (Bean 1980). Its history as an ornamental in the United States is somewhat less clear. An early accession at the Arnold Arboretum (AA # 17333*A) dates to 1910, though it seems likely *Styrax americanus* was cultivated in its native southeast prior. Regardless, the species seems well suited for the landscape, flowering profusely when removed from its indigenous, shaded woodland habitat (Raulston 1991). The heavily reflexed nature of the petals provides an interesting shape to the flower, even if it is admittedly small in size.

Styrax americanus is the most widely distributed species of the genus in North America, with provenance playing a large role in its hardiness. The species was not generally considered hardy in the Philadelphia area as of 1950 (Gall 1962), though would later be estimated as hardy to USDA Zone 6, possibly 5 (Raulston 1992). Recent research based on stem hardiness has suggested tolerance to USDA Zone 4 for germplasm from northern Illinois, though its ornament at these temperatures could be inhibited. However, hardiness was only suggested as USDA Zone 7 for germplasm from Florida populations (Lenahan et al. 2010). Earl Cully (Heritage Trees Inc.) collected and grew seedlings of *Styrax americanus* from the northernmost portion of the range near Kankakee, IL, USA. These plants proved hardy to USDA Zone 5, though reached a shorter height (ca. 1.5-2 m) as compared to the straight species. They were sold and distributed by Ellen Hornig of Seneca Hill Nursery as *Styrax americanus* Northern-hardy, and later as *Styrax americanus* Kankakee Form. (Ellen

Hornig, pers. comm.) Neither of these are cultivars, merely forms representing this northern population.

Plants with “shorter pedicels and more densely pubescent new shoots, leaves, and inflorescences”, most noticeable at the southern range of the species (Fritsch 2009), have historically been split at the varietal (*Styrax americanus* var. *pulverulentus* Michaux), or species level (*Styrax pulverulentus* Michaux) Current thought seems to take the numerous intermediates between both forms as evidence that they should be considered synonymous (Spongberg 1976, Fritsch 2009). However, some (Lasseigne 2001) argue for upholding a distinction at the forma level (*Styrax americanus* f. *pulverulentus* Michaux), feeling that the characteristics are significantly distinct, as some specimens can even appear to have grey leaves, particularly from a distance, due to the dense pubescence (Lasseigne 2001). Such a form of the species would be interesting to trial in the landscape. The grey undersides of the leaves perhaps could allow for a similar effect on windy days as the silvery-backed leaves of *Hydrangea arborescens* Linnaeus ssp. *radiata* (Walter) E.M. McClint. Such a cultivar however might not be as hardy as the straight species, since the most densely pubescent forms occur at southernmost portion of the range.

Seeds are singly dormant and readily germinate following 3 months cold stratification. Softwood cuttings root readily in 1000 or 4000 ppm IBA solution (Dirr & Heuser 2006).

The species can generally be diagnosed by examining the leaves, which are smaller and paler green in color than most other cultivated species.

Styrax calvescens Perkins
Reference: Pflanzenr. (Engler) Styracac. 32. 1907
Type: China, Hubei. *A. Henry 721*.
= *Styrax dasyanthus* var. *cinerascens* Rehder, Pl. Wilson. 1(2): 289. 1912

Balding Snowbell. Deciduous tree or shrub to 5-15 m; branchlets sparsely stellate puberulent. Leaves alternate; elliptic to obovate, densely grey stellate tomentose; lamina 3-8 × 1.5-4.5 cm (1.8-2.0 × longer than wide), margin apically serrulate, apex acuminate to acute, base subrounded; 6-7 secondary vein pairs, tertiary veins reticulate and conspicuously raised; petiole 1-3 mm, vasculature an arc with two invaginated ends accompanied by 2-4 bundles. Flowers white, 1-1.5 cm; pedicel 5-10 mm; many-flowered pseudoterminal and axillary racemes or panicles, 3.5-9 cm, bearing many flowers in April to June (Figure 2); calyx 5-toothed, 3-5 × 3-4 mm, densely grey-yellow stellate tomentose; corolla lobes 5, oblong, 8-10 × 2-2.5mm, valvate in bud; stamens inserted; fruit ca. 8 × 6mm, obovoid; densely gray-yellow stellate tomentose and pubescent, apex sharply pointed; seeds brown, glabrous.

Wood diffuse porous; rays uniseriate or biseriate, uniseriate ray width ca. 12-16(18) μm; biseriate ray width ca. (16)18-29(31) μm; 3-4(7) uniseriate rays and 0-2(3) multiseriate rays per 1.73 mm^2 (21% of rays biseriate). Vessel elements ca. 21-24(26) μm × (22)23-29(34) μm (1.2 × wider than long), (20)28-45(50) per 1.73 mm^2, with a mean of (1.9)2.3-3.0(3.3) per multiple, rarely occurring solitarily (4% of vessels solitary).

Native to forest edges on slopes of Southeastern China; 500-1200m. Flowering May-June.

Figure 2 Branchlet of *Styrax calvescens* Perkins. Flowering April, 1992 (Raleigh, NC, USA). Photograph by J.C. Raulston (Slide 105-0328), provided by JC Raulston Arboretum.

Styrax calvescens is rare in cultivation, more strongly represented in North American collections than elsewhere. Grimshaw & Bayton (2009) list zone hardiness to USDA 7-8. One accession of this species at the JC Raulston Arboretum (No number, located in bed A08 as of 5/26/2012) is approximately 12’ in height, confirming this range. The species is often difficult to propagate from seed due to low germination rates (Raulston 1991b).

Though this species should hypothetically be easy to diagnose based on its distinct leaf pubescence and short petiole, it proves much more difficult due to a discrepancy in this foliage pubescence. Sargeant (1916) claimed the species possessed densely tomentose leaf undersides, though Hillier Nurseries (1991) described the leaves as thin and lustrous green on both surfaces. Raulston (1992) notes the *Styrax calvescens* he trialed possessed a glabrous leaf. This is somewhat problematic as the tomentose leaf indumentum is an important characteristic in keys such as Hwang & Grimes (1996) for separating the plant from other uncommonly cultivated species such as *Styrax confusus*, *Styrax dasyanthus*, *Styrax formosanus*, *Styrax faberi*, and *Styrax serrulatus* likely to be confused in nurseries and botanic gardens.

The specific epithet *calvescens* describes becoming bald, probably in reference to the glabrescent nature of this supposedly diagnostic leaf indumentum. Hwang & Grimes (1996) refer to the adaxial plane of the leaf as sparsely stellate pubescent but glabrescent, though it may be possible that the abaxial indumentum is glabrescent as well. More glabrous specimens will prove difficult to separate from *Styrax dasyanthus* and particularly *Styrax confusus*, though petiole length (3-7 mm in *Styrax dasyanthus*, <3 mm in *Styrax calvescens*), leaf margin (denticulate in *Styrax dasyanthus* vs. apically serrulate in *Styrax calvescens*), and fruit morphology (ovoid to globose in *Styrax dasyanthus* vs. obovoid in *Styrax calvescens*) should be sufficient to differentiate it from the former, and flower number per inflorescence (3-8 in *Styrax confusus*, many in *Styrax calvescens*) should aid in separation from the latter. Leaf morphology (serrulate with cuneate to broadly cuneate base in *Styrax confusus* vs. apically serrulate with subrounded base in *Styrax calvescens*) may also prove sufficient when material is sterile.

Aside from the accession mentioned at the JC Raulston Arboretum, the University of Washington Botanical Garden also collects the species (UW# 321-94*A). The Arnold Arboretum obtained seeds of the species as part of the 1994 NACPEC Hubei Expedition (AA# 765-64), though appeared to suffer germination failure.

The JC Raulston Arboretum uses the common name "bald snowbell" for the species which seems appropriate if one is desired, though "balding snowbell", listed above, helps to clarify the glabrescent as opposed to glabrous nature of the leaves.

Styrax confusus Hemsley
Reference: Bull. Misc. Inform. Kew 1906, 162
Type: China: Guangdong, May 1888, *Mr. Ford's native collector s.n.*

Chinese Snowbell. Deciduous tree or shrub, 2-8 m; branchlets densely brownish stellate pubescent. Leaves alternate; dark green, narrowly oblong, obovate elliptic, or oblong-elliptic, densely stellate pubescent, quickly glabrescent; Lamina 4-14 × 2.5-7 cm (1.6-2.0 × longer than wide), Margin serrulate, apex acute to shortly acuminate, base rounded to broadly cuneate; 5-7 secondary vein pairs, tertiary veins reticulate and conspicuously raised; petiole 1-3 mm, vasculature an arc with invaginated ends, accompanied by several vascular bundles. Flowers white, 1.3-2.2 cm, pedicel 1-1.5 cm. Pseudoterminal racemes 3-8 flowered, 4-10 cm; calyx 5-toothed, 3-10 × 4-6 mm, densely yellowish to grey stellate tomentose and villose (Figure 3); Corolla lobes 5, lanceolate to oblong-lanceolate. Capsule 0.8-1.5 cm diameter (wall thickness: 1-2 mm), subglobose to ovoid and oblique, densely yellowish stellate tomentose (Figure 4). Seeds brown, ovoid, smooth or deeply rugose.

Wood ring porous, corresponding to Carlquist (1988) Type 1C, though first ring formed may appear diffuse porous porous. Rays uniseriate, biseriate, or triseriate; uniseriate ray width ca. (16)17-20(21) µm, multiseriate ray width ca. (23)24-33(39) µm; 4-7(8) uniseriate rays and 2-4 multiseriate rays per 1.73 mm^2 (34% of rays multiseriate). Vessel elements ca. (20)21-27(31) µm x (19)22-26(27) µm (approximately as wide as long); (27)32-61(71) per 1.73 mm^2, with a mean of (2.7)3.0-4.2(4.4) per multiple, rarely occurring solitarily (4% of vessels solitary).

Native to Eastern and Central China; 100-1700m. Flowering April-October. Three lower taxa.

- *Styrax confusus* var. *confusus*
  = *Styrax serrulatus* var. *vestitus* Hemsley, J. Linn. Soc., Bot. 26(173): 77. 1889; *Styrax philadelphoides* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 32. 1907; *Styrax mollis* Dunn, Bull. Misc. Inform. Kew 1911, 273; *Styrax fukienensis* W.W.Smith. & Jeffrey, Notes Roy. Bot. Gard. Edinburgh 9: 130. 1916; *Styrax juncudus* Diels, Notizbl. Königl. Bot. Gart. Berlin 9: 198. 1924
  Calyx 5-8mm, Lamina sparsely stellate pubescent, flowers ca. 1.5cm. Likely represents the majority of germplasm in cultivation.

- *Styrax confusus* var. *microphyllus* Perkins, Pflanzenr. 30(IV. 241): 24
  Calyx ca. 3mm, Lamina glabrous, flowers ca. 1.5cm. Hubei Province; 800m.

- *Styrax confusus* var. *superbus* (Chun) S.M.Hwang, Acta Phytotax. Sin. 18(2): 161.
  = *Styrax philadelphoides* var. *superbus* Chun, Sunyatsenia 1(4): 296. 1934
  Calyx 5-8mm, Lamina glabrous, flowers ca. 2.2cm. Guangdong Province; 1000m.

Figure 3 *Styrax confusus* Hemsley (UD #06-8*1). Flowering 5/26/2012 at the University of Delaware Botanic Gardens (Newark, DE, USA). Photograph by the Author.

Figure 4 Fruit-bearing branch of *Styrax confusus* Hemsley (AA# 1082-89*B), Fruiting 8/13/2012 at the Arnold Arboretum of Harvard University (Jamaica Plain, MA, USA). Photograph by the Author.

An early collection by Wilson, though typically referred to under the synonym *Styrax philadelphoides* in early literature. Hwang & Grimes (1996) describe as a tree, though plants many observed in cultivation seem to prefer a more multi-stemmed habit. Raulston (1992) theorized hardiness to USDA Zone 8 and recommended it for the Pacific Northwest. More recently, Grimshaw & Bayton (2009) suggested USDA Zones 7-8, though Accessions at the Arnold Arboretum (AA# 1082-89, AA# 312-2004) suggest USDA Zone 6b hardiness.

The species is rare in cultivation, with most collections apparently in North America. Living collections examined at Arnold Arboretum, Polly Hill Arboretum, and University of Delaware Botanic Gardens all displayed heavy pubescence to newest leaves in late August, a sharp contrast to the somewhat leathery, largely glabrous leaves on older branchlets. This characteristic should help to separate the species from similar species, with examination of leaf morphology as described above for separation from the reportedly glabrescent *Styrax calvescens*.

One specimen at the Arnold Arboretum showed weak flowering in late August, while UDBG accession 06-8*1 entered a second period full bloom in early September 2012. There may be potential for a reblooming cultivar which would drastically improve the landscape merit of the species. The species is commercially available in the United States. The larger flowers represented by *Styrax confusus* var. *superbus* may be desirable for cultivation as well, particularly if a specimen exhibits reblooming, though the southern provenance probably restricts hardiness.

The specific epithet indicates confusion, though Hemsley (1906) does not reference as to what. The common name “chinese snowbell” is used by the JC Raulston Arboretum, appropriate based on its wide range throughout that country.

Styrax dasyanthus Perkins
Reference: Bot. Jahrb. Syst. 31(4-5): 485. 1902.
Type: China: Hubei, 1885-1888, *A. Henry 5977*
= *Styrax argyi* H. Léveillé, Repert. Spec. Nov. Regni Veg. 11: 64. 1912
= *Styrax rubifolius* Guillaumin, Bull. Soc. Bot. France 70: 884. 1924
= *Styrax dasyanthus* var. *hypoleucus* Pampanini, Nuovo Giorn. Bot. Ital., n.s., 17(4): 688

Deciduous tree or shrub, 3-20 m; branchlets densely grey-yellow stellate pubescent, glabrescent. Leaves alternate; obovate elliptic to elliptic, sparsely stellate pubescent (particularly on veins), glabrescent; lamina 7-14(16) × 3.5-6.5(8) cm (2.0-2.2 × longer than wide), margin denticulate and slightly revolute to subentire, apex acute to shortly acuminate, base cuneate to broadly cuneate; 5-7 secondary vein pairs, tertiary veins reticulate, and somewhat conspicuously raised; petiole (1)3-4(6) mm, vasculature an arc with invaginated by ends, accompanied by two bundles. Flowers somewhat reflexed, 0.9-1.6 cm; pedicel 6-10(12) mm; pseudoterminal or axillary panicles, many-flowered, 4-8 cm; calyx 5-toothed, ca. 4 × 3 mm; corolla lobes 5, oblong to oblong-lanceolate, 6-8.5 × 1.5-2.5(3) mm, valvate in bud; fruit 9-13 × 5-7 mm (wall thickness ≤1mm), ovoid to globose; apex sharply pointed; densely greyish stellate tomentose; seeds brown, smooth.

Wood diffuse porous; rays uniseriate, biseriate, and rarely multiseriate (3-celled), uniseriate rays ca. (13)15-19(21) μm wide; multiseriate rays (22)23-34(39) μm wide, 32% of rays multiseriate; (1)2-5(6) uniseriate rays and 1-2(3) multiseriate rays per 1.73 mm^2. Vessel elements ca. (17)19-24(27) × (21)23-27(29) um (1.2 × wider than long), with a mean of (2.0)2.4-3.5(4.1) per multiple, rarely occurring solitarily (4 % of vessels solitary), (29)31-43(45) vessels per 1.73 mm^2.

Native to mixed forests of Southeastern and South-central China; 100-1700m. Flowering March-May. A lower taxon, *Styrax dasyanthus* var. *cinerascens* Rehder, was described as a more pubescent form, but now is considered a synonym of *Styrax calvescens* (Huang et al. 2003).

An E.H. Wilson introduction, collected from Hubei province and accessioned at the Arnold Arboretum in 1907 (AA #6764A). Bean (1980) references a 1900 introduction from Sichuan, though notes it differed morphologically from the Hubei specimen due to its larger flowers, on less floriferous inflorescences. Without examining specimens from the Sichuan province, it is difficult to determine whether this is within the variability expected from this species, though the modern interpretation allows for some variability in flower size.

Today, *Styrax dasyanthus* is uncommon in cultivation, in the collections of a few gardens, more frequently those of Europe as opposed to North America. The species appears to reach a shorter height in cultivation. Though typically listed as 2-8m, 930409 at the JC Raulston Arboretum appeared to be ca. 4m in Spring 2012 though is growing in partial shade.

USDA Zone 6b hardiness is confirmed by a thriving plant at the Arnold Arboretum (Jamaica Plain, MA). Hardiness has been estimated as low as USDA Zone 5 (Rehder 1940). Though *Styrax japonicus* and *Styrax obassia* are USDA Zone 5 hardy as well, *Styrax dasyanthus* may be a superior choice for cooler climates owing to its later flowering, alleviating the concern of frost damage to the blossoms.

There was some confusion between *Styrax dasyanthus* and *Styrax japonicus* when the species first entered cultivation (Bean 1980), though they should be easy to distinguish when flowering as *Styrax dasyanthus* contains more flowers per inflorescence, as well as a pedicel which is shorter (as opposed to as long or longer) as the subtended flower. Separation from *Styrax confusus* and *Styrax calvescens* as described above is proves more difficult. One accession of *Styrax dasyanthus* observed at the Arnold Arboretum in mid-August 2012 (164-2008*A) displayed largely glabrous leaves and branchlets as compared to nearby accessions of *Styrax confusus*, indicating the species may glabresce more rapidly.

Attempts to propagate the species are noted by Dirr & Heuser (2006). Seeds are doubly dormant, with a recommended three months warm and three months cold stratification for germination, whereas softwood cuttings root easily following treatment with 1000-4000ppm IBA.

The specific epithet generally defines thickly hairy flowers, possibly referencing the dense villose indumentum of the filaments.

Styrax faberi Perkins
Reference: Pflanzenr. (Engler) Styracac. 33. 1907.

Faber Snowbell. Deciduous shrubs to 2m; branchlets slender, densely villose. Leaves alternate; ovate, elliptic, or obovate, sparsely brown to grey stellate pubescent, glabrescent; lamina 4-11 × 3-3.5 cm (1.3-3.1 × longer than wide), margin serrulate to remotely serrate, apex acuminate, base broadly cuneate, auriculate, or subrounded; 5-6 secondary vein pairs, tertiary veins reticulate; petiole 1-2 mm, vasculature a medullated cylinder (Schadel & Dickison 1979). Flowers white and slightly pendulous, 1.2-1.5(2) cm; pedicel 0.8-1.5 cm, in 3-5-flowered pseudoterminal racemes, 3-4 cm; calyx 5-toothed, 4-5 mm, membranous; corolla lobes 5, lanceolate to oblong, 5-15 × 2.3 mm, valvate in bud. Capsule 6-8 × 5-7 mm (wall thickness ca. <0.5 mm), obovoid to subglobose, densely gray stellate pubescent.

Native to Southeastern and South-central China, Taiwan. 100-1000m. Flowering time uncertain, though based on May-October fruiting (Hwang & Grimes 1996), April seems likely. Three lower taxa.

- *Styrax faberi* var. *amplexifolius* Chun & How ex S. M. Hwang
  Reference: Acta Phytotax. Sin. 18(2): 161. 1980
  Type: China: Hunan: Dongkou Xian, mixed forests or thickets, 800-1000 m, 17 July 1954, *Z.T. Li 2673*
  Lamina not orbicular, base auriculate. China (Hunan); 600-1000m.

- *Styrax faberi* var. *faberi*
  = *Styrax faberi* var. *acutiserratus*, Pflanzenr. (Engler) 4, Fam. 241: 33. 190; *Styrax iopilinus* Diels, Notizbl. Königl. Bot. Gart. Berlin 9: 1028. 1926
  Lamina not orbicular, base broadly cuneate to rounded.
  Southeastern & South-central China, Taiwan.

- *Styrax faberi* var. *formosanus*
  Reference: Novon 4(3): 254. 1994
  Type: China: Taiwan: Byolistu, thickets on mountain slopes, ca. 1000 m, *Honda 31*
  = *Styrax rugosus* var. *formosanus* Matsumura, Bot. Mag. (Tokyo) 15(172): 76. 1901; *Styrax matsumuraei* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 34. 1907; *Styrax faberi* Perkins var. *matsumurae* (Perkins) S.M.Hwang, Acta Phytotax. Sin. 18(2): 161. 1980; *Styrax formosanus* var. *matsumuraei* (Perkins) Y.C. Liu, Novon 4(3): 254. 1994
  Lamina orbicular. Taiwan; 1000m.

Styrax faberi is rare in cultivation, with some gardens collecting in Europe but only one in North America. Grimshaw & Bayton (2009) suggest USDA Hardiness to Zone 8. The Arnold Arboretum obtained seed from China and accessioned (556-94), though appeared to suffer germination failure.

Styrax faberi may prove difficult to separate from the similar, also shrubby *Styrax formosanus*, though Hwang & Grimes (1996) key based on a longer calyx (4-5 mm) and smooth as opposed to rugose fruit.

The specific epithet likely honors one with the surname Faber, though the original publication is unclear as to who exactly this is. Though the author abbreviation “Faber” refers to Friedrich Carl von Faber (1880-1954), who worked primarily with algae, fungi, and lichens in Indonesia, the species is more likely named in honor of Rev. Ernst Faber (1839-1899). Rev. Faber collected in Guangdong and Zhejiang, and during the article Perkins cites a collection of the species by “Faber” from mountains of the latter province.

Styrax formosanus Matsumura
Reference: Bot. Mag. (Tokyo) xv. 75.
Type: China: Taiwan: Tooseikaku, *Y. Tashiro 81*

Taiwan Snowbell. Deciduous tree or shrub, 3-9 m; branchlets densely brownish stellate pubescent, glabrescent; Leaves alternate; obovate, elliptic-rhomboid, or elliptic; sparsely brownish stellate pubescent, glabrescent; lamina 2-5(7) × 1.5-2.5 cm (1.3-2.0 × longer than wide); margin apically irregularly coarsely serrate to (rarely) 2-4 lobed, apex caudate to acuminate, base cuneate; 3-5 secondary vein pairs, tertiary veins reticulate; petiole 3-4 mm, vasculature an arc with two invaginated ends with accompanying bundles (Schadel & Dickison 1979). Flowers white and slightly pendulous, 1.2-1.4 cm; pedicel 0.8-1.2 cm; in 3-5-flowered pseudoterminal racemes, 2.5-4.5 cm; calyx truncate to obscurely 5-toothed, 2.5-3 × 3-4 mm, densely grey stellate tomentose; corolla lobes 5(6), lanceolate to oblong-lanceolate, 8-11 × 2.4-3 mm, (sub)valvate in bud; androecium of 10 (rarely 9 or 11) stamens, inserted; fruit ca. 1 × 6 mm, ovoid; apex rostrate to apiculate; seeds brown, ovoid, glabrous.

Wood ring porous, corresponding to Carlquist (1988) Type 1C, though first ring formed may appear diffuse porous. Rays uniseriate, biseriate, and rarely triseriate; uniseriate ray width ca. (11)12-16(17) μm; multiseriate ray width ca. (19)20-28(34) μm; (6)7-10 uniseriate rays and 1-3 multiseriate rays per 1.73 mm^2 (18% of rays multiseriate). Vessel elements ca. (11)13-17(18) × (15)16-19(20) μm (1.2 × wider than long), with a mean of (1.6)2.0-3.1(3.7) per multiple, rarely occurring solitarily (8 % of vessels solitary); (13)26-69(85) per 1.73 mm^2.

Native to Southeastern China and Taiwan (endemic to Taiwan per Huang et al. (2003); 500-1300 m. Flowering time uncertain though based on May-August fruiting (Hwang & Grimes 1996), April seems likely. Two lower taxa.

- *Styrax formosanus* var. *formosanus*. Sparse stellate tomentose indumentum to petioles, pedicels, and bracteoles. Southeastern China & Taiwan; 500-1300 m.

- *Styrax formosanus* var. *hirtus* S.M.Hwang. Dense stellate pubescent indumentum to petioles, pedicels, and bracteoles. Southeastern China; 800-1000 m.

Styrax formosanus is a relatively uncommon and new addition to the cultivated component of *Styrax*, evidenced by its notable absence from the thorough trials of J.C. Raulston (1991). It is present in the collections of both North American and European gardens, including the JC Raulston Arboretum (011483), Charles R. Keith Arboretum, University of California Botanical Garden at Berkeley (2001.0224), and Sir Harold Hillier Gardens (1993.0675).

The species is morphologically similar to *Styrax japonicus* albeit more often shrubby in habit. It can be distinguished by its shorter pedicel and tendency towards valvate corolla aestivation (Huang et al. 2003). In opposition to the distribution cited in Hwang & Grimes (1996), Huang et al. (2003) suggest *Styrax formosanus* as endemic to Taiwan, an area from which *Styrax japonicus* is not present, theorizing it shared a common ancestor with that species, and speciated due to its isolated habitat.

The apparent contradiction as to the distribution of the species has yet to be clarified. Grimshaw & Bayton (2009) note that all germplasm in cultivation can be traced to Taiwanese origin (and are thus likely *Styrax formosanus* var. *formosanus*), as well as share the habit of a single stemmed tree, as opposed to multi-stemmed shrubs as listed by Hwang & Grimes (1996). Additionally, the 3m height provided in the Flora of China appears to be a low estimate, as HH# 1993.0675 at the Sir Harold Hillier Gardens was recorded as 8.9m in height with an 11.9 cm DBH in the winter of 2011.

Despite its similarity to *Styrax japonicus*, *Styrax formosanus* may be more challenging to propagate; Griffin & Lasseigne (2005) found rooting with 3000 or 8000 ppm K-IBA poor to ineffective. Grimshaw & Bayton (2009) suggest hardiness to USDA Zones 8-9.

The specific epithet references its location (Formosa an older name for the island of Taiwan). The common name Taiwanese Snowbell may be more appropriate to help clarify it as an Old World rather than New World species (Formosa is also the name of an Argentinian Province, ironically its antipode), as well as emphasize its endemic nature.

Styrax glabrescens Bentham
Reference: Pl. Hartw. [Bentham] 66.
Type: Mexico, Oaxaca: [Chinantla region], planitie Llano Verde, *Hartweg 489*
= *Styrax guatemalensis* Donnell Smith., Bot. Gaz. 15: 27. 1890
= *Styrax glabrescens* var. *pilosus* Perkins, Pflanzenr. IV. 241(Heft 30): 72. 1907
= *Styrax pilosus* (Perkins) Standley, Contr. U.S. Natl. Herb. 23: 1129. 1924
= *Styrax vestitus* Lundell, Wrightia 4: 121. 1969

Mexican Snowbell. Deciduous tree to 30 m; branchlets glabrous to densely whitish-yellowish stellate pubescent, with bark often exfoliating into long strips.

Leaves alternate; ovate or obovate (though most terminal leaf sometimes rhombic to suborbiculate, and basal leaf pair on each branchlet opposite, and sometimes ovate-oblong), glabrous to white stellate pubescent, veins and most basal leaves often with stalked orange stellate hairs (Figure 5); lamina 3.5-14 × 1.5-10 cm (1.4-2.3 × longer than wide), up to 20 cm in length on sterile shoots; margin glandular and entire to serrate, apex cuspidate to long-acuminate, base narrowly cuneate to rounded, rarely truncate or attenuate; 6-8 secondary vein pairs; petiole 6-16 mm, vasculature in an arc with invaginated ends accompanied by two dorsal cortical bundles (Schadel & Dickison 1979). Flowers white; in (1)2-12(21)-flowered pseudoterminal or 1-5(17)-flowered axillary racemes (rarely panicles), calyx campanulate or broadly cupuliform, 0-7-toothed, 4-6 × 4-6 mm, grayish green stellate pubescent; corolla lobes 5-10, elliptic or broadly elliptic, 14-28 mm, imbricate in bud; anthers 4-6 mm in length; fruit 10-15(17) × 9-15(19) mm, globose, stellate pubescent.

Native to evergreen cloud forests, montane rainforests (on steep slopes near waterways), and pine-oak forests of Southeastern Mexico (Queretaro, Veracruz) extending south to SW Costa Rica; 550-2500 m. Flowering December-May.

Figure 5 *Styrax glabrescens* Bentham. August, 1995 (Raleigh, NC, USA). Photograph by J.C. Raulston (Slide 122-0241), provided by JC Raulston Arboretum.

A very rare and recent introduction to cultivation, *Styrax glabrescens* is somewhat of an oddity in its indigenous range: all the other species in the region are suckering shrubs as opposed to deciduous trees (Fritsch 1997). This characteristic, combined with imbricate corolla aestivation, separates it readily from most similar species.

Styrax glabrescens is very rare in cultivation, with only two accessions known: 91.0718 at the University of California Botanical Garden at Berkeley, and a collection at the Jardin Botanico Francisco Javier Clavijero (Xalapa, Veracruz, Mexico). One accession survived at the JC Raulston Arboretum for 10 years though perished in a late freeze (Grimshaw & Bayton 2009). USDA Hardiness is likely to Zone 9 based on the native range, though Raulston et al. (1995) suggests USDA Zone 7.

The specific epithet likely references a glabrescent nature to the leaves as described by Bentham (1840), though Fritsch (1997), the basis for the above treatment, instead describes the leaves as white stellate pubescent or more often glabrous with no reference to glabrescence. Raulston et al. (1995) list with the common name of "mexico styrax", which could easily be modified to "mexican snowbell" if such a name is desired.

Styrax grandifolius Aiton
Reference: Hortus Kew. (W. Aiton) 2: 75. 1789
= *Styrax officinalis* sensu Walt., Fl. Carol. 140. 1788

Bigleaf Snowbell. Deciduous shrub or tree to 6 m, suckering from roots and with stems often of a twisting habit; branchlets orange brown stellate pubescent. Leaves alternate; obovate to broadly elliptic or broadly rhombic, grey stellate tomentose; lamina 7-20 × 4-14.3 cm (1.4-1.8 × wider than long), largest leaves on sterile shoot, margin denticulate to serrate or rarely weakly lobed, apex narrowly acuminate, base cuneate to broadly cuneate; 5-8 secondary vein pairs, tertiary veins subparallel; petiole 4-12 mm, vasculature in an arc with two accompanying bundles, or a medullated cylinder. Flowers white, slightly reflexed; pedicel 4-9mm; in (1)2-19-

flowered pseudoterminal inflorescences, 3.0-11.5 cm), often accompanied by axillary flowers (Figure 6); calyx 5-toothed,4-6 × 3-6mm; corolla 10-21mm, of 5(6) elliptic lobes, imbricate in bud; stamens exserted. Fruit nutlike and generally indehiscent, globose to subglobose, grey to grey-yellow stellate pubescent. *2n=2x=32*.

Wood diffuse porous. Rays uniseriate, biseriate, and rarely triseriate, uniseriate rays ca. (14)17-19 µm wide; multiseriate rays ca. 22-30(34) µm wide (16% of rays multiseriate); 5-6(9) uniseriate rays and 0-3(5) multiseriate rays per 1.73 mm^2. Vessel elements ca. 22-24(25) × (26)27-30(31) µm (1.2 × wider than long) with a mean of (2.1)2.6-4.5(5.6) per multiple, or rarely occurring solitarily (5% of vessels solitary), (21)31-66(84) vessel elements per 1.73 mm^2.

Native to upland woods of Central and Southeastern United States; 0-300 m. NatureServe Ranking G5 (Globally secure). Flowering April-May.

Figure 6 *Styrax grandifolius* Aiton (UD# 01-145*1). Flowering 5/10/2012 at the University of Delaware Botanic Gardens (Newark, DE, USA). Photograph by the Author.

The bigleaf snowbell is similar to its close relative, *Styrax americanus*, but differs on the basis of larger leaves as well as a greater height. It is relatively uncommon in cultivation, though has gained popularity in recent years in North American gardens to the point where it is the fourth most commonly collected species. According to Raulston (1992), *Styrax grandifolius* was introduced into European cultivation in 1765, though it is currently virtually unrepresented there. Though the species was likely somewhat trialed in the American Southeast prior, the earliest North American evaluation to my knowledge is by the Arnold Arboretum, which received seed and accessioned a plant in 1924 (18246*A), though it died in the nursery, surviving only 1-2 years.

Much of the species' newfound prominence in cultivation is likely due to J.C. Raulston trialing and recommending the species in the Southeast, where many were pleasantly surprised by the dense growth and flowering exhibited when removed from its native, shaded habitat. It is likely hardy to USDA Zone 6 (Raulston 1992).

Despite the globally secure ranking assigned by NatureServe, the species is declining somewhat in the northern components of its range, thought largely as a result of habitat conversion, possibly exacerbated by its suspected sexual self-incompatibility. It is presumably extirpated in Ohio, and considered endangered in Illinois and Indiana (Hill 2007). The specific epithet references the large leaves of the species.

Seed is likely singly dormant, though cuttings seem difficult to root. Dirr & Heuser (2006) reported no success. I attempted with 8000 ppm IBA/talc (Hormodin 3) on late spring cuttings, though none rooted.

Styrax hemsleyanus Diels
Reference: Bot. Jahrb. Syst. 29(3-4): 530. 1900
Type: China, Sichuan: Wushan Xian, 1885-1888, *A. Henry 5676*
= *Styrax hemsleyanus* var. *griseus* Rehder, Pl. Wilson. 1(2): 291. 1912
= *Styrax huanus* Rehder, J. Arnold Arbor. 11: 167 (-168). 1930

Hemsley Snowbell. Deciduous tree, 5-12 m; branchlets densely brown stellate pubescent, older twigs dark brown and glabrescent. Leaves alternate; elliptic to ovate elliptic (oblong to ovate-oblong per Hwang & Grimes 1996); lamina 8-12 × 4-6 cm (2 × longer than wide though largest leaves usually less so), margin serrate to subentire, apex slightly curved, acute to weakly acuminate,; base oblique to subrounded to broadly cuneate; 7-10 secondary vein pairs, tertiary veins reticulate to subparallel and prominently raised abaxially; petiole 0.7-1.5 cm, vasculature an arc with two invaginated ends, sometimes with an integrated bundle, and accompanied by two bundles. Flowers white, 1.5-2.5 cm; pedicel slightly curved, 2-4 mm; in 8-15(20)-flowered pseudoterminal 2-3 branched racemes, 9-15 cm, often joined by 4-9-flowered axillary racemes, of similar length (Figure 7); calyx sharply 5-toothed, 4-8 × 3-6 mm, yellow brown stellate tomentose; corolla lobes 5(6), elliptic to elliptic-obovate, 12-15 × 4.5 mm, imbricate in bud; androecium of 10(12) inserted stamens, anthers 3.5-4.5 mm in length; capsule 0.8-1.3 × 1.0-1.5 cm, globose to ovoid, densely yellow brown to grey-yellow stellate tomentose, apex apiculate; seeds brown, smooth to rugose, 1-2 per fruit.

Native to Mountain slopes and forest edges of Central China; 300-900 m. Flowering May-June.

Figure 7 Flowers and foliage of *Styrax hemsleyanus* Diels (UD# 99-104*1). Flowering 5/10/2012 at the University of Delaware Botanic Gardens (Newark, DE, USA). Photograph by the Author.

Styrax hemsleyanus was first introduced to cultivation by E.H. Wilson in 1900 (Bean 1980). Raulston (1991) thought highly of the plant's floriferous nature, listing it (specifically of *Styrax huanus*, now a synonym) as a high priority for further evaluation. Today, *Styrax hemsleyanus* is uncommon but represented in both European and North American collections. The seeds produced are known to have been utilized for soaps and lubricating oils (Huang et al. 2003). It is a mid-sized tree native to China, similar to *Styrax obassia* in terms of its height, form, and many-flowered pseudoterminal inflorescences. Though its leaves are larger than many other species of *Styrax*, they are still generally smaller than those of *Styrax obassia* and less prone to wilting during drought conditions. The smaller leaves are also less likely to fully obstruct the inflorescence, an ornamental deficit of similar species such as *Styrax obassia* and *Styrax odoratissimus*. Bean (1980) stated it is fast growing and reaches flowering ages more quickly than *Styrax obassia*, and recommends growing in a sheltered position with a moist soil. Raulston (1992) suggested hardiness to USDA Zone 6, though an accession at Cornell Plantations may suggest USDA Zone 5 potential for the species given a suitable location.

Dirr & Heuser (2006) recommend treating seed in the same fashion as *Styrax obassia* (3-5 months warm stratification and 3 months cold stratification)

Styrax hemsleyanus can be diagnosed by the relatively sharp teeth of the calyx as well as prominently raised tertiary venation of the leaf. Though the leaf size may elicit confusion with *Styrax obassia*, *Styrax hemsleyanus* has a less pubescent leaf and will never have a petiole encasing the winter bud. Named in honor of the English botanist William Botting Hemsley (1843-1924).

Styrax hookeri C.B.Clarke
Reference: Fl. Brit. India [J. D. Hooker] iii. 589.
Type: India. Sikkim: 1828-2121 m, *J.D. Hooker s.n.*
= *Styrax macranthus* Perkins, Bot. Jahrb. Syst. 31. 487. 1902
= *Styrax caudatus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 74. 1907
= *Styrax hookeri* var. *yunnanensis* Perkins, Repert. Spec. Nov. Regni Veg. 8: 84. 1910
= *Styrax roseus* Dunn, Bull. Misc. Inform. Kew 1911, 273.
= *Styrax perkinsiae* Rehder, Pl. Wilson. 1(2): 292. 1912
= *Styrax shweliensis* W.W.Smith., Notes Roy. Bot. Gard. Edinburgh 12: 236. 1920

Hooker Snowbell. Deciduous tree or shrub to 10m; branchlets grey-brown stellate puberulent, older twigs purplish brown glabrescent. Leaves alternate oblong to lanceolate ovate to narrowly elliptic, glabrous or sparsely grey white stellate pubescent (generally on veins); lamina 6-8(12) × 3-4(6) cm (2 × longer than wide), margin glandular-serrulate, apex acuminate to caudate (rarely acute) and slightly oblique, base rounded to broadly cuneate (rarely acute) and often slightly oblique; 5-7 secondary vein pairs, tertiary veins subparallel; petiole (2.5)4-5(10) mm. Flowers white to pink, (1.3)1.5-2.5 cm; pedicel (2)5-8(13) mm; in 1-2 flowered pseudoterminal inflorescences or (1)2-3(6)-flowered racemes, 2-4c m (rachis yellow stellate tomentose), joined by 1-3-flowered axillary inflorescences; calyx truncate, 2-3, or 5-toothed, (3.5)5-7(9) × 4-6(11) mm, yellow stellate tomentose; corolla lobes (4)-5, obovate to obovate-elliptic, (11)12-18 mm × (4)5-10 mm, imbricate in bud; androecium of (8)10 stamens, anthers 3-5mm in length; capsule (1)1.5-2 × (0.7)1-1.5 cm, subglobose to ovoid, grey yellow stellate tomentose, apex acute to short rostrate; seeds beige to brown, subglobose or ovoid, smooth. *2n=4x=32?*

Native to open or semi open wooded habitats and forest edges of mountains of Bhutan, Southwestern China, India, Myanmar, and Nepal;730-3352 m. Flowering March-September.

Though it is likely less hardy than many other species listed due to its native range, *Styrax hookeri* has been cultivated historically, with the majority of the material coming from the northern part of the range (Western Sichuan Province; 2000 m), previously considered distinct at the species level as *Styrax perkinsiae* or *Styrax schweliensis*. Seeds collected from the latter synonym as part of George Forrest's 1917-1919 expedition to China served as the first introduction of the species to the west. Raulston (1992) listed USDA Zone 9 for synonym *Styrax schweliensis*, giving the native range as Yunnan Province to Myanmar, and estimated the species would be hardier so long as the summer temperatures were high enough. Grimshaw & Bayton (2009) list USDA Zone 9 hardiness.

Styrax hookeri is very rare in cultivation today, with only one accession known in a North American Botanic Garden. It is overall quite similar to *Styrax japonicus* though perhaps with a greater tendency towards a shrubby habit, and though the range of flower sizes is similar, *Styrax hookeri* seems to be disposed to having flowers on the larger end of said range. If sufficiently hardy material can be sourced, likely from higher altitudes in China, the species could prove quite interesting for further evaluation, particularly in USDA Zone 8 areas of the American Southeast providing summer heat.

The specific epithet honors likely honors either William Jackson Hooker (1785-1865), his son Joseph Dalton Hooker (1817-1911), or both, though the original publication does not specify.

Styrax japonicus Siebold & Zuccarini
Reference: Fl. Jap. (Siebold) 1: 53, t. 23. 1838
Type: Japan. Kyushu: Kumamoto Pref., Simabara, *I. Keiske s.n.*
= *Styrax grandiflorus* Griffith, Not. Pl. Asiat. 4: 287. 1854
= *Styrax seminatus* Farges, Vilm. & Bois, Frutic. Vilm. 181 (1904)
= *Styrax bodinieri* H. Léveillé, Repert. Spec. Nov. Regni Veg. 4: 332. 1907
= *Styrax duclouxii* Perkins, Repert. Spec. Nov. Regni Veg. 8: 83. 1910
= *Styrax touchanensis* H. Léveillé, Repert. Spec. Nov. Regni Veg. 11: 64. 1912
= *Styrax kotoensis* Hayata & Hayata, Icon. Pl. Formosan. 9: 68. 1920
= *Styrax japonicus* var. *kotoensis* (Hayata) Masamune & Suzuki, Annual Rep. Taihoku Bot. Gard. 3: 65. 1933
= *Styrax jippei-kawamurai* Yanagita, J. Soc. Forest. 15: 693. 1933
= *Styrax japonicus* var. *iriomotensis* Masamune, Masam., Trans. Nat. Hist. Soc. Taiwan 25: 250. 1935
= *Styrax philippinensis* Merrill & Quisumbing, Philipp. J. Sci. 56: 313. 1935
= *Styrax japonicus* var. *zigzag* Koidzumi, Acta Phytotax. Geobot. 6: 212. 1937
= *Styrax japonicus* f. *parviflorus* Y. Kimura, J. Jap. Bot. 16: 59. 1940
= *Styrax japonicus* var. *angustifolius*, Acta Phytotax. Geobot. 10: 55. 1941
= *Styrax japonicus* var. *tomentosus* Hatusima, J . Jap. Bot. 29: 230. 1954
= *Styrax japonicus* f. *rubicalyx* Satomi, J . Geobot .6: 110. 1957.
= *Styrax japonicus* var. *longipedunculatus* Z.Y.Zhang, F1. Tsinlingensis 1 (4): 395. 1983
= *Styrax japonicus* var. *nervillosus* Z.Y.Zhang, F1. Tsinlingensis 1 (4): 395. 1983
= *Styrax japonicus* f. *jippei-kawakamii* (Yanagita) T.Yamaz., Fl. Jap. (Iwatsuki et al., eds.) 3a: 104. 1993
= *Styrax japonicus* f. *pendulus* T.Yamaz., Fl. Jap. (Iwatsuki et al., eds.) 3a: 104. 1993

= *Styrax japonicus* f. *tomentosus* (Hatusima) T.Yamaz., Fl. Jap. (Iwatsuki et al., eds.) 3a: 104. 1993

Japanese Snowbell. Deciduous shrub or small tree, 4-8(10) m; branchlets brown, sparsely grey yellow to pale yellow stellate pubescent, older twigs glabrescent; stem greyish brown; bark relatively smooth except on oldest stems, there developing orange to brown fissures. Leaves alternate; elliptic, oblong elliptic, ovate elliptic, ovate-lanceolate, or subrhombic, glabrous except for veins of younger leaves; lamina 3-11 × 2-5(7) cm (1.5-2.2 × longer than wide), margin weakly serrate apically, though some leaves subentire, apex acute to short-acuminate, base cuneate to broadly cuneate or subrounded; 5-8 secondary vein pairs, tertiary veins reticulate and conspicuously raised; petiole (2)4-7(10) mm; vasculature in an arc with invaginated ends, accompanied by bundles. Flowers white to pink, slightly pendulous, (1.2)1.5-2.5(3) cm; pedicel slender, 1.5-3.5 cm (generally at least as long as flower it subtends); in 5-8 flowered pseudoterminal racemes, 5-8 cm, joined by numerous axillary 2-5 flowered racemes, 2-5 cm; calyx irregularly 5-toothed, 4-5(7) × 3-5 mm, glabrous to sparsely stellate pubescent; corolla lobes 5(6) ovate, obovate, oblong ovate, or ovate lanceolate, (0.8)1.0-1.6(2.3) mm, imbricate in bud; androecium of 10(12) stamens, exserted, anthers 4-5(10) mm long; capsule 0.8-1.5 × 0.8-1.0 cm, ovoid or ellipsoid, densely grey-yellow stellate pubescent, apex sharply pointed; seeds brown, ellipsoid, smooth to rugose, 1-2 per fruit. *2n=2x=16, 2n=5x=40, 2n=6x=48*.

Wood diffuse porous; rays uniseriate and biseriate, uniseriate ray width ca. 14-16µm; multiseriate ray width ca. (19)23-29 µm, 24% of rays multiseriate; (3)4-7(9) uniseriate rays and 1-2 multiseriate rays per 1.73 mm^2. Vessel elements ca. (18)21-28(31) × (27)28-34(38) µm (1.3× wider than long), with a mean of (1.6)1.9-2.8(3.3) per multiple, or occurring solitarily (18% of vessels solitary). (21)25-37(41) vessel elements per 1.73 mm^2.

Native to open wooded habitats (forest edges, successional areas) of Central and Eastern China, Japan, Korea, India, Laos, Myanmar, Philippines, and Vietnam. Naturalized in Northeastern United States. Flowering April-July.

Though its specific epithet references Japan, *Styrax japonicus* is found over a large portion East and Southeast Asia, possessing the largest distribution of a *Styrax* species. Morphological variation of the species is significant over its broad range, and the species has been interpreted as a variety of taxa at either the species or lower levels. Huang et al. (2003) subsumed all of these under *Styrax japonicus*. *Styrax japonicus* is also, by far, the most common species in cultivation. Though it was almost certainly cultivated in East Asia prior, the first records of introduction in the west are by Richard Oldham to Kew Gardens in 1862 (of Japanese & Korean provenance), and again by E.H. Wilson (of Chinese provenance) in the early 1900s (Bean 1980). Despite its early introduction and current commonality, it would remain little known in North American gardens until the close to the turn of the 21st century. Gall (1962) states the species was little known then, and Dirr (1978) notes that asking for a "snowbell" in an American nursery would probably lead to confusion with the more commonly cultivated "silverbell" (various species of *Halesia*), though was impressed with the species particularly on the value of its lustrous foliage, profuse flowering, and ornamental striated bark (Figure 8). It was likely through the efforts of himself and Raulston that the species is now better known.

Figure 8	*Styrax japonicus* Siebold & Zuccarini (UD# 88-83*1), exhibiting ornamental bark with orange longitudinal fissures. 1/15/2013 at the University of Delaware Botanic Gardens (Newark, DE, USA). Photograph by the Author.

Styrax japonicus is hardy to USDA Zone 5-8 depending on provenance, though growing the plant in cooler climates presents the risk of damage to the flowers during a late frost. In such a situation, *Styrax dasyanthus* may be a superior choice.

The plant produces a heavy fruit set (Figure 9) with a profusion of seedlings often found germinating under the canopy. Some have suggested weedy or invasive potential for the species. Though Trueblood (2009) judged the plant noninvasive and recommended for use, at least in North Carolina, the establishment of a sterile cultivar may be desirable to alleviate conservation and maintenance concerns.

Figure 9 Heavy seed load of *Styrax japonicus* Siebold & Zuccarini (UD# 89-102*2) underneath tree canopy. 1/15/2013 at the University of Delaware Botanic Gardens (Newark, DE, USA). Photograph by the Author.

Seed of *Styrax japonicus* is doubly dormant and difficult to germinate. It benefits from acid scarification, and requires warm and cold stratification (three months and four months, respectively) for acceptable germination rates (Dirr & Heuser 2006). The species roots readily and is probably better propagated from softwood cuttings, though cuttings should be taken as early in the season as possible to alleviate their difficulties overwintering (Raulston 1992). Dirr & Heuser (2006) recommend treating cuttings with 1000-3000ppm IBA. Griffin & Lasseigne (2005) note that cuttings later in the summer (July) need a higher concentration of 7000ppm IBA for acceptable rooting.

Owing to both its prevalence in cultivation and variety over its range, *Styrax japonicus* is the only species of *Styrax* with any registered cultivars. The cultivar selection overall offers a variety of forms which are pink-flowered, weeping, of superior form, dwarf (many of them of dubious dwarfness when mature), and variegated or burgundy-leaved. Dirr (2009) mentions red flowered and double-flowered forms, though these do not appear to be named or widely distributed.

- 'Angyo Dwarf'. Dwarf form collected by Barry Yinger and introduced by Brookside Gardens. Dirr (2009) lists 8-10'. An accession at the Arnold Arboretum obtained from Brookside Gardens (AA# 549-85*A) was slightly larger ca. 15', though still below the height expected of a specimen near 30 years of age.

- Benibana Group ('Benibana'). A Japanese name used to describe any pink-flowered seed grown form.

- 'Camellia Forest Dwarf'. Raulston (1992) mentions this form was being trialed. It proved to not maintain a dwarf habit and is no longer produced or distributed.

- 'Carillon' ('Pendula', 'Shidare'). Smaller than straight species and weeping in habit, 8-12'. Can be trained to a more tree-like form by staking main leader until the desired height is achieved. Collected from Shibamichi Nursery (Angyo, Japan) by Barry Yinger. Likely originated from *Styrax japonicus* f. *pendulus* Yamazaki.

- 'Crystal'. Vigorous grower with upright habit. Darker leaves than straight species, purple coloration to pedicels and sepals, and variety in petal number (2-9) (Figure 10). Korean origin. Apparently easier to propagate via softwood cuttings as compare to other cultivars (Raulston 1994). Introduced by the JC Raulston Arboretum.

Figure 10 *Styrax japonicus* Siebold & Zuccarini ‘Crystal’ exhibiting darker foliage and higher petal merosity as compared to straight species. Flowering July, 1994 (Raleigh, NC, USA). Photograph by J.C. Raulston (Slide 097-0284), provided by JC Raulston Arboretum.

- ‘Emerald Meadow’. Upright, pyramidal habit with larger and darker green leaves than the straight species. 20-30’ × 15-25’. Introduced by Gary Handy of Handy Nursery (Boring, Oregon, US).

- ‘Emerald Pagoda’ (‘Sohuksan’). Foliage darker green, more leathery, and 2-4 × larger than the straight species, flowers variable in petal number (2-8) and 2-3 × larger than straight species (Figure 11). Raulston (1991) theorized these two features may indicate polyploidy for the cultivar, though Dr. Tom Ranney of the North Carolina State University compared the common *Styrax japonicus* cultivars through use of flow cytometry and found no differences in ploidy level (Ranney, pers. comm.) It is apparently more difficult to root than other cultivars (Griffin & Lasseigne 2005). Introduced by J.C. Raulston in 1985. Korean Origin. Dirr (2009) rates as one of Dr. Raulston’s best introductions. Dr. Dennis Werner once noticed a yellow/green variegated shoot on a landscape planting at the North Carolina State University, though it also proved difficult to propagate (Dennis Werner, pers. comm.).

Figure 11 *Styrax japonicus* Siebold & Zuccarini 'Emerald Pagoda' (UD#91-22*1). Flowering 5/10/2012 at the University of Delaware Botanic Gardens (Newark, DE, USA). Photograph by the Author.

- 'Evening Light'. A burgundy-leaved form named by Henny Kolster in Boskoop, Netherlands. Has a darker and glossier leaf than 'Purple Dress'. Also appears to be more vigorous and cold hardy.

- 'Fargesii'. Leaves darker and larger than straight species. Pedicels purple, flowers pure white. Flowering two weeks later than straight species. Introduced by Pere Farges in 1898. Sometimes listed or distributed as *Styrax japonicus* var. *fargesii*.

- 'Fat Man'. Semi-dwarf form with a rounded habit. Selected by John Allen of Shiloh Nursery (Harmony, North Carolina, USA). Sir Harold Hillier Gardens is growing the cultivar (HH#2004.0400), currently a young plant 2 m in height (Wolfgang Bopp, pers. comm.)

- 'Fragrant Fountain' (PP 19,664). Dark green leaves and fragrant flowers. Dirr (2009) suggests parentage as *Styrax japonicus* 'Rosea' × *Styrax japonicus* 'Carillon'. Sometimes circulated as 'Fragrant Fountains' or 'Fragrant Mountain'. Introduced by Crispin Creations Nursery (Molalla, Oregon, US).

- 'Frosted Emerald'. Variegated form with white leaf margins. Some tendency for reversion. Introduced by Crispin Creations Nursery (Molalla, Oregon, US).

- ‘Hyme’. Little information exists though the cultivar appears to be sold mainly in Europe. Internet photos depict a pink-colored calyx and pedicel, suggesting this cultivar probably originates from *Styrax japonicus* f. *rubricalyx* Satomi. Larch Cottage Nurseries (Penrith, Cumbria, UK) has carried the plant.

- ‘Issai’. Fast growing selection, free-flowering, larger foliage, 20-30’. Barry Yinger Brookside Garden. Griffin & Lasseigne (2005) found rooting with 3000 or 8000 ppm K-IBA to be ineffective to negative.

- ‘JFS-D’ = [Snowcone®]. Dense, pyramidal habit. 25’ × 20’. Introduced by J.F. Schmidt & Son Co. (Boring, Oregon, US).

- ‘JFS-E’ = [Snow Charm®]. Darker green leaves, rounded habit. 20’ × 20’. Introduced by J.F. Schmidt & Son Co (Boring, Oregon, US).

- ‘Kusan’. Introduced by Bob Tichnor (Oregon State University). A Compact, slow growing, globe shaped form. The Miller Garden collects a specimen ‘Kizan’, likely a transcription error. Mr. Richie Steffan, the curator of the garden, notes ‘Kizan’ appears in Mrs. Miller’s first inventory of the garden and though no source information is listed, likely was an acquaintance of Mr. Tichnor’s and may have received the plant directly from him (pers. comm.). The plant lacks a dwarf habit, currently standing 40’ × 30’ in a woodland condition, indicating that this cultivar lacks the dwarf habit or the plant at the Miller Garden is instead a straight species.

- ‘Lady Bell’. Collected by the JC Raulston Arboretum. No further information.

- ‘Masaku’. Distributed by Spinner’s Garden (Boldre, Hampshire, UK). One accession at the Royal Horticultural Society‘s Garden, Wisley. No further information.

- ‘Nana’. Distributed by the JC Raulston Arboretum in 1985. No further information.

- ‘Pink Chimes’. Somewhat upright in habit. Flowers (Figure 12) are pink and fragrant, though may fade to white in late spring heat. May be distributed under erroneous names such as ‘Pink Charm’. Initially introduced in Angyo, Japan by Shibarnichi Kanjiro as ‘Benibana-ego-no-ki’, and brought to the United States by Barry

Yinger in 1978, then distributed by Brookside Gardens. ‘Rosea’ is likely a synonym (Dirr 2009).

Figure 12 *Styrax japonicus* Siebold & Zuccarini ‘Pink Chimes’ (UD# 94-80*1), Flowering 5/10/2012 at the University of Delaware Botanic Gardens (Newark, DE, USA). Photograph by the Author.

- ‘Purple Dress’. Some tendency towards purple leaves and pink flowers, though displays these characteristics far less prominently than ‘Evening Light’ and ‘Pink Chimes’, respectively. Apparently of limited vigor.

- ‘Rosea’. Similar to ‘Pink Chimes’ though apparently of limited height. Possibly a synonym.

- Rubra Pendula Group: Weeping, pink flowered forms, some of which have been distributed by the JC Raulston Arboretum. ‘Pink Cascade’ at the Atlanta Botanical Garden appears to be a named form of the group. Griffin & Lasseigne (2005) found rooting ‘Pink Cascade’ with 3000 or 8000 ppm K-IBA to be ineffective to negative.

- ‘Ryan’s Weeping’ (‘Ryan’s Weeper’). Slow growing weeping form with dark stems and leaves. Introduced by Gary Handy of Handy Nursery (Boring, Oregon, US)

- ‘Salty Dog’. Offered for sale spring 2013 at Ronney’s Garden Word (Smyrna, DE, USA). No information as to significant characteristics compared to straight species.

- ‘Snowfall’. Denser than straight species with rounded habit, flowers fragrant. Introduced by the JC Raulston Arboretum. Griffin & Lasseigne (2005) found this cultivar rooted better with 8000 ppm K-IBA as opposed to 3000 ppm K-IBA, whereas the opposite was true for other cultivars.

- ‘Spring Showers’ (PP 660970). Dirr (2009) references a breeding program by Dr. Sandra Reed at the United States National Arboretum, which would result in the production of this plant. ‘Spring Showers’ (NA71587) has a conical habit and breaks bud later than the straight species, and is thus more suitable for use in areas prone to spring species. As for the other forms from this program, NA71580 was similar but did not propagate well, and NA71589 and NA71590 proved to lack vigor (Sandra Reed, pers. comm.)

- ‘Wespelaar’ (Suggested parentage *Styrax japonicus* ‘Fargesii’ × *Styrax hemsleyanus*). Occurred as an open pollinated seedling of *Styrax japonicus* ‘Fargesii’ (Arboretum Wespelaar #84402), collected by nurseryman Dominique Duhaut. The foliage of the plant differs strongly from *Styrax japonicus* in its prominent venation as well as tendency to turn a dull brown color in early summer. Flowers pale pink. (Koen Camelbeke, pers. comm.). Controlled hybrids between *Styrax japonicus* and *Styrax hemsleyanus* would likely be the best way to confirm this parentage, though determining the ploidy level of AW#84402 is likely a necessary prerequisite.

- ‘Yatsubusa’. Dwarf form accessioned at Moore Farms Botanic Garden (Lake City, SC, USA).

Styrax limprichtii Lingelsheim & Borza
Reference: Repert. Spec. Nov. Regni Veg. 13: 386. 1914
Type: China. Yunnan: Chuxiong Shi, Tschu-hsiung-fu, 2000 m, 24 Aug. 1913, *K. G. Limpricht 920*
= *Styrax langkongensis* W.W.Smith. & Handel-Mazzetti, Symb. Sin. Pt. vII. 803 (1936), descr. ampl

Limpricht Snowbell. Deciduous shrub, 1.0-2.5 m; branchlets grey-yellow or yellow-brown stellate tomentose, older twigs purple and glabrescent. Leaves alternate; elliptic to obovate, white stellate tomentose or rarely subglabrous; lamina 3.5-7(9.5) × 2-4.5 cm (1.6-1.8 × longer than wide), margin serrate to subentire (if subentire, still glandular) and often apically serrulate, apex obtuse to weakly acuminate, base rounded to broadly cuneate; 5-6 secondary vein pairs, tertiary veins reticulate; petiole 1-3 mm, vasculature in an arc with invaginated ends accompanied by two bundles (Schadel & Dickison 1979). Flowers white, 1.5-2.0 cm; pedicel densely pubescent, 3-4 mm; in 2-3(4)-flowered pseudoterminal racemes, 3-4 cm, joined by small 1(2)-flowered axillary inflorescences; calyx 5-toothed, 5-6 × 5-6mm, yellow-brown or orange stellate tomentose; corolla lobes 5, elliptic to ovate elliptic lobes, 9-11 × 4-6 mm, imbricate in bud; androecium of 10 stamens, anthers 4-5mm long; capsule 1.4-1.6 × 1-1.5cm (wall thickness: 0.3-0.6mm), globose, rugose, densely grayish stellate pubescent, apex rounded to apiculate; seeds brown, glabrous, ovoid.

Native to forests of South-central China (Sichuan and Yunnan); 1700-2400 m. Flowering February-October.

A similar species to *Styrax hookeri* albeit shrubbier in nature and with smaller leaves, this was also an introduction from George Forrest's 1917-1919 expedition (as *Styrax langkongensis* W.W. Smith). Raulston (1991) estimated USDA Zone 8-9 hardiness, though doubted it would perform well in the hot, moist conditions of the

American southeast. Grimshaw & Bayton (2009) suggest USDA Zone 8, and note the species appears to grow much taller in gardens, reaching 6 m but still maintaining a shrubby, multi-stemmed habit. To the best of my knowledge, *Styrax limprichtii* is currently not represented at all in Botanical Gardens. It is a very similar taxa to *Styrax wilsonii,* though typically has larger leaves and never with a lobed margin. From a horticultural standpoint, it shares the same potential flaw of a heavy fruit load. Due to its limited hardiness, *Styrax limprichtii* is likely an inferior species to *Styrax wilsonii* in cultivation.

The specific epithet likely honors Hans Wolfgang Limpricht, a German botanist who collected spermatophytes in China and Japan.

Styrax macrocarpus Cheng
Reference: Contrib. Biol. Lab. Sc. Soc. China, Bot. Ser. x. 242 (1938)
Type: China. Hunan: Yizhang Xian, Mang-shan, 800 m, 21 Aug. 1937, *W.C. Cheng 700*
= *Styrax zhejiangensis* S.M.Hwang & L.L.Yu, Acta Bot. Austro Sin. 1: 75. 1983

Deciduous trees or shrubs (2)6-9 m; branchlets terete, densely gray-brown stellate pubescent, becoming gray and glabrescent. Leaves alternate; elliptic to obovate-elliptic, glabrous (though veins stellate pubescent when young); lamina 2.5-17 × 2-7.5 cm (1.3-2.7 × longer than wide), margin entire and apically serrulate, apex acute, base cuneate to broadly cuneate or rounded; 6-10 secondary vein pairs, tertiary veins subparallel, raised abaxially and sunken adaxially; petiole typically very short (<1 mm), though rarely approaching 2 mm. Flowers white, precocious, 2.3-3.2 cm; pedicel white stellate tomentose, 7-12 mm; solitary on axillary inflorescences restricted to wood of previous growing season; calyx 5-6-toothed, 5-6 × 7-9mm, subglabrous; corolla lobes 5-7, elliptic to narrowly elliptic, 1.6-2.6 cm, imbricate in bud; androecium of 10-12 inserted stamens, anthers 5-6 mm; fruit indehiscent, 1.8-3.0

× 1.0-2.5cm (wall thickness: (1.0)1.5-3.0 mm), ovoid to pyriform, densely gray to brownish stellate tomentose or smooth, apex rounded to apiculate; seeds brown to dark brown, ellipsoid to ovoid-ellipsoid, glabrous to sparsely white stellate villose, sometimes rugose.

Native to forest thickets, slopes, and ravines of Southeastern China (Hunan and Guangdong); 500-800 m. Flowering May-June.

A relatively new and very rare species in cultivation, with only three plants known: two in Chinese Botanical Gardens and one in a New Zealand area garden. It has been grown to some extent in the west at the private collection of Tom Hudson at Tregrehan (England) though did not perform well (Grimshaw & Bayton 2009). The species is likely only hardy to USDA Zone 9 based on its native range, though still would be an interesting species for further trial due to its significantly larger flowers as compared to other species in the genus, as well their precocious nature.

S. macrocarpus is the only species of *Styrax* to produce inflorescences on old as opposed to new wood, though this characteristic is seen in other genera of the family, namely *Huodendron* (Huang et al. 2003). The specific epithet references the large fruit of the species.

Styrax obassia Siebold & Zuccarini
Reference: Fl. Jap. (Siebold) 1: 93, t. 46. 1839
Type: Japan. *I. Keiske 287*

Fragrant Snowbell. Deciduous tree, 10-15 m; branchlets somewhat flattened, brown stellate pubescent, older twigs dark purple and glabrescent with bark exfoliating; Leaves alternate; broadly elliptic, ovate, or rounded, densely gray stellate tomentose; lamina 5-17 × 4-15 cm (1.1-1.3 × longer than wide), margin subentire to coarsely serrate, apex acute to acuminate, base subrounded to cuneate; 5-8(10) secondary vein pairs, tertiary veins subparallel; petiole 1.0-1.5 cm, forming a sheath enclosing the winter bud. Basal leaf pair on each branchlet subopposite to opposite, smaller in size with shorter petiole (3-5 mm, not enclosing winter bud), elliptic to ovate with rounded to acute apex; Flowers white to pink, 1.2-2.0 cm; pedicel 3-5 mm; in 10-20-flowered pseudoterminal racemes, 6-15 cm, joined by shorter axillary racemes (Figure 13); calyx of 5-6 irregularly distributed teeth, 5-6 × 4-5 mm, white stellate tomentose; corolla lobes 5-6, elliptic, 13-16 × 4-5 mm, imbricate in bud; androecium of 10(12) inserted stamens, anthers 4-5mm; capsule 1.4-2.0 × 0.7-1.2 cm (wall thickness 0.2-0.5 mm), ovoid to subovoid, white or yellow-brown stellate tomentose, apex rounded to apiculate; seeds dark brown, smooth, oblong to ellipsoid. *2n=16*.

Native to wet forests of Southeastern China, Japan, and Korea; 9-1500m; flowering May to July.

Figure 13 Inflorescences and foliage of *Styrax obassia* Siebold & Zuccarini. Flowering 5/1/2012 at a private garden in Landenberg, PA, USA. Photograph by the Author.

Styrax obassia is the second most common species to cultivation. It was first introduced by Maries for Messrs. Veitch in 1879 (Bean 1980). Since then it has remained an uncommon species, though many have extolled its landscape value for its neat habit and profuse flowering. On the few plants I've observed, the flowers appeared to have a somewhat displeasing fragrance, casting doubt on the common name "fragrant snowbell", though others such as Bean (1980) disagree. Raulston (1991) noted problems with summer root rot prevented it from being a recommended species in the American southeast, though did recommend it to for the Mid-Atlantic region. It is hardy to USDA Zone 5 so likely can be utilized in upper parts of New England and much of the Midwest as well. Dirr & Heuser (2006) recommend 3-5 months warm followed by 3 months cold stratification for seed propagation, and 1000-3000 ppm IBA for softwood cuttings.

The large leaves serve as somewhat of a diagnostic characteristic, as they much larger than that of any commonly cultivated *Styrax* species. The leaves are somewhat of a detriment to its ornamental value however: in the spring, they tend to obstruct the inflorescences making the flowers difficult to see (Figure 14), whereas in the summer they are very prone to wilting in heat and drought conditions.

Figure 14 Inflorescence of *Styrax obassia* Siebold & Zuccarini obstructed by large leaf. Flowering 5/1/2012 at a private garden in Landenberg, PA, USA. Leaf captured in side view displays diagnostic petiole encasing winter bud. Photograph by the Author.

The most ideal method for diagnosing *Styrax obassia* however, is by examination of the petiole. It is one of only two species to dilate towards the basal portion and form a sheath completely encasing and protecting the winter bud (somewhat visible in the leaf captured in side view in Figure 14). The other species to possess this characteristic, *Styrax shiraianus*, is far rarer in cultivation and contains a unique leaf type described under the entry for that species.

There are no listed cultivars for *Styrax obassia*, likely due not only to the fact that it is less popular in cultivation than *Styrax japonicus*, but also that unlike *Styrax japonicus*, it is much less variable over its range.

Styrax odoratissimus Champion ex Bentham
Reference: Hooker's J. Bot. Kew Gard. Misc. 4: 304. 1852
Type: China. Hong Kong: ravines of Mt. Victoria, *J. G. Champion 138*
= *Styrax prunifolius* Perkins, Bot. Jahrb. Syst. 31. 486. 1902
= *Styrax veitchiorum* Hemsley & E.H.Wilson, Bull. Misc. Inform. Kew 1906, 161.

Deciduous tree, 4-10 m; branchlets flattened to terete, glabrous, purple to dark purple; stem grey-brown; Leaves alternate (including basal pair on each branchlet), ovate to ovate elliptic, glabrous (though abaxial veins sometimes densely brown stellate pubescent); lamina 4-15 × 2-8 cm (1.9-2.0 × longer than wide), margin entire (sometimes weakly serrulate apically), apex acuminate to acute, base broadly cuneate to rounded; 6-9 secondary vein pairs, tertiary veins subparallel and conspicuous; petiole 5-10 mm; Flowers white, 1.0-1.5 cm; pedicel 1.5-1.8 cm; in 5-7(11)-flowered pseudoterminal raceme (rarely panicles), 3-8 cm (rachis densely yellow stellate tomentose), joined by shorter axillary racemes or 1-2 flowered inflorescences; calyx 5-toothed (typically weakly so to truncate), 3-4(5) × 3-4 mm, yellow stellate tomentose; corolla lobes 5(6), elliptic to obovate-elliptic, 9-11 mm × 4-6mm, imbricate in bud; androecium of 10-12 inserted stamens; capsule 8-10 × 6-8 mm (wall thickness: 0.5-1.0 mm), subglobose (rarely ovoid), densely grey-yellow stellate tomentose, apex rostrate (rarely apiculate); seeds brown, oppressed stellate pubescent, ovoid.

Native to shaded ravines and semi-open forest thickets of Southwestern, South-central China; 600-1600 m; flowering March-July.

Discovered by E.H.Wilson (as *Styrax veitchiorum*, now a synonym) and introduced on his behalf by Messrs Veitch, *Styrax odoratissimus* is a similar species to *Styrax obassia* and *Styrax hemsleyanus*, sharing a single stemmed habit, profuse flowering, and large leaves that often obscure the inflorescences. Unlike these taxa however, *Styrax odoratissimus* has yet to be cultivated to any significant extent. It remains relatively rare in cultivation, accessioned at a scant few Botanic Gardens including the University of California Botanical Garden at Berkeley (91.0888). The Arnold Arboretum has accessioned plants of this species twice in recent years: one of cultivated origin (AA# 326-96A) and one tracing its lineage to Zhejiang Province (AA# 909-89*N1), though both died in the nursery.

Though it is less hardy than *Styrax obassia*, estimated to USDA Zone 6 (Raulston 1991), the species is far more variable across its range than either *Styrax obassia* or *Styrax hemsleyanus* in terms of leaf size, flowers per inflorescence, and inflorescence length, and may be a suitable candidate for breeding in order to select a superior cultivar. The most accurate way to diagnose this species is likely by observing the appressed pubescence on the seeds, a characteristic similar taxa lack (Huang et al. 2003).

Styrax serrulatus Roxburgh
Reference: Fl. Ind., ed. 1832. 2: 415. 1832

Sawtooth Snowbell. Deciduous tree, 4-12 m; branchlets densely brown stellate pubescent. Leaves alternate; ovate, oblong, or ovate lanceolate, sparsely stellate pubescent to glabrous; lamina 5-14 × 2-4(5.5) cm (2.5-3.5 × longer than wide), margin serrate to (rarely) entire, apex acuminate or weakly so, base broadly cuneate to rounded; 5-7 secondary vein pairs, tertiary veins reticulate and conspicuously raised;

petiole 3-5 mm; vasculature in an arc with two invaginated ends usually accompanied by one small bundle, ends splitting into individual bundles towards distal third of petiole, or in a medullated cylinder with no accompanying bundles Schadel & Dickison (1979); Flowers white, 1.0-1.3 cm; pedicel 3-8 mm; in many-flowered racemes or panicles, 3-10 cm; calyx 5-toothed, 3-4 × 3-4 mm, densely yellow stellate tomentose; corolla lobes 5, oblong lanceolate, 7-9 mm, valvate in bud; stamens inserted; fruit 8-16 × 6-8 mm, ellipsoid to ellipsoid ovoid, densely gray-brown stellate tomentose, sometimes sparsely stellate villose, apex slightly oblique and acute to apiculate; seeds dark brown, stellate puberulent to glabrous, 1-2 per fruit.

Wood diffuse porous; rays uniseriate and biseriate, uniseriate ray width ca. (13)14-16 μm; biseriate ray width ca. 17-28(31) μm, (3)4-8(10) uniseriate rays and 0-2 biseriate rays per 1.73 mm^2 (16% of rays biseriate). Vessel elements ca. 20(21-24) μm × (23)25-28(30) μm (1.2 × wider than long), with a mean of (2.1)2.3-2.9(3.2) per multiple, or rarely occurring solitarily (4% of vessels solitary), (30)37-58(64) vessel elements per 1.73 mm^2.

Native to sparse forests of Southern China, Taiwan, Bhutan, India, Laos, W Malaysia, Myanmar, Nepal, Thailand, Vietnam; 500-1700 m. Flowering March-May.

Despite the wide range of the species, it seems to be a recent introduction to cultivation, conspicuously missing from both Bean and Raulston's treatments. Grimshaw & Bayton (2009) estimate hardiness to USDA Zone 7-8 (presumably for plants of northern provenance). The species remains rare in cultivation, though accessioned at the JC Raulston Arboretum (#940340) and the Sir Harold Hillier Gardens (#1976.1802 and #1978.2807).

Diagnosis of *Styrax serrulatus* can prove difficult to the large amount of morphological variation over its distribution (Fritsch 1999), often apparent by examining the leaf margin One specimen I observed at the Cultivated Herbarium of the Arnold Arboretum displayed the serrulate leaf margin (the genesis of the specific epithet) prominently, though many others can be subentire to entire. The shape of the leaf is likely more unique, as it is far more narrow than other species in cultivation, approaching or exceeding a length three times longer than its width. The species has been utilized for resin production, though apparently produces a benzoin resin of inferior quality (Langenheim 2003).

Styrax shiraianus Makino
Reference: Bot. Mag. (Tokyo) 1898, 50.
Type: Japan. Honshu: Shizuoka Pref., Sugura, Araizawa in Abe-gori, *Herb. Sc. Coll. Imp. Univ. Tokyo s.n*

Deciduous tree, 3-8 m; branchlets purple-gray, yellow or brown stellate tomentose, aging to gray and glabrescent; Leaves alternate; broadly obovate to rhomboid orbicular, sparsely stellate pubescent, glabrescent; lamina 8-10 × 7-9.5 cm (As long as wide or slightly longer); margin serrulate towards base, dentate towards apex, apex rounded to short-caudate, base cuneate to broadly cuneate; 4-6 secondary vein pairs, tertiary veins parallel and conspicuous; petiole 8-15 mm, dilated at base and forming sheath covering winter bud (except in basal leaf pair on each branchlet) (Figure 15). Flowers white, 1.5-2.0 cm; pedicel densely white or brown stellate villose, <1mm; in 3-11-flowered pseudoterminal racemes, 2-3 cm (rachis yellow stellate tomentose), joined by axillary 1-flowered inflorescences; calyx 5-8-toothed, 4-6.5 × 4-6 mm, stellate tomentose; corolla lobes 5, ovate, 6-8mm × 3mm, imbricate in bud; androecium of 10 stamens, anthers 2-3 mm in length; fruit 0.8-1.0 × 0.6-0.8 cm (wall thickness 0.3-0.7 mm), ellipsoid to subglobose, white stellate tomentose, apex rounded or apiculate; seeds brown, smooth, ellipsoid.

Rare in open deciduous forests of Japan & South Korea; 600-1500 m. Flowering in June.

Figure 15 *Styrax shiraianus* Makino exhibiting apically dentate foliage. June, 1990. Seattle, WA, USA. Photograph by J.C. Raulston (Slide 100-0341), provided by JC Raulston Arboretum.

Introduced to the US in 1915 and accessioned at the Arnold Arboretum (AA# 7727*A), the species would not reach Europe until nearly 30 years later (Bean 1980). *Styrax shiraianus* is very rare in cultivation today, though one mature accession exists at the Washington Park Arboretum (61-92*A). It is also present in at least one European garden: The Botanic Garden of the University of Copenhagen.

Like *Styrax obassia*, leaves of *Styrax shiraianus* possess a petiole which flares at the basal portion of the petiole to form a sheath encasing the winter bud, though differs from that species in flower and leaf morphology. The corolla is fused much further towards the distal end than in other species, resulting in a longer tube, shorter lobes, and narrower appearance to the flower. Most distinctive however are the leaves, which due to a dentate margin apically, resemble several members of the Hamamelidaceae (Raulston 1992 and Bean 1980 specifically mention *Hamamelis japonica*). Raulston (1992) listed its hardiness as USDA Zones 6-7, and theorized it would be well adapted to the American Southeast.

Styrax supaii Chun & F. Chun
Reference: Sunyatsenia 3: 34. 1935
Type: China. Guangdong: RuyuanYaozu Zizhixian, Chut-sien Dun [Qi-xian-gou], 9 May 1934, *Styrax P. Kwok 80419*

Shrub or small tree, 2-6 m; branchlets terete, brown to dark brown densely stellate pubescent, aging to dark purple and glabrescent; stem dark brown; bark exfoliating. Leaves alternate; ovate to obovate, sparsely stellate pubescent, glabrescent; lamina 4-8 × 2-5 mm (1.6-2.0 × longer than wide), margin coarsely serrate to weakly 3-5 lobed (basal leaves of each branchlet usually entire), apex acute to acuminate, base rounded to broadly cuneate; 3-5 secondary vein pairs, tertiary veins reticulate and conspicuously raised; petiole 2-5 mm; Flowers white, 1.5-1.8 cm; pedicel slender, sparsely stellate pubescent, 1.0-1.5 cm; in 2-3-flowered pseudoterminal racemes, 2-4 cm, joined by several shorter 1-2 flowered axillary inflorescences; calyx prominently 5-toothed, ca. 12 × 4mm, sparsely appressed pubescent; corolla of 5 elliptic-lanceolate lobes, 1.4-1.5 × 0.4-0.5 cm, imbricate in bud; androecium of 10 stamens, conspicuously unequal in length, anthers 4-6 mm;

capsule 1.0-1.5 × 0.7-0.9(1.3) cm (wall thickness ca. 0.3-0.6 mm); ovoid or ellipsoid, densely white stellate villose; apex apiculate to shortly rostrate; seeds brown, ovoid, smooth.

Rare in dry, disturbed areas (forest edges, roadsides) of Southeastern China (Hunan and Guangdong); 300-900 m. Flowering May-June.

S. supaii is very rare in cultivation, present in one Asian garden and probably not cultivated in the west. The exfoliating bark could serve to extend its ornament when not flowering, though I have not observed this characteristic myself. The species is unlikely hardy past USDA Zone 9 due to its native range. It is probably most easily diagnosed by its stamens, which are unequal in length, and long calyx teeth relative other similar species (Hwang & Grimes 1996).

Styrax rugosus Kurz
Reference: J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40(1): 61. 1871
Type: Myanmar, Pegu: hills between Sittang & Salween, 1212 m, *Brandis s.n.*

Rugose Snowbell. Deciduous trees or shrubs to 6 m; branchlets terete and densely stellate tomentose, becoming purple and glabrescent. Leaves alternate, ovate-oblong, ovate, or elliptic, densely grey-yellow stellate tomentose; lamina 3-7 × 2-3 cm (ca. 1.5-2.3 × longer than wide), up to 9 × 4.5 cm on sterile branches; margin serrate, sometimes dentate apically; apex acuminate or rarely acute; base broadly cuneate to rounded, often slightly oblique; 4-7 secondary vein pairs, tertiary veins parallel and conspicuous on young leaves; petiole 2-3 mm. Flowers white, 1.4-1.6 cm; pedicel 3-4 mm; in 3-6-flowered pseudoterminal racemes, rachis yellow stellate tomentose, (2)4-6 cm, and joined 1-2 flowered axillary inflorescences; calyx 4.5-5 mm × 3.5-5 mm, densely yellow-brown stellate tomentose, 5-toothed, margin dentate; corolla 1.0-1.2

cm, lobes 5, elliptic to obovate, imbricate in bud; stamens 10; capsule 0.7-0.9 cm × 0.5-0.6 cm, ovoid, densely yellow-brown stellate pubescent; apex rounded to apiculate; seeds ovoid, brown, ribbed, glabrous, 1-2 per fruit.

Native to forests of Tropical China (Southern Yunnan), India, Myanmar, and Thailand; 1000-1500m. Flowering March-July.

A shrubby species probably not hardy past USDA Zone 9 due to its southern provenance. It has been trialed at the private garden of Tom Hudson at Tregrehan (Southern United Kingdom), though was unsuccessful (Grimshaw & Bayton (2009). Species such as *Styrax wilsonii* and *Styrax limprichtii* are likely to be hardier and probably of higher priority for evaluation.

Styrax tonkinensis (Pierre) Craib ex Hartwich
Reference: Apotheker-Zeitung xxviii. 698 (1913)
Type: Vietnam, Province unknown: Tu Phap, 12 May 1887, *B. Balansa 4332*
= *Styrax hypoglaucus* Perkins, Bot. Jahrb. Syst. 31. 486. 1902
= *Styrax macrothyrsus* Perkins, Bot. Jahrb. Syst. 31. 485. 1902
= *Styrax subniveus* Merrill & Chun, Sunyatsenia 1: 78. 1930

Tonkin Snowbell. Deciduous tree, 6-30 m; branchlets gray-brown stellate tomentose, older twigs dark brown, glabrescent. Leaves alternate (including basal pair on each branchlet), elliptic to ovate, densely grey to glaucous stellate pubescent; lamina 5-18 × 4-10cm (1.3-1.8 × longer than wide), margin entire, sometimes apically serrate, apex shortly acuminate, base rounded to cuneate; 5-6 secondary vein pairs, tertiary veins subparallel, conspicuous; petiole 8-12(15) mm, vasculature in an arc with invaginated ends accompanied by two bundles (Schadel & Dickison 1979). Flowers white, 1.2-1.5(1.7) cm; pedicel 5-10 mm, yellow stellate tomentose; in (6)8-18(23)-flowered pseudoterminal racemes or panicles, (5)7-20 cm, joined by axillary 1-2-flowered inflorescences or 1-7-flowered racemes, 3-5 cm; calyx 3-4 × 3 mm, truncate to 5-toothed, usually with a distinct dentate margin, densely gray-white stellate pubescent; corolla lobes 5, ovate lanceolate to oblong elliptic, 10-15 × 3-4 mm, imbricate in bud; androecium of 10 stamens, anthers ca. 5 mm in length; capsule, 0.8-1.2 × 0.7-1.1 cm (wall thickness: 0.8-1.1 mm), subglobose, densely grey stellate tomentose, apex rostrate; seeds brown to dark brown, stellate tomentose, ovoid & tuberculate.

Wood diffuse porous; rays uniseriate, biseriate and rarely triseriate, uniseriate ray width ca. 13-18(21) μm; multiseriate ray width ca. (19)20-27(31); (5)6-10(11) uniseriate rays and (0)1-2(3) multiseriate rays per 1.73 mm^2 (18% of rays multiseriate). Vessel elements ca. (18)21-30(33) μm × (19)21-29(33) μm (approximately as wide as long), with a mean of (2.1)2.2-3.3(4.2) per multiple, or rarely occurring solitarily (5% of vessels solitary), (20)25-34(38) vessel elements per 1.73 mm^2.

Common in open forests and disturbed sites of Southeastern China, Laos, and Vietnam; 30-2400m. Flowering April-July.

Styrax tonkinensis, along with *Styrax benzoin*, is one of the most important sources of Styrax resin. The resins have been historically confused in the literature, though the resin produced by *Styrax tonkinensis* is generally clarified as Siam Benzoin, whereas that of *Styrax benzoin* is Sumatra Benzoin. It differs from the latter in having a vanilla as opposed to a balsamic odor, and according to Pinyopusarerk (1994), is recognized as a superior product. The tree however is seldom tapped today for benzoin resin due to a decline in the market value, but has found economic use as timber plant for production of pulpwood (Pinyopusarerk 1994).

For ornamental purposes however, *Styrax tonkinensis* is very rare in cultivation. One accession at the JC Raulston Arboretum (JCR# 960302) purports to be this plant. The above wood description is based on said accession. Grimshaw & Bayton mention accessions at the David C. Lam Asian Garden in Vancouver, Tregrehan, and Cornwall. Though requiring a protected area, it seems to be a fast growing plant, sometimes semi-evergreen in a mild winter. The Arnold Arboretum accessioned seed in 1994 (AA# 565-94), though no plants appear to have entered the collection.

Raulston (1991) suggested hardiness to USDA Zones 9-10, noting it was likely not cultivated in the US. Grimshaw & Bayton list USDA Zones 8-9. This discrepancy is likely a result of provenance, as Raulston refers to the plant a Thailand native whereas Grimshaw & Bayton list the northern distribution of the plant in Southern China.

The species may be difficult to separate from *Styrax hookeri*, or *Styrax limprichtii* but differs from the former due to its dentate calyx and by latter due to its longer petiole and densely tuberculate seeds (Huang et al. 2003). The specific epithet references northern Vietnam.

Styrax wilsonii Rehder
Reference: Pl. Wilson. (Sargent) 1(2): 293. 1912
Type: China, Sichuan: Baoxing Xian, Mu-pin, 1300-1700 m, June 1908, *E. H. Wilson 884*

Wilson Snowbell. Deciduous shrub, 1-2 m; branchlets densely reddish-brown stellate pubescent, glabrescent to dark brown. Leaves alternate; obovate, rhomboid, or rarely elliptic-ovate, grayish stellate tomentose; lamina 1-2.5(4) × .7-2(2.6) cm (1.3-1.4 × longer than wide), margin 2-4 lobed or apically serrate, apex acute to shortly acuminate, base cuneate; 4-6 secondary vein pairs, tertiary veins inconspicuous; petiole 1-2 mm, vasculature an arc with invaginated ends, in this case the phloem forming a complete ring around the xylem, often containing minute accompanying bundles, larger accompanying bundles present towards distal portion. Flowers white, 0.9-1.1(1.3) cm; pedicel 2-3 mm; in 3-5-flowered pseudoterminal racemes, 1-2 cm; calyx 5-toothed, unevenly distributed, 2-3 × 3-3.5 mm, densely stellate tomentose; corolla 0.6-0.8(1.0) cm, lobes 5(6), 6-7 × 3.5-4 mm, imbricate in bud; androecium of 10(12) stamens, anthers ca. 3 mm; fruit 0.5-0.6 × 0.4-0.5 cm (wall thickness: 0.2-0.3 mm), subglobose, densely grey tomentose, apex rounded to shortly apiculate; seeds brown, ovoid to globose, smooth, 1-2 per fruit.

Wood diffuse porous; rays uniseriate, biseriate, or rarely triseriate, uniseriate ray width ca. (12)13-16(19) μm; multiseriate ray width ca. (15)16-31(32) μm; (4)6-10(11) uniseriate rays and 0-2(3) multiseriate rays per 1.73 mm^2 (12% of rays multiseriate). Vessel elements ca. (17)18-19 × (16)17-24(26) μm (1.1 × wider than long), with a mean of (2.7)3.0-3.7(4.2) per multiple, or rarely occurring solitarily solitary (3% of vessels solitary). (27)32-46(55) vessel elements per 1.73 mm^2.

Native to openings of forests or scrub of Central China (endemic to Baoxing Xian, Sichuan); 1300-1700m. Flowering May-June (September).

The plant was introduced by E.H. Wilson in 1908, and named for him by Rehder. In 1911 it was accessioned at the Arnold Arboretum (AA# 6763*A). Bean (1980) thought very highly of the plant, stating a 6' height specimen observed in 1913 in at Mr. Chenault's nursery at Orleans was "one of the most beautiful objects I have ever seen."

Today *Styrax wilsonii* is uncommon in cultivation, though much more commonly represented in North American gardens than those of Europe. It flowers at a very young age when only inches in height, though some (Raulston 1992) feared it would be short-lived in cultivation due to a heavy fruit set. Mature accessions at the Polly Hill Arboretum (PHA#2007-30*A) and JC Raulston Arboretum (JCR#001612) indicate this may not be as detrimental as first thought. However, the profuse flowering of the plant at a young age likely makes it a very suitable candidate for further evaluation, and production of a sterile cultivar would alleviate this potential issue.

It is easily separated from other species due to its distinct foliage, which is small and strongly dentate to weakly lobed Though described in the literature as a shrub, Bean (1980) mentions it is sometimes tree-like, a condition observed on accessions at the Polly Hill Arboretum (PHA#2007-30*A) and JC Raulston Arboretum (JCR#001612).

Styrax wuyuanensis S.M.Hwang
Reference: Acta Phytotax. Sin. 18(2): 160 (1980).
Type: China: Jiangxi: Wuyuan, ca. 2000 m, 6 April 1959, *G.H. Li & C. Chen 183*

Wuyuan Snowbell. Deciduous shrub, 1.5-3.0 m; branchlets terete, sparsely brown stellate pubescent. Leaves alternate elliptic to elliptic-pyriform, glabrous, though veins sparsely brown stellate pubescent; lamina 3.5-6 × 1-3 cm (2.0-3.5 × longer that wide), margin remotely serrulate, apex acuminate to caudatley so, base cuneate to broadly so; 3-5 secondary vein pairs, tertiary veins reticulate; petiole 2-5 mm. Flowers white, ca. 1 cm, pedicel 1.5-2 cm, glabrous; inflorescences reduced, present as a 2-3 flowered pseudoterminal racemes, accompanied by axillary flowers; calyx 5-toothed, ca. 3 × 3.5 mm, brown, glabrous; corolla tube ca. 3 mm, valvate in bud; stamens slightly inserted; capsule ca. 1cm × 1cm, globose; apex shortly pointed; seeds brown, ovoid, glabrous. Native to damp, shady areas and forest thickets of Southeastern China (Anhui, Jiangxi); ca. 2000 m. Flowering in April.

Very rare in cultivation, present in one European garden and likely not cultivated in North America at all. Based on its native range, *Styrax wuyuanensis* is likely hardy to at least USDA Zone 8, maybe even 6-7 as it seems to grow in high elevation. The description above is from Hwang & Grimes (1996), though clarification is needed as to the length of the corolla lobes and overall size of the flowers before its ornament can be estimated. Based on the description above the plant is likely of further interest mainly due to hardiness. The specific epithet likely refers to the Wuyuan County of Jiangxi Province, China, and the species should be relatively easy to diagnose on the basis of valvate corolla aestivation and a glabrous calyx and pedicel.

***Styrax* series *Styrax* P.W.Fritsch**

> Leaf margins entire, lobed, or coarsely toothed, but never glandular denticulate or glandular serrate; inflorescences strictly terminal. 3 species; California, Texas, Mediterranean region (Fritsch 2001). All 3 species in cultivation, two uncommon, one rare.

Styrax officinalis Linnaeus
Reference: Sp. Pl. 1: 444. 1753
Type: LT: *Herb. Clifford 187*, Styrax no. 1; ; (BM) LT designated by Barrie, Regnum Veg. 127: 92 (1993)

Deciduous shrub (rarely tree) to 6 m (Figure 16); branchlets subterete, whiteish stellate pubescent, glabrescent. Leaves alternate; broadly elliptic to broadly ovate or ovate oblong, densely whiteish stellate tomentose; lamina 4.5-9.5 × 3.7-6.5 cm (1.2-

1.5 × longer than wide); margin entire, apex acute to rounded, base rounded to weakly cuneate; 5-7 secondary vein pairs; petiole ca. 0.5-1.0 cm. Flowers white, fragrant, ca. 1.5-2.5 cm; pedicel ca. 1-2 cm; in 2-6-flowered pseudoterminal racemes, 4.5-5.0 cm; calyx densely stellate tomentose, teeth 5, minute; corolla 1.5 × 0.6 cm, lobes 5-8, oblong lanceolate, imbricate in bud; stamens 12, of equal length; capsule 1.2-1.4 × 1.2-1.4 cm, globose, densely stellate tomentose; seeds brown, subglobose.

Native to Eastern Mediterranean region, extending westwards to Italy (Albania, Croatia, Cypress, Greece, Israel, Italy, Jordan, Lebanon, Syria, Turkey).

Figure 16 Espalier trained *Styrax officinalis* Linnaeus flowering May, 1988 at Chelsea Physic Garden (Chelsea, London, England). Photograph by J.C. Raulston (Slide 095-0017), provided by JC Raulston Arboretum.

Cultivated since antiquity for the exudation of resin, this plant is often referred to as the “True Storax Tree”. This common name is not preferable, inviting further confusion between the resin produced by *Styrax* and the resin produced by

Liquidambar which is more commonly termed “storax”. To colloquially refer to the species as the “Styrax-tree” is probably more appropriate. Interestingly, recent attempts by Zeybek (1970) to extract such resin have proven unsuccessful. It is theorized that provenance may have an impact on the resin production of this species (Langenheim 2003). Regardless, a record exists of medicinal use of *Styrax officinalis* resin, such use serving as the genesis of the specific epithet.

As an ornamental, *Styrax officinalis* is uncommon in cultivation and more strongly represented in European than North American Gardens. The Arnold Arboretum obtained seed of Turkish provenance in 1990 (AA# 608-90*N1), though the plants perished in the nursery. Its flowers differ significantly from many others in the genus both in their pleasant fragrance, as well the numerous, narrow corolla lobes causing the flower to resemble an orange blossom with a greatly reduced gynoecium.

Zone hardiness for the species appears to be strongly dependent on summer heat, required for proper ripening of the wood (Bean 1980). Raulston (1992) suggests USDA Zone 7 hardiness for areas with warm summers, and USDA Zone 9 hardiness for areas with relatively cool summers, recommending it particularly for the Pacific Northwest due to its close relationship to the California-native *Styrax redivivus* (discussed below).

Styrax platanifolius Engelmann ex Torrey
Reference: Smithson. Contrib. vi. (1854) 4, in nota.
Type: U.S.A. Texas: Comal Co., near New Braunfels, 1851, *Lindheimer s.n.*

Sycamore-leaved Snowbell. Deciduous shrub, 3-6m; branchlets glabrous to densely white stellate pubescent; older twigs with exfoliating bark. Leaves alternate;

suborbiculate to broadly ovate, glabrous to densely stellate pubescent (indumentum more prominent on veins and lower, subopposite leaf pair); lamina 4.5-9.0(12.0) × 4.2 - 9.0(11.5) cm (approximately as long as wide), margin entire to 3-lobed, apex rounded to obtuse (rarely acute or cuspidate), base rounded, sometimes attenuate and oblique; 5-6 secondary vein pairs, tertiary veins evident but not conspicuous; petiole 0.6-2.0 cm (Figure 17); vasculature in an arc with invaginated ends with evident sclerenchymous ring surrounding phloem. Flowers white, slightly reflexed, ca. 1-2 cm; pedicel 4-9 mm; in 1-7 flowered pseudoterminal racemes, 2-5 cm; calyx entire or irregularly 1-7-toothed, 3.0-5.0(6.0) × 4.5-5.5 mm, glabrous or densely white-stellate pubescent; corolla 1.2-2.1 cm, lobes 5-6, elliptic, imbricate in bud; stamens slightly exserted, anthers 3.0-5.5 mm long; capsule 7-10 × 7-11 mm (wall thickness: 0.3-0.5 mm), globose, grey-white stellate pubescent; seeds glabrous.

Native to South-central United States (Texas) and Mexico; South-central US (Texas), Mexico. NatureServe ranking G3 (Globally Vulnerable). Flowering April-May. Five recognized lower taxa, all narrow endemics.

- *Styrax platanifolius* ssp. *mollis* P.W. Fritsch
  Reference: Ann. Missouri Bot. Gard. 84(4): 742, f. 66. 1998
  Type: Mexico. Coahuila: Mpio. de Muzquiz, Rancho Agua Dulci, E slope of the Sierra de San Manuel, 28 June 1936, *E L. Wynd & C. H. Mueller 340*
  = Styrax platanifolius var. *mollis* (P.W.Fritsch) B.L.Turner
  Sida 19(2): 261. 2000
  Lamina, pedicel, and calyx white stellate pubescent (lamina only sparsely so). Similar to ssp. *stellatus* but stellate hairs usually <1 mm and leaves somewhat rough to the touch. Rare in wooded canyons of Mexico (Coahuila, Tamaulipas); 1200-1400 m.

- *Styrax platanifolius* ssp. *platanifolius* (Cory) P.W. Fritsch. Leaf, pedicel, and calyx glabrous. Extremely rare in dry bottomlands, and ledges of Texas (Edwards Plateau); 200-700 m.

- *Styrax platanifolius* ssp. *stellatus* (Cory) P.W.Fritsch
  Reference: Ann. Missouri Bot. Gard. 84(4): 743. 1998
  Type: U.S.A. Texas: Bandera Co., Sabinal Canyon, 16 June 1940, *V L. Cory 34765*
  = *Styrax platanifolius* var. *stellatus* Cory, Madroño 7: 111. 1943
  Hairy Sycamore-leaved Snowbell. Lamina, pedicel, and calyx white stellate pubescent (lamina only sparsely so). Similar to ssp. *mollis* but stellate hairs often >1 mm and leaves soft to the touch. Rare in dry bottomlands, and ledges of Texas (Edwards Plateau); 500-700 m. Subspecific epithet referencing stellate indumentum.

- *Styrax platanifolius* ssp. *texanus* (Cory) P.W.Fritsch.
  Reference: Ann. Missouri Bot. Gard. 84(4): 743. 1998
  Type: U.S.A. Texas: Edwards Co., Polecat Creek, 4 July 1941, *V L. Cory 34940*
  = Styrax texanus Cory, Madroño 7: 112. 1943; *Styrax platanifolius* var. *texanus* (Cory) B.L. Turner, Sida 19(2): 261. 2000
  Texas Snowbell (Figure 19). Lamina, pedicel, and calyx white stellate pubescent; branchlets glaucous, subglabrous. Rare on limestone cliffs and ledges of Texas (Edwards Plateau); 500-700 m. Rarest of the five subspecies, <20 populations known. Subspecific epithet referencing distribution.

Figure 17 Foliage of *Styrax platanifolius* Engelmann ex Torrey ssp. *texanus* (Cory) P.W.Fritsch (PHA# 2009-90*A) at the Polly Hill Arboretum (West Tisbury, MA, USA). 8/20/2012. Photograph by the Author.

- *Styrax platanifolius* ssp. *youngiae* (Cory) P.W.Fritsch
  Reference: Ann. Missouri Bot. Gard. 84(4): 743. 1998.
  Type: U.S.A. Texas: Limpia, canyon, Davis Mountains, 12 May 1914, *M. S. Young s.n*
  = *Styrax youngiae* Cory, Madroño 7(4): 113-115. 1943
  = *Styrax platanifolius* var. *youngiae* (Cory) B.L.Turner, Sida 19(2): 261. 2000
  Young Snowbell (Figure 18). Lamina, pedicels, calyx, and branchlets white stellate pubescent. Rare on limestone substrates of Davis Mountains (Texas) and Coahuila (Mexico); elevation uncertain. Once thought extinct.

Figure 18 *Styrax platanifolius* Engelmann ex Torrey ssp. *youngiae* (Cory) P.W.Fritsch flowering May, 1995 in Raleigh, NC, USA. Photograph by J.C. Raulston (Slide 116-0187), provided by JC Raulston Arboretum.

The date of introduction for this species to cultivation is unclear, though Spongberg (1976) lists as being collected by the Henry Foundation for Botanical Research (Gladwyne, PA, USA). The Arnold Arboretum received plants from Yucca Do Nursery and attempted cultivation (AA 281-93*A and 281-93*B), though both died in the nursery within ten years.

Currently, all lower taxa save for *Styrax platanifolius* ssp. *stellatus* are represented in botanical garden collections, though exclusively in those of North America. *Styrax platanifolius* ssp. *texanus* is the most common accession, though still rare relative to other species of *Styrax*, collected by 8 gardens including the Polly Hill Arboretum (PHA# 2009-90*A), JC Raulston Arboretum (JCR# 031738), and Lady Bird Johnson Wildflower Center. Efforts by J. David Bamberger and others of The Bamberger Ranch Preserve (Johnson City, TX, USA) have been very successful in terms of scouting populations on private land, collecting seed, germinating, and reintroducing the species. Though many more populations must be established before the species can be considered restored, their model for collaboration with private landowners should be reviewed by any non-profit organization with an interest in plant conservation.

Figure 19 *Styrax platanifolius* Engelmann ex Torrey ssp. *texanus* (Cory) P.W.Fritsch flowering April, 1986 in Dallas, TX, USA. Photograph by J.C. Raulston (Slide 031-1036), provided by JC Raulston Arboretum.

All other lower taxa are very rare in cultivation, with *Styrax platanifolius* ssp. *platanifolius* collected by two institutions: The Ladybird Johnson Wildflower Center and the United States National Arboretum. *Styrax platanifolius* ssp. *mollis* and *Styrax platanifolius* ssp. *youngiae* are only collected by one garden each, the former at the University of California Botanical Garden at Berkeley (UCB# 91.1305), and the latter at another North American Botanical Garden. The JC Raulston Arboretum has collected *Styrax platanifolius* ssp. *youngiae* in the past, finding no damage to the plant at 2°F (Raulston 1995).

Styrax redivivus (Torrey) L.C. Wheeler
Reference: Bull. S. Calif. Acad. Sci. 44: 94. 1946
= *Styrax officinalis* Linnaeus var. *californicus* (Torrey) Rehder, Mitt. Deutsch. Dendrol. Ges. 1915: 226.
= *Styrax officinalis* Linnaeus var. *fulvescens* (Eastwood) Munz & I. M. Johnston, Bull. Torrey Bot. Club 51: 297. 1924
= *Styrax officinalis* Linnaeus var. *redivivus* (Torrey) R.A.Howard, Sida 5(5): 337. 1975

California Snowbell. Deciduous shrub to 4 m. Leaves alternate; broadly elliptic, obovate, or orbiculate; lamina 3.0-7.5(11.7) cm × 2.5-6.5(8.8) cm (1.2 × longer than wide), margin entire, apex acute to obtuse, base obtuse to rounded; (6)7-8(9) secondary vein pairs; petiole 0.3-1.4 cm, vasculature in an arc with invaginated ends accompanied by two bundles (Schadel & Dickison 1979). Flowers white, slightly reflexed, ca. 1.5-2.5 cm; pedicel 4-9 mm; in 1-6-flowered pseudoterminal inflorescences, 2-5 cm; calyx shallowly toothed, 5-7 mm, pubescent; corolla lobes 5-7(8), oblong to obovate, 12-15 m, imbricate in bud; stamens inserted; capsule 11-15 × 10-12 mm (wall thickness: 0.3-0.5 mm), globose, tawny or fulvous stellate-pubescent. *2n=16*.

Native to Chaparral and yellow pine forest of Western United States (California); 0-1500 m. Conservation Status: NatureServe G2G3 (Globally Imperiled to Vulnerable). Flowering April to May.

Fritsch (2009) does not describe the branchlets for this species. I suspect them to be subterete and white stellate pubescent and glabrescent as in *Styrax officinalis*, though have elected to not describe as such above without examining specimens of this taxa.

The identity of this taxon has long been confused in the literature, due to its near identical morphological appearance to *Styrax officinalis.* Perkins (1907) considers it identical to such, whereas Gonsoulin (1974) assigns it varietal status (as *Styrax officinalis* var. *californica*). Molecular analysis by Fritsch (2001), specifically focusing on the ITS region of nuclear ribosomal DNA and chloroplast restriction sites of the genes trnK, rpoC1, and proC2, suggested *Styrax platanifolius* and *Styrax redivivus* are more closely related to each other than to *Styrax officinalis*, justifying recognition of the taxon at the species level.

Adding to the nomenclatural confusion, the taxon has been treated with two specific epithets: *californica* and *redivivus*, with a var. *fulvescens* also in the literature. As described by Fritsch (2009), *Styrax californicus* Torrey is a superfluous name, as the basionym *Darlingtonia rediviva* Torrey, was published two years earlier in 1951, giving *Styrax redivivus* priority over *Styrax californicus*. *Styrax officinalis* var. *fulvescens* was a lower taxon supposedly distinct by a heavy tawny pubescence on the underside of the leaves (the term fulvescens indicates a tawny/yellowish-brown coloration), a rufous pubescence to the calyx, and a more southern provenance. Fritsch

(2009) rejected this lower taxon due to the variability of these characteristics over the range of the species.

In summation, though earlier treatments often interpreted *Styrax officinalis* as containing three lower taxa, one distributed in the Old World and two in the New World, modern treatments consider the new both New World taxa as a single, separate, species: *Styrax redivivus*.

In cultivation, the species is uncommon, though better represented in North American Gardens, particularly those of the Pacific Northwest, than in European Gardens. The specific epithet, *redivivus,* means an ability to revive from a dry state.

Styrax section *Valvatae* P.W.Fritsch

> Plants evergreen; bases of young shoots without stalked ferrugineous or fulvous stellate hairs unless these accompanied by a dense tomentum consisting of hairs of the same general color and type; sides of the corolla straight or nearly so in bud; corolla lobes subcoriaceous. 86 species, eastern and southeastern Asia, Neotropics (Fritsch 1999).

***Styrax* series *Benzoin* P.W.Fritsch**

> Mesocarp dry; endocarp at maturity adherent to the mesocarp, not the seed; seeds depressed-globose; seed coat crackled. 9 species, eastern and southeastern Asia (Fritsch 1999). Three species (33% of series) in cultivation: One rare, two very rare.

Styrax benzoin Dryander
Reference: Phil. Trans. lxxvii. II. 308., t. 12. 1787
Type: Dryander, Philos. Trans. 77: *tab.* 12 (1787).
= *Styrax benjuiferus* Stokes, Bot. Mat. Med. 2: 517. 1812
= *Styrax dealbatus* (Miers) Gurke, Nat. Pflanzenfam. [Engler & Prantl] iv. I. (1891) 178.

Benjamin-tree. Evergreen tree to 8 m; branchlets brownish stellate pubescent, glabrescent. Leaves alternate; ovate, ovate-oblong, or ovate-lanceolate, grey or brown yellow pubescent (though veins glabrous), lamina 6.0-15.0 × 2.5-6.0 cm (ca. 2.5 × longer than wide), margin entire to subentire, apex acuminate, base broadly cuneate to rounded; 7-13 secondary vein pairs, tertiary veins subparallel and conspicuous; petiole 6-12 mm. Flowers white, ca. 1.5 cm; pedicel 1-5 mm; in pseudoterminal and axillary racemes 3-7 cm (rachis greyish stellate pubescent); calyx entire to 5-toothed, 3 mm long, pubescent; corolla lobes 4-5, linear oblong, 10-14 mm, valvate in bud; stamens 8-10, exserted; dry drupes 1.5-2.0 × 1.8-2.2 cm, subglobose, grey stellate pubescent; seeds glabrous, 1(-2) per fruit.

Native to dense forests of Peninsular Malaysia, Indonesia, India, Myanmar, Thailand, Cambodia. Laos, and Vietnam; 200-500(1600) m. Flowering February-June.

Likely one of the most important species historically cultivated, though more frequently for its resin than for ornamental quality. As an ornamental, *Styrax benzoin* is very rare in cultivation, with only four accessions known worldwide, all in African or Asian gardens. Though it is an interesting specimen due to its history of resin exudation, it is probably not hardy past USDA Zone 9-10 (Raulston 1991), and would likely only be suitable for conservatory use in North America.

Styrax chinensis Hu & S.Ye Liang
Reference: Acta Phytotax. Sin. 18(2): 230(1980)
Type: China: Guangxi: Du'an Xian, dense forests, 740-800 m, 27 April 1979, *S. Y. Liang 7904271*

Evergreen Chinese Snowbell. Evergreen tree, 10-20 m; branchlets subterete, densely yellow-brown stellate pubescent. Leaves alternate; oblong elliptic to obovate elliptic, densely gray-brown stellate tomentose; lamina 8-23 × 3-12 cm (2.0-2.7 × longer than wide); margin entire, apex obtuse to shortly pointed; 7-12 secondary vein pairs, tertiary veins subparallel; petiole quadrangular, 1.0-1.5 cm. Flowers white, 1.2-

1.5 cm; pedicel 1-3 mm; inflorescences pseudoterminal and axillary racemes or panicles, 4-12 cm; calyx 5-toothed, 6-7 × 6-7 mm, densely yellowish stellate tomentose; corolla 5-lobed, 10-12 × 2-3mm, lobes valvate in bud; stamens exserted; capsule 1.8 × 1.8 cm, globose, densely tomentose and sparsely pubescent with gray stellate hairs, apex obtuse to shortly pointed; seeds brown, globose, rugose, glabrous.

Native to dense forests of South-central China (Guangxi & Yunnan) and Laos; 300-1200 m. Flowering April-May.

Very rare in cultivation, with two accessions known: one at an east Asian garden, and one in the west at Arboretum Wespelaar. The plant is young and in a sheltered environment, though its native range suggests it may not be hardy past USDA Zones 9-10. The JC Raulston Arboretum has also historically collected (960300).

Styrax suberifolius Hooker & Arnott
Reference: Bot. Beechey Voy. 196, t. 40. 1837
Type: China: Taiwan: Tamsui, 1864, *R. Oldham 293*

Evergreen tree, 4-20 m; branchlets red brown to grey brown stellate tomentose. Leaves alternate; elliptic, oblong, or elliptic lanceolate, densely brownish stellate tomentose; lamina 5-15(18) cm x 2-5(8) cm (2.5-3.0 × longer than wide), margin subentire, apex acuminate, base cuneate; 5-12 secondary vein pairs, tertiary veins subparallel; petiole subquadranglar, 1.0-1.5(2.0) cm, vasculature in an arc with two invaginated ends, accompanied by two bundles (Schadel & Dickison 1979). Flowers white, 1.0-1.5 cm; pedicel 1-3 mm; in many-flowered axillary and terminal racemes, 6-12cm; calyx 5-toothed, 3-5(7) × 2-4(7) mm, densely gray yellow tomentose; corolla lobes 4(5), lanceolate to oblong, 11-13 × 2-3mm, valvate in bud; stamens 8(10), exserted; capsule 1-1.8 cm; ovoid-globose; densely gray to brown stellate tomentose; seeds brown, glabrous.

Native to Southeastern and South-central China, Taiwan, Myanmar, and Vietnam; 100-3000m. Flowering March-May. 2 lower taxa.

- *Styrax suberifolius* var. *suberifolius*
  = *Styrax caloneurus* Perkins, Bot. Jahrb. Syst. 31. 484. 1902
  = *Styrax suberifolius* var. *caloneurus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 61. 1907
  = *Styrax suberifolius* var. *fargesii* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 61. 1907
  = *Styrax oligophlebius* Merrill ex H.L.Li, J. Arnold Arbor. 24: 451. 1943
  Lamina densely brownish stellate tomentose. China, Taiwan, Vietnam; 100-3000 m

- *Styrax suberifolius* var. *hayataianus*
  Reference: Trans. Nat. Hist. Soc. Taiwan 25: 418
  = *Styrax hayataianus* Perkins, Repert. Spec. Nov. Regni Veg. 8: 82. 1910
  = *Styrax formosanus* var. *hayataianus* (Perkins) H.L. Li, Woody Fl. Taiwan 753. 1963
  Lamina densely greyish-white stellate tomentose. Taiwan; 1000 m.

Rare in cultivation, with the majority of gardens accessioning located in East Asia. The species is somewhat present in the west as well, having been trialed by Raulston (1991,1992). There is one plant living at the University of California Botanical Garden at Berkeley (UCB# 81.0024).

The origin of the specific epithet is unclear, as “Suber” typically refers to cork which does not seem to describe the leaves.

***Styrax* series *Valvatae* P.W.Fritsch**

> Mesocarp juicy; endocarp at maturity adherent to the seed, not the mesocarp; seeds ellipsoid; seed coat not crackled. 77 species, Neotropics (Fritsch 2001). Four species cultivated (5% of series): three very rare, one historic.

Styrax argenteus C. Presl.
Reference: Reliq. Haenk. ii. 60.
Type: Mexico. Guerrero: "Ad portum et urbem Acapulco" (protologue), *T Haenke s.n.*
= *Styrax polyanthus* Perkins, Bot. Jahrb. Syst. 31: 479. 1901
= *Styrax myristicifolius* Perkins, Bot. Jahrb. Syst. 31: 481. 1902

Silver Snowbell. Evergreen tree to 20(30) m. Branchlets grey yellow, yellow brown, orange brown, or light brown stellate pubescent. Leaves alternate; ovate to elliptic or lanceolate, weakly green to grey-green stellate pubescent (though veins generally glabrous) (Figure 20); lamina 6.5-18.0 × 2.4-7.5 cm (2.4-2.7 × longer than wide), margin entire, apex acute to acuminate, base cuneate to rounded (sometimes slightly oblique); 9-11 secondary vein pairs; petiole 1.0-2.5 cm, vasculature in an arc with invaginated ends accompanied by two bundles (Schadel & Dickison 1979). Flowers white, reflexed to recurved with petals not overlapping, ca. 1.5 cm; pedicel 2-11(15) mm; in 3-22-flowered pseudoterminal or axillary racemes (rarely panicles), 3.0-14.0cm; calyx 5-toothed, 2.5-5.0mm × (3.5)4.0-6.0(7.0) mm, greyish green stellate pubescent; corolla, 1.0-1.6 cm, lobes 5, 8-14 mm x 1.7-2.3 mm, valvate in bud; anthers 6.8-8.0 mm long; drupes ellipsoid to ovate-ellipsoid, rugose, 1.3-1.8 × 0.8-1.4 cm; seeds glabrous. $n=x=8$.

Native to tropical, deciduous, and evergreen forests of tropical Mexico to Panama and Belize. Flowering August-March.

Figure 20 *Styrax argenteus* C. Presl. September, 1992 in Raleigh, NC, USA. Photo by J.C. Raulston (Slide 105-0298), provided by JC Raulston Arboretum.

Styrax argenteus is very rare in cultivation, with only one collection known in a Mexican Botanical Garden. Still, the species is quite common through Mexico and Central America and thus a likely collection during expeditions to this region, and worth mention here due to the history of taxonomic confusion as well as difficult identification of the species.

The interpretation of this species changed significantly in Fritsch's (1997) revision, who argued that Gonsoulin's (1974) interpretation of the species, which had essentially lumped all evergreen Mexican taxa save for *Styrax conterminus* Donnell Smith. together as *Styrax argenteus*, was far too broad. Gonsoulin also named two lower taxa, *Styrax argenteus* var. *hintonii* (Bullock) Gonsoulin, and *Styrax argenteus* var. *ramirezii* (Greenman) Gonsoulin, both currently considered synonymous with *Styrax ramirezii* Greenman (described below).

Additionally, though neither appear to currently be in cultivation to any significant extent, Fritsch (1997) warns it is quite difficult to separate between *Styrax argenteus*, *Styrax nicaraguensis*, and *Styrax warscewiczii* (two species considered synonymous with *Styrax argenteus* per Gonsoulin). The easiest way to separate *Styrax argenteus* from *Styrax nicaraguensis* is to seek out orange-brown trichomes on the leaves and calyx, possessed by *Styrax nicaraguensis* but not *Styrax argenteus*. Separation from *Styrax warscewiczii,* is more difficult, and often impossible unless the plant in question is flowering. The key by Fritsch (1997) recommends examination of the androecium, as the stamens of *Styrax argenteus* possess longer hairs to the filaments (1-2 mm long as opposed to 0.5 mm), as well as connective prolonged past the anthers sacs, a characteristic lacking in *Styrax warscewiczii*. Of the two species, confusion with *Styrax nicaraguensis* during collection is less likely due to its restricted range (high elevation cloud forests (1100-1550 m) of NW Costa Rica and NW Nicaragua).

The specific epithet *argenteus* refers to a silvery color, possibly in reference to the leaf or branchlet indumentum, and thus the common name “silver snowbell” is appropriate if one is desired.

Styrax glaber Swartz
Reference: Prodr. [O. P. Swartz] 74. 1788
= *Styrax roraimae* Perkins, Bot. Jahrb. Syst. 31: 478. 1901
= *Styrax micrasterus* Perkins, Repert. Spec. Nov. Regni Veg. 2: 24. 1906
= *Styrax glaber* Swartz var. *micranthus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 63. 1907
= *Styrax fanshawei* Sandwith, Kew Bull. 1948: 321.
= *Styrax costanus* Steyermark., Fieldiana, Bot. 28: 490. 1953
= *Styrax tepuiensis* Steyermark. & Maguire, Mem. New York Bot. Gard. 17(1): 456, fig. 7. 1967

Tree or shrub 6-18 m. Leaves alternate; elliptic to elliptic-oblong, pale stellate pubescent; lamina 8-15cm × 3.5-5.5cm (2.3-2.7 × longer than wide), margin subentire, apex acuminate, base cuneate, petiole 1.2-1.4 cm; vasculature in an arc with two invaginated ends or medullated cylinder accompanied by two vascular bundles (Schadel & Dickison 1979). Flowers white, ca. 1.5 cm; pedicel 9-14 mm; in 4-7-flowered axillary racemes, 2-3.5(7) cm; calyx truncate or minutely toothed, 4-5 × 4-6 mm; corolla lobes oblong-linear, 16-18 mm, valvate in bud; stamens inserted; drupes 2 × 1 cm, ovoid or globose-ovoid; seeds pale brown, smooth, 1 per fruit.

Native to dwarf forests of Brazil, Guyana, Suriname, Venezuela, and the Caribbean; 300-2200 m. Flowering April-June.

Very rare in cultivation. Only one accession is known, at a botanic garden in the Lesser Antilles. No horticultural information available; based on its provenance, likely suitable only for conservatory use in North American gardens.

Styrax lanceolatus P.W. Fritsch
Reference: Ann. Missouri Bot. Gard. 84(4): 733, nom. nov. 1998
Type: Mexico. Queretaro: Mpio. de Arroyo Seco, ± 2 km al W de Agua Fría de los Fresnos, 23 Apr. 1992, *E. Carranza 4033*

Lanceolate Snowbell. Evergreen tree to 6 m; branchlets grayish green or brown stellate pubescent. Leaves alternate; lanceolate, greenish white stellate pubescent;

lamina 7.7-9.7 × 3.0-3.9 cm (2.5 × longer than wide), margin entire, apex narrowly acute to acuminate, base broadly cuneate to rounded (sometimes weakly oblique); 8-9 secondary vein pairs; petiole 7-12 mm. Flowers white, ca. 1.5 cm; pedicel 3-5 mm; in 1-8-flowered pseudoterminal or axillary racemes or panicles, 1.7-5.0 cm; calyx 5-toothed (teeth sometimes absent), 3.5-4.5 × 4.5-6.0 mm, grayish green-stellate pubescent; corolla lobes 5, linear-deltoid, valvate in bud; anthers 0.3-0.5mm long; drupes 9-10(11) × 7-8(9) mm; ovoid-cylindric, rugose; seeds glabrous.

Rarely in wet forests, hillsides, and disturbed areas of Mexico (Tamaulipas and Queretaro). Flowering in October.

Raulston (1992) mentions a species *Styrax globosa,* in cultivation at Yucca Do Nursery (then located in Hemstead, TX, USA). The genesis of this name is uncertain, and it is conspicuously absent from online citation databases such as IPNI and Tropicos. According to Grimshaw & Bayton (2009), the species Raulston was referring to is actually *Styrax lanceolatus* P.W.Fritsch. Though it is not currently in cultivation, the species apparently is quite ornamental when bearing flower buds, as the yellow anthers are visible through the white petals, making the buds appear a pastel orange in color. It is likely best suited for the San Francisco Bay Area or mild areas of England (Raulston 1992). The specific epithet likely references the lanceolate shape of the leaves.

Styrax ramirezii Greenman
Reference: Proc. Amer. Acad. Arts xxxiv. 568.
Type: Mexico. Morelos: Mountain canyons above Cuernavaca, 15 May 1898, *C. G. Pringle 6848*
= *Styrax cyathocalyx* Perkins, Repert. Spec. Nov. Regni Veg. 2: 24. 1906
= *Styrax micranthus* Perkins, Repert. Spec. Nov. Regni Veg. 2: 17. 1906
= *Styrax orizabensis* Perkins, Repert. Spec. Nov. Regni Veg. 2: 25. 1906
= *Styrax ramirezii* var. *micranthus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 54. 1907
= *Styrax ramirezii* var. *orizabensis* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 54. 1907
= *Styrax hintonii* Bullock, Bull. Misc. Inform. Kew 1936: 9
= *Styrax argenteus* C.Presl var. *hintonii* (Bullock) Gonsoulin, Sida 5: 226. 1974
= *Styrax ramirezii* var. *hintonii* (Bullock) Gonsoulin, Sida 5: 226. 1974
= *Styrax argenteus* var. *micranthus* (Perkins) D'Arcy, Ann. Missouri Bot. Gard. 66: 169. 1979
= *Styrax argenteus* var. *ramirezii* (Greenman) Gonsoulin, Sida 5: 227. 1974

Ramirez Snowbell. Evergreen tree to 20(25-27) m; branchlets yellow-brown, orange-brown, or dark-brown stellate pubescent, older twigs not exfoliating. Leaves alternate; ovate-oblong to elliptic (sometimes ovate), greenish white stellate pubescent (rarely glabrous); lamina (10.1)11.0-22.5cm × 2.9-9.5(10.5)cm (2.4-2.8 × longer than wide), margin entire, apex rounded to acuminate, base cuneate to rounded (sometimes slightly oblique); 10-15 secondary vein pairs; petiole 5-25 mm. Flowers white to pink, ca. 1.5 cm; pedicel 4-11 mm; in (2)5-17-flowered pseudoterminal or axillary racemes (rarely panicles), 2.5-12.0 cm; calyx 5-toothed, (1.5)3-6 × (3)3.5-6.5 mm, greyish-green stellate pubescent; corolla lobes 5, (8)11-14 mm, valvate in bud; anthers 3.0-4.8 mm long; drupe (7)9-15 × 5-9 mm, ellipsoid, rugose; seeds glabrous.

Common in deciduous and cloud forests of Mexico. Flowering time variable. Named for Sr. Dr. José Ramirez, Director of El Instituto Médico Nacional, City of Mexico (Greenman 1899).

In 1991, the Arnold Arboretum obtained and accessioned both divisions and seed of the species from an expedition to Mexico (520-91 and 535-91, respectively). Though these were likely the first attempts to introduce the species to cultivation, neither accession entered the collection, likely due to hardiness failure. *Styrax ramirezii* remains very rare in cultivation today, with only two accessions known: 73.0293 at the University of California Botanical Garden at Berkeley, and 1985-0136 at the San Francisco Botanical Garden.

Conclusions

Several species of *Styrax* are worthy of further growth and evaluation. Priorities should likely focus on those species which differ significantly from *Styrax japonicus*, for example the unique leaf type possess by *Styrax shiraianus*, profuse flowering and shrubbier habit of *Styrax wilsonii*, in subtropical areas perhaps the evergreen nature of *Styrax suberifolius*, and in tropical or conservatory conditions, the precocious and large flowers of *Styrax macrocarpus*. Isolating cultivars which display the heavily pubescent nature of *Styrax americanus* or the reblooming potential of *Styrax confusus* would help to increase the landscape potential of those species, already somewhat present in cultivation. Sterile cultivars would be desirable for *Styrax japonicus* to alleviate concerns as to weedy potential, as well as for *Styrax wilsonii* to prevent injury due to heavy fruit load. More research as to effective rooting procedures and seed stratification techniques is desirable to improve production techniques, as in numerous cases whether single vs. double dormancy is exhibited by certain species is unclear.

The history of resin exudation and confusion as to which species produce it raises interesting questions as well. Wounding of specimens of known wild origin of *Styrax officinalis* could help to confirm Zeybeck’s (1970) theory as to certain races more prone to resin production following injury, and shed more light on whether or not *Styrax officinalis* “storax” was historically utilized.

Chapter 3

ANATOMICAL CONTRIBUTIONS TO TAXONOMY

Introduction

Several authors such as Howard (1979) have proposed anatomical or morphological examination of the petiole as a diagnostic characteristic, particularly in the case when sterile or non-flowering material must be identified. Such diagnosis is based on both the shape of the vasculature and presence and number of accompanying bundles. As many species of *Styrax* are difficult to separate even when in flower, such a characteristic would prove valuable.

Schadel & Dickison (1979) sectioned and examined the petioles of multiple species of *Styrax*, determining five basic patterns as observed in the distal portion: an arc with invaginated ends, an arc with invaginated ends accompanied by two dorsal cortical bundles, a medullated cylinder, a medullated cylinder accompanied by two dorsal cortical bundles, and a medullated cylinder accompanied by medullary vascular tissue and two dorsal cortical bundles. The possibility that the characteristic may differ between different individuals of the same species should be considered, particularly since some species observed by Schadel & Dickison as displaying different vascular patterns are now considered synonymous based on subsequent revisions of the genus (Hwang & Grimes (1996), Fritsch (1997). To test the effectiveness of petiole vasculature as a diagnostic characteristic, as well as to gain an understanding of its diversity over a given species, petioles from several *Styrax* species were sectioned and examined.

Wood anatomy of stems of the Styracaceae was examined qualitatively by Dickison & Phend (1985) and concluded to be rather uniform, though one unique aspect is the simple as opposed to scalariform perforation plates in two species (*Styrax platanifolius* and *Styrax redivivus*), which when considered as a group are now understood as the American component of *Styrax* sect. *Styrax* ser. *Styrax*. In order to determine whether such peculiarities existed in species of *Styrax* sect. *Styrax* ser. *Cyrta*, a larger series spanning East Asia, the Southeastern United States, and Mexico, wood samples were collected, sectioned, and examined.

Though the base number for the genus *Styrax* is typically $n=x=8$, *Styrax japonicus*, the most widespread member of the genus in temperate regions of East Asia, has been implied as a pentaploid or higher, listed as $2n>40$ (Manshard 1936). However, Yamazaki (1993), listed as $2n=16$, more in line with the base number for the genus. Huang et al. (2003) questioned the validity of the earlier number, though Baranec & Murin (2003) would soon confirm as $2n=40$. None of these publications included figures, drawings, or photographs. The only count with a supporting diagram appears to be by Shiuchi & Fujita (2006), who determined $2n=48$ for *Styrax japonicus* var. *tomentosus,* confirming hexaploidy for the species.

Though not a recognized lower taxa by Huang et al. (2003), who recognize none, *Styrax japonicus* var. *tomentosus* appears closely allied with *Styrax japonicus* var. *kotoensis*. Yamazaki (1993) treats it as a forma of such, *Styrax japonicus* var. *kotoensis* f. *tomentosus* (Hatusima) Yamazaki. Both plants are described as possessing a thick stellate tomentose vestiture to branchlets, petioles and undersides of leaves, as well as larger leaves and corollas as compared the straight species (4-11 × 3-7 cm as opposed to 3-9 × 2-4 cm and 2.5-3 cm across as opposed to 2-2.5 cm, respectively). This latter characteristic is consistent with the *gigas* effect noted in many polyploids.

Multiple ploidy levels are not unheard of in a species with a widespread range, however the actual chromosome number or numbers remain of interest for a variety of topics including potential phylogenic hypotheses involving autoduplication events and breeding applications. Even for intraspecific breeding, the multiple ploidy levels of *Styrax japonicus* could potentially establish prezygotic barriers. Though Ranney (pers. comm.) determined through use of flow cytometry that no differences in ploidy level exist between the common *Styrax japonicus* cultivars (refuting the hypothesis that *Styrax japonicus* 'Emerald Pagoda' was of a higher ploidy level than other cultivars), the ploidy level represented by these cultivars, be it diploid, pentaploid, hexaploid, or other, is still unknown. In order to both shed some light on this issue as well as to provide diagrams for diploid and possibly pentaploid specimens, an attempt was made to determine the chromosome number using a variety of squash techniques.

Materials & Methods

Petiole

Petioles were collected from several species (Table 6) contained in the collections of the University of Delaware Botanic Gardens, Arnold Arboretum, Polly Hill Arboretum, and JC Raulston Arboretum. Petioles from the Arnold Arboretum and Polly Hill Arboretum were stored in vials containing 50% ethanol for preservation and transport. Those obtained from the JC Raulston Arboretum arrived in the mail and were shipped dry. Though the lamina had visibly desiccated, the petioles were still intact and were removed and placed in 50% ethanol. Specimens from the University of Delaware Botanic Gardens were sectioned and observed immediately following collection.

Table 6 Sources of *Styrax* petioles for sectioning and examination. PHA: Polly Hill Arboretum (West Tisbury, MA, USA), UDBG: University of Delaware Botanic Gardens (Newark, DE, USA), JC Raulston Arboretum (Raleigh, NC, USA), Arnold Arboretum (Jamaica Plain, MA, USA).

Taxon	**Source**	**Acc. Num.**
S. americanus	PHA	70-085*A
S. americanus	UDBG	96-15*1
S. calvescens	JCR	(None)
S. confusus	AA	1082-89*C
S. confusus	AA	1082-89*D
S. confusus	PHA	2009-56*A
S. confusus	UDBG	06-8*1
S. dasyanthus	AA	162-2008*A
S. grandifolius	PHA	2009-35*A
S. grandifolius	UDBG	06-95*1
S. hemsleyanus	PHA	2003-70*A
S. hemsleyanus	UDBG	99-104*1
S. japonicus	UDBG	88-83*1
S. platanifolius ssp. *texanus*	PHA	2009-90*A
S. serrulatus	JCR	940340
S. wilsonii	PHA	2007-30*A

Petioles were sectioned freehand with double-edged razor blades, aided by use of a dissecting microscope. The pulvinus was first removed and discarded. Next several transverse sections were cut from the basal, medial, and distal thirds of the petiole. Sections were cut as thin as possible, and transferred to water to prevent desiccation. Approximately three sections from each of the three regions of the petiole were cut, with the sections cut thinnest and most evenly selected for observation. Typically only one petiole from each accession was sectioned; though in cases where observable sections could not be produced due to freehand sectioning, additional attempts were made.

Sections were then stained with 0.1% Toluidine Blue O (0.1g/100ml H_2O) for ca. five minutes or until satisfactory staining of the vasculature was evident. A wet mount was prepared for each section, with the edges of the cover slip sealed with nail polish to prevent desiccation. Slides were examined under 40× magnification, with diagnostic drawings (available in Appendix B) prepared through use of a Wild M20 drawing tube. The overall shape of the major leaf vein and number of accompanying vascular bundles were recorded.

For the major vein, the terms “arc with invaginated ends” or “medullated cylinder,” as used by Schadel & Dickison (1979), were used to describe the shape. Both the number and location of accessory bundles were recorded. Three different categories were proposed in order to accurately depict their location: “accompanying bundle,” referencing one present near the margins of the transverse section and well into the cortical tissue, “associated bundle,” referencing those which are in close proximity to the main vasculature but not a part of it, and “integrated bundle,” one present within the phloem region of the main vasculature.

Wood

A stem segment approximately 1 cm in diameter was cut from an individual of each of the eleven following species growing at the JC Raulston Arboretum or University of Delaware Botanical Gardens: *Styrax americanus*, *Styrax calvescens*, *Styrax confusus*, *Styrax dasyanthus*, *Styrax formosanus*, *Styrax grandifolius*, *Styrax japonicus*, *Styrax serrulatus*, *Styrax tonkinensis*, *Styrax wilsonii*, and *Sinojackia rehderiana* Hu (Table 7). The latter, an East Asian member of the Styracaceae, was sampled as an outgroup. The samples were preserved in vials of 50% ethanol. Cross sections were cut to a thickness of 40μm with an American Optical Model 860 sliding microtome.

Table 7 Sources of stem material examined and diameter of cross sections. UDBG: University of Delaware Botanic Gardens (Newark, DE, USA), JCR: JC Raulston Arboretum (Raleigh, NC, USA).

Species	**Distribution**	**Source**	**Acc. Num.**	**Cross sect. diam.**
Styrax				
S. americanus	North America	UDBG	96-15*1	8 mm
S. calvescens	East Asia	JCR	(None)	5 mm
S. confusus	East Asia	JCR	001628	8 mm
S. dasyanthus	East Asia	JCR	930409	7 mm
S. formosanus	East Asia	JCR	011483	8 mm
S. grandifolius	North America	UDBG	06-95*1	11 mm
S. japonicus	East Asia	UDBG	88-83*1	10 mm
S. serrulatus	East Asia	JCR	940340	5 mm
S. tonkinensis	East Asia	JCR	960302	6 mm
S. wilsonii	East Asia	JCR	001612	6 mm
Sinojackia				
Si. rehderiana	North America	JCR	880421	8 mm

Specimens were stained with 0.5% safranin (0.1g/100ml of 50% ethanol) for one hour, and then transferred into 100% ethanol for five minutes in order to completely dehydrate the samples. The ethanol was then drained, and the samples were transferred to toluene. A slide was then prepared holding several cross sections, with one drop of Cytoseal 60 mounting medium applied per section. The slide was then sealed with a cover slip, and given one hour to dry and become permanent before examination.

Cross sections were examined under 200× magnification, with each field representing a view 0.55 mm in diameter and with an area of approximately 1.73 mm^2. Eight fields were examined for each species: four from the first growth ring, and four from later growth rings. A tracing was prepared for each field of view in order to aid in interpretation of the wood. Rays and vessels were traced with a Wild M20 drawing tube. The number of uniseriate or multiseriate rays per each field of view was counted, with the width (number of cells) of the latter recorded. As there was sometimes difficulty in distinguishing axial parenchyma cells occurring in radial rows from the radial parenchyma cells of rays; therefore all radially aligned parenchyma cells were interpreted as rays. Vessels were counted and distinguished from fiber-tracheids by the thinner walls of the former, as well as their distinct scalariform intervessel pitting. The number of vessels which occurred solitarily rather than as part of a multiple was also recorded.

The following characteristics were measured from each tracing: ray width, vessel width, and vessel length as seen in cross section. All of these were measured on the drawings through use of a ruler, and then converted from mm to μm. A proportion to convert was obtained through use of a stage micrometer, producing a drawing of 0.4 mm at 200× magnification; 0.1 mm on this drawing was equivalent to 3.2 cm on the ruler used for measurement, resulting in a conversion proportion of 32 mm/100 μm.

Due to the semi-rectangular appearance of the vessel in cross section, measurements of the radial and tangential walls were determined to be the most appropriate method for representing their size. The cross sections were also used to determine if the wood of each species is diffuse porous or ring porous. As these terms can often be somewhat imprecise, the definitions proposed by Carlquist (1988) are referenced in order to more accurately describe the stem wood of *Styrax*.

Measurements were entered into JMP 10 Statistical Software for analysis. Additional characteristics calculated were percentage of rays multiseriate (calculated by dividing the number of multiseriate rays by the total number of rays), mean number of vessels per multiple (calculated by dividing the vessel element density by vessel element multiple density), percentage of vessels solitary (calculated by dividing the number of solitary vessels by the total number of vessels), and the ratio of the vessel width to length in cross section (henceforth referred to as the vessel ratio). To determine the effect of species on all characteristics examined, ANOVA analysis was run at α=.05. F-tests were run to determine whether any characteristic differed significantly from species to species, with Student's T-tests run with a connecting letter report to determine which species could be statistically separated through use of each characteristic. The overall number of characteristics in which species could not be significantly separated from each other was tallied, and a percentage of similarity between each species sampled was calculated. The following ten characteristics were used for this index: uniseriate ray density, uniseriate ray width, multiseriate ray density, multiseriate ray width (both metric and number of cells wide), vessel element density, vessel element multiple density, the percentage of solitary vessels, vessel tangential wall length, and vessel radial wall length.

Additionally, ANOVA was run between all various characteristics and cross section diameter as well as source to determine if either accounted for variability observed to the same extent as species.

Chromosome Count of *Styrax japonicus*

Two stains were utilized to aid in examination of chromosomes: acetocarmine and Schiff's reagent, though the latter was only used during root squash techniques. Acetocarmine was prepared according to the procedure listed by Jensen (1962), which follows Darlington & Lacour (1960) and Johansen (1940): 55 ml of distilled water, 45ml of glacial acetic acid, and 0.5 g of carmine mixed together, brought to a boil, and allowed to boil gently for five minutes. The solution was then shaken, allowed to cool, and filtered.

Schiff's reagent was prepared according to the procedure listed by Jensen (1962), following that of Longley (1952): 0.5 g of basic fuchsin and 0.5 g of sodium metabisulfite were dissolved in 100 ml of .15*N* HCl. Next, 300 mg of decolorizing charcoal was added. The mixture was shaken vigorously for five minutes, and then filtered. The now colorless mixture was refrigerated and stored in a foil-covered bottle in order to prevent spoilage.

Flower buds were collected, as a source for anthers to be squashed, from the JC Raulston Arboretum on 3/26/12. Though the spring was uncharacteristically warm and progressing rapidly, all accessions of *Styrax* observed there, save for 960302 (purportedly *Styrax tonkinensis*) had not begun to flower and reproductive buds were still tightly sealed. Buds were preserved in 50% ethanol for later analysis.

With the aid of fine forceps and a dissecting microscope, the flower buds were dissected and the minute, still unpigmented, anthers removed. One anther was then transferred to a slide. A wet mount was prepared using one drop of acetocarmine. After a coverslip was affixed, significant pressure was applied using a pencil eraser in order to squash the naturally soft tissue and spread out the cells without risking breakage of the cover slip. A match was lit and held under the slide to heat the preparation, but removed prior to causing the acetocarmine to boil. The underside of the slide was then wiped to clean the resulting residue, and the edges of the coverslip were sealed with clear nail polish to prevent desiccation.

After the nail polish dried, the slide was examined using at 1000× magnification. Actively dividing cells with satisfactorily stained chromosomes were photographed. Slides were stored in a refrigerator to preserve the slide and to remain available for later examination. In some cases, the anthers were incubated in acetocarmine for 1, 3, or12 hours prior to preparation of the wet mount. Several anthers were squashed and observed.

Cuttings of *Styrax japonicus* ‘Pink Chimes’ (ca. 4” length) were taken on 6/7/12, treated with 1000 ppm IBA in talc (Hormodin 1), and rooted in perlite under mist (Mist rate: 15 seconds every 10 minutes during daylight). After three weeks in mist, rooted cuttings were transplanted into 2.5” plastic pots, again using perlite as the medium. These rooted cuttings were treated with a Dosatron fertilizer injector on a weekly basis.

Root tips were harvested from the cuttings exhibiting the most rapid growth. The plant was removed from its container, and the terminal 1 cm of an elongating root was removed and placed in tap water and transported to the lab. Immediately thereafter, the root tips were stained in acetocarmine for six hours. The root tips were then removed from the solution, and the terminal 1-2 mm was harvested from each root section. Each root tip was then transferred to a slide, with a wet mount prepared using one drop of 45% acetic acid. After a coverslip was affixed, the squash technique proceeded as described for the anther though in some cases the tissue necessitated smearing in order to truly tease apart the cells. Heating, examination, and preservation occurred as described above. Several root tips were squashed and observed.

In a few preparations, the freshly harvested root tips received a three hour pretreatment with p-dichlorobenzene prior to staining in hopes it would arrest dividing cells at metaphase. An alternate technique, utilized only for a few root tip squashes, involved staining with Schiff's reagent, according to the procedure listed by Jensen (1962), which follows Darlington & Lacour (1960) and Johansen (1940). In this case, after the root tips were harvested, they were fixed for 30 minutes in a 3:1 mixture of ethanol and glacial acetic acid. The root tips were then transferred to 70% ethanol, then immediately to 1 *N* HCl (at ca. 60°C) for 15 minutes. Next the root tips were transferred to Schiff's reagent, where they were stained in the dark for 60 min. Root tips were then removed from the solution and washed in distilled water. They were then bleached for 10 minutes in a mixture of 1 part sodium metabisulfite ($Na_2S_2O_5$), 3 parts 1 *N* HCl, and 3 parts distilled water. This process was repeated once for a total of two changes. Next the root tips were transferred to tap water for 30 minutes. Finally, each root tip was then transferred to a slide, with a wet mount prepared using one drop of 45% acetic acid. Squashing, heating, examination, and preservation occurred as described above.

Petals were harvested also from the flower buds collected for anther squashes. Petals were dissected from the flowers buds using fine forceps, and placed on a slide with a wet mount prepared using a drop of acetocarmine. As with the anther squashes, some preparations involved a 1, 3, or 12 hour incubation of the petal in acetocarmine prior to preparation of the wet mount. The squashing, preservation, and examination procedures took place in the same fashion as the anther and root tip squashes, though in this case far less pressure to the cover slip was required due to the naturally flattened nature of the petal.

Results

Petiole

Petioles of 16 accessions representing 10 species were successfully sectioned and their vascular patterns described (Table 8). Though a different stain than used by Schadel & Dickison (1979), Toluidine Blue O provided acceptable staining of the vascular tissue. Lignified secondary walls of the xylem vessels stained dark blue and were easily separated from the dirty grey-green phloem and the grey to light blue cells of the cortex. Individual phloem parenchyma cells, sieve tube members, or companion cells were difficult to observe, likely due to the thickness or slight bias of the section. As is the nature of freehand sectioning, multiple sections prepared were inadvertently cut on a bias or torn, though the majority of sections were easily observable.

Table 8 Sources of *Styrax* petioles and vascular patterns observed in cross section of distal portion (near lamina). PHA: Polly Hill Arboretum (West Tisbury, MA, USA), UDBG: University of Delaware Botanic Gardens (Newark, DE, USA), JCR: JC Raulston Arboretum (Raleigh, NC, USA), AA: Arnold Arboretum (Jamaica Plain, MA, USA).

Taxon	**Source**	**Acc. Num.**	**Vasculature Shape**	**Accomp. Bundles**	**Assoc. Bundles**	**Integ. Bundles**
S. americanus	PHA	70-085*A	Arc w/ invaginated ends	2	1	0
S. americanus	UDBG	96-15*1	Arc w/ invaginated ends	2	0	0
S. calvescens	JCR	(None)	Arc w/ invaginated ends	2	1	1
S. confusus	AA	1082-89*C	Arc w/ invaginated ends	2	2	0
S. confusus	AA	1082-89*D	Arc w/ invaginated ends	2	3	0
S. confusus	PHA	2009-56*A	Arc w/ invaginated ends	1	0	2
S. confusus	UDBG	06-8*1	Arc w/ invaginated ends	2	1	0
S. dasyanthus	AA	162-2008*A	Arc w/ invaginated ends	2	0	0
S. grandifolius	PHA	2009-35*A	Arc w/ invaginated ends	2	0	2
S. grandifolius	UDBG	06-95*1	Medullated cylinder	2	1	0
S. hemsleyanus	PHA	2003-70*A	Arc w/ invaginated ends	2	0	1
S. hemsleyanus	UDBG	99-104*1	Arc w/ invaginated ends	2	0	0
S. japonicus	UDBG	88-83*1	Arc w/ invaginated ends	2	0	0
S. platanifolius ssp. *texanus*	PHA	2009-90*A	Arc w/ invaginated ends	2	0	0
S. serrulatus	JCR	940340	Arc w/ invaginated ends	0	2	0
S. wilsonii	PHA	2007-30*A	Xylem in arc, sheathed by ring of phloem	2	3	0

Only two petioles examined exhibited a medullated cylinder, making the arc the more common condition for the central vascular component. The petiole of *Styrax wilsonii* displayed a condition seemingly distinct, in which the xylem appeared as an arc with invaginated ends, though the phloem completely sheathed and formed a ring around the xylem (Figure 21). *Styrax platanifolius* ssp. *texanus* exhibited a wide ring of non-conductive sclerenchyma within the main trace which was not observed in any other petiole sectioned to the same degree (Figure 22). Whether the central trace for each species displayed an arc with invaginated ends or a medullated cylinder was consistent except in the case of *Styrax grandifolius.* The petiole of *Styrax grandifolius* obtained from the Polly Hill Arboretum (2009-35*A) exhibited an arc with invaginated ends (Figure 23), whereas the specimen from the University of Delaware Botanic Gardens instead displayed a medullated cylinder (Figure 24).

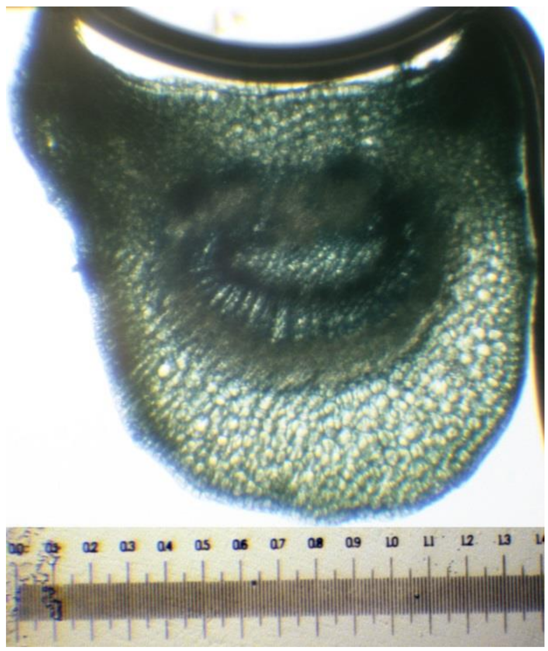

Figure 21 Cross section of the distal portion of a petiole from *Styrax wilsonii* Rehder (PHA# 2007-30*A), the xylem in an arc with invaginated ends and sheathed by a ring of phloem. 40× Magnification, stained with 0.1% Toluidine Blue O. Scale bar representing 1.4 mm. Photograph by the Author & T.D. Pizzolato. Interpretive drawing available in Appendix B.

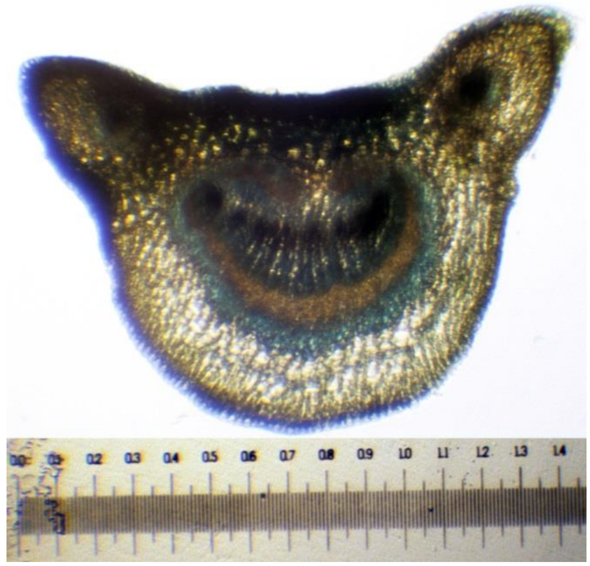

Figure 22 Cross section of the distal portion of a petiole from *Styrax platanifolius* Engelmann ex Torrey ssp. *texanus* (Cory) P.W.Fritsch (PHA #2009-90*A), exhibiting a broad band of phloem sclerenchyma. 40× Magnification, stained with 0.1% Toluidine Blue O. Scale bar representing 1.45 mm. Photograph by the Author & T.D. Pizzolato. Interpretive drawing available in Appendix B.

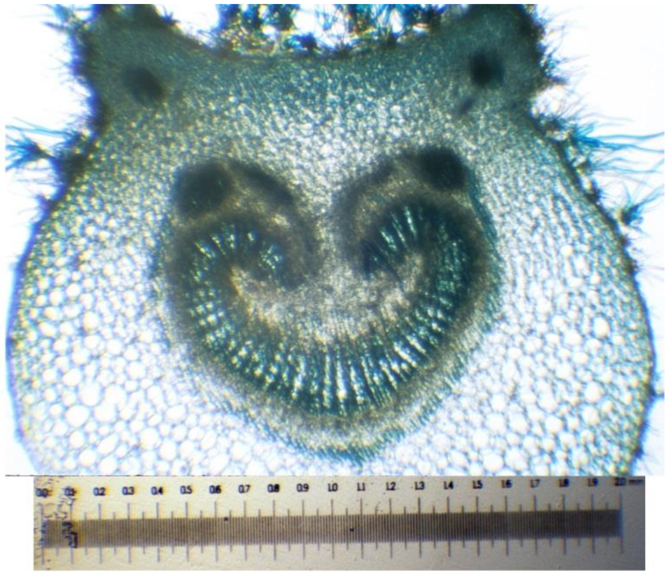

Figure 23 Cross section of the distal portion of a petiole from *Styrax grandifolius* Aiton (PHA 2009-35*A), the vasculature in the shape of an arc with two invaginated ends and joined by two accompanying and two integrated bundles. 40× Magnification, stained with 0.1% Toluidine Blue O. Scale bar representing 2.0 mm. Photograph by the Author & T.D. Pizzolato. Interpretive drawing available in Appendix B.

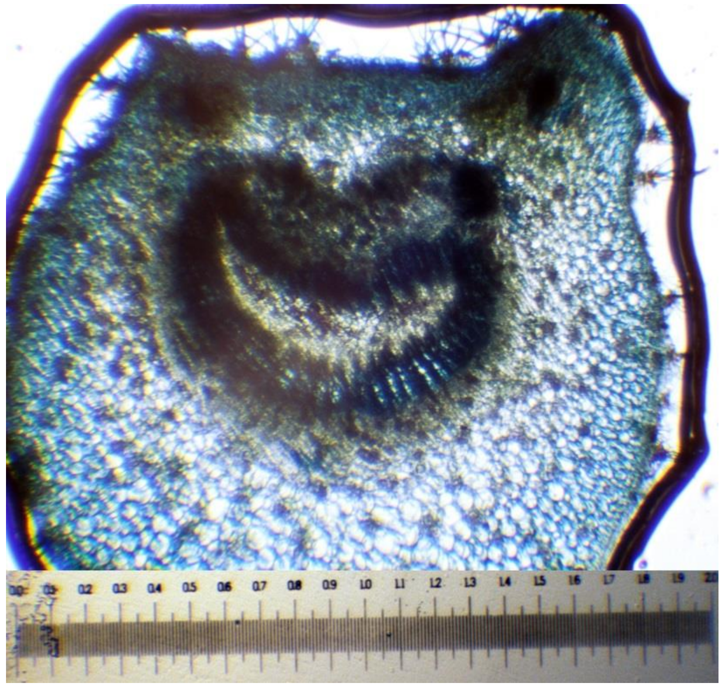

Figure 24 Cross section of the distal portion of a petiole from *Styrax grandifolius* Aiton (UDBG 06-95*1), the vasculature in the shape of a medullated cylinder. 40× Magnification, stained with 0.1% Toluidine Blue O. Scale bar representing 2.0 mm. Photograph by the Author & T.D. Pizzolato. Interpretive drawing available in Appendix B.

The greatest amount of variability observed was in the presence, number, and position of the small accessory vascular bundles. Every petiole sectioned exhibited at least two accessory bundles in addition to the main trace. In all cases these bundles were located in the dorsal as opposed to ventral portion of the petiole in relation to the main trace. Two accompanying bundles located in the cortical tissue a significant distance from the main trace were observed on all petioles save for that of *Styrax confusus* PHA# 2009-56*A, which exhibited only one, and *Styrax serrulatus* JCR #940340, which had no such bundles (Figure 25). Associated bundles, those bordering or immediately adjacent to the main trace were observed in eight (50%) of the petioles sectioned. Of these, four species (50%) had one associated bundle, two species (25%) had two, and two species (25%) had three. No petioles representing *Styrax dasyanthus*, *Styrax hemsleyanus*, *Styrax japonicus*, or *Styrax platanifolius* ssp. *texanus* exhibited any bundles in this fashion. Integrated bundles, small traces appearing within the vascular of the main trace, appeared more rarely and were only observed in four petioles (25%). *Styrax calvescens* and *Styrax hemsleyanus* PHA# 2003-70*A exhibited one bundle, whereas petioles of *Styrax confusus* PHA# 2009-56*A and *Styrax grandifolius* PHA# 2009-35*A contained two.

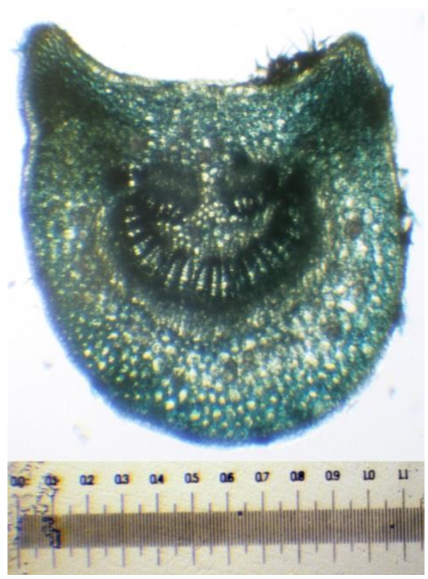

Figure 25 Cross section of the distal portion of a petiole from *Styrax serrulatus* Roxburgh (JCR# 940340), lacking prominent dorsal cortical accompanying bundles. 40× Magnification, stained with 0.1% Toluidine Blue O. Scale bar representing 1.15 mm. Photograph by the Author & T.D. Pizzolato. Interpretive drawing available in Appendix B.

Wood

Though an attempt was made to collect stems at as uniform as a size as possible (ca. 1 cm diameter), in many cases this was difficult due to the limited size and rarity of these taxa. Wider cross sections contained larger vessel elements, though oddly only significantly so in terms of the length of the tangential wall but not the radial wall. Wood samples with wider cross sections were also correlated with both a greater number and percentage of solitary vessel. Additionally, there was a positive correlation between cross section diameter and the vessel ratio.

The species of North American origin (*Styrax americanus, Styrax grandifolius*) differed significantly from the East Asian members of *Styrax* ser. *Cyrta* (Table 9). North American species possessed a significantly higher density of uniseriate rays (8.75 per 1.73 mm^2 as opposed to 6.07 per 1.73 mm^2) though the uniseriate rays were narrower (14.01 µm as opposed to 15.62 µm). The density of multiseriate rays and the total percentage of multiseriate rays were also significantly lower in the species distributed through North America (1.19 per 1.73 mm^2 as opposed to 1.53 per 1.73 mm^2 and 11.67% as opposed to 21.87%). Differences between multiseriate ray widths were insignificant.

Table 9 The effect of species distribution on uniseriate and multiseriate ray density, uniseriate and multiseriate ray width, and percentage of total rays multiseriate. Density refers to number of rays observed in a 1.73 mm^2 field of view. Means not connected by the same letter are significantly different according to Student's t-test ($\alpha = 0.05$).

Distribution	**Uni-seriate Ray Density**		**Uni-seriate Ray Width**		**Multi-seriate Ray Density**		**Multi-seriate Ray Width**		**Multi-seriate Ray Width (# cells)**		**% of Rays Multi-seriate**	
North America	8.75	A	14.01	B	1.19	B	22.55	A	2.03	A	11.67%	B
East Asia	6.07	B	15.62	A	1.53	A	25.06	A	2.08	A	21.87%	A

More variability resulting from species distribution was observed in regards to the vessel elements (Table 10). North American species appeared to contain a higher density than East Asian species (59.63 per 1.73 mm^2 as opposed to 37.81) in a greater number of multiples (17.38 per 1.73 mm^2 as opposed to 14.01). The tangential wall was significantly longer in North American species (27.58 µm as compared to 24.72 µm), though there were no significant differences in radial wall length. The vessel ratio also differed, with North American species on average with a tangential wall 1.23 × longer than the radial wall as opposed to 1.11× longer. Differences between the percentages of solitary vessel elements were not significant.

Table 10 The effect of species distribution on vessel element density, vessel element multiple density, vessel tangential and radial wall lengths, and ratio of tangential to radial wall length (vessel ratio). Density refers to number of rays observed in a 1.73 mm^2 field of view. Means not connected by the same letter are significantly different according to Student's t-test ($\alpha = 0.05$).

Distribution	**Vessel Element Density**		**Vessel Element Multiple Density**		**% Vessels Solitary**		**Vessel Tangential Wall Length**		**Vessel Radial Wall Length**		**Vessel Ratio**	
North America	59.63	A	17.38	A	4.30	A	27.58	A	22.52	A	1.23	A
East Asia	37.81	B	14.01	B	8.32	A	24.72	B	22.62	A	1.11	B

In the majority of cases, the significant differences observed in the rays when considering distribution as a factor could also be explained by source (Table 11). Again, there were significant differences occurring in uniseriate ray density and width (with a higher uniseriate ray density and narrower rays in sections collected from the University of Delaware Botanic Gardens). As with considering distribution as a factor, differences in multiseriate ray width were also insignificant when considering source. However, in this case the differences between multiseriate ray density and the percentage of total rays multiseriate were also not significant.

Table 11 The effect of cross section source on uniseriate and multiseriate ray density, uniseriate and multiseriate ray width, and percentage of total rays multiseriate. Density refers to number of rays observed in a 1.73 mm^2 field of view. JCR: JC Raulston Arboretum (Raleigh, NC, USA), UDBG: University of Delaware Botanic Gardens (Newark, DE, USA). Means not connected by the same letter are significantly different according to Student's t-test (α = 0.05).

Source	**Uni-seriate Ray Density**		**Uni-seriate Ray Width**		**Multi-seriate Ray Density**		**Multi-seriate Ray Width**		**Multi-seriate Ray Width (# cells)**		**% of Rays Multi-seriate**	
JCR	6.13	B	15.70	A	1.52	A	24.93	A	2.10	A	21.51%	A
UDBG	7.71	A	14.34	B	1.33	A	23.85	A	2.02	A	15.88%	A

Considering the effect of cross section source on the vessels, a significantly higher density was observed in those obtained from the University of Delaware Botanic Gardens as compared to the JC Raulston Arboretum, though the density of vessel multiples was not significantly different (Table 12). Much as was the case when considering distribution, the tangential wall was significantly longer in sections from UDBG though there were no significant differences in radial wall length. The vessel ratio also differed, with sections from UDBG exhibiting a tangential wall 1.26× longer than the radial wall as opposed to 1.09× longer. Differences between the percentages of solitary vessel elements were not significant.

Table 12 The effect of cross section source on vessel element density, vessel element multiple density, vessel tangential and radial wall lengths, and ratio of tangential to radial wall length (vessel ratio). Density refers to number of rays observed in a 1.73 mm^2 field of view. JCR: JC Raulston Arboretum (Raleigh, NC, USA), UDBG: University of Delaware Botanic Gardens (Newark, DE, USA). Means not connected by the same letter are significantly different according to Student's t-test (α = 0.05).

Distribution	**Vessel Element Density**		**Vessel Element Multiple Density**		**% Vessels Solitary**		**Vessel Tangential Wall Length**		**Vessel Radial Wall Length**		**Vessel Ratio**	
JCR	38.67	B	14.09	A	7.16	A	23.89	B	22.40	A	1.09	B
UDBG	50.04	A	16.04	A	8.72	A	28.84	A	23.13	A	1.26	A

All species examined exhibited the diffuse porous condition save for *Styrax dasyanthus* and *Styrax formosanus* which appeared somewhat ring porous (Table 13). These species had a noticeably lower density of vessel elements in the latewood, though the size of the vessels appeared roughly the same. This ring porous condition appeared to correspond to Carlquist (1988) Type 1C, in which the wood exhibits moderate differentiation into growth rings and the vessels are more numerous in the earlywood, but not noticeably larger. This condition is often less precisely described by other authors as semi-diffuse porous (Carlquist 1988). It is also noteworthy that in the first growth ring, both species appeared diffuse porous with no noticeable difference in vessel density between earlywood and latewood. The ring porous condition was most evident in *Styrax formosanus* (Figure 26).

Table 13 Porosity of *Styrax* stem wood as examined in cross section.

Species	**Porosity**
<u>*Styrax*</u>	
S. americanus	Diffuse
S. calvescens	Diffuse
S. confusus	Diffuse
S. dasyanthus	Ring (Carlquist Type 1C)
S. formosanus	Ring (Carlquist Type 1C)
S. grandifolius	Diffuse
S. japonicus	Diffuse
S. serrulatus	Diffuse
S. tonkinensis	Diffuse
S. wilsonii	Diffuse
<u>*Sinojackia*</u>	
Si. rehderiana	Diffuse

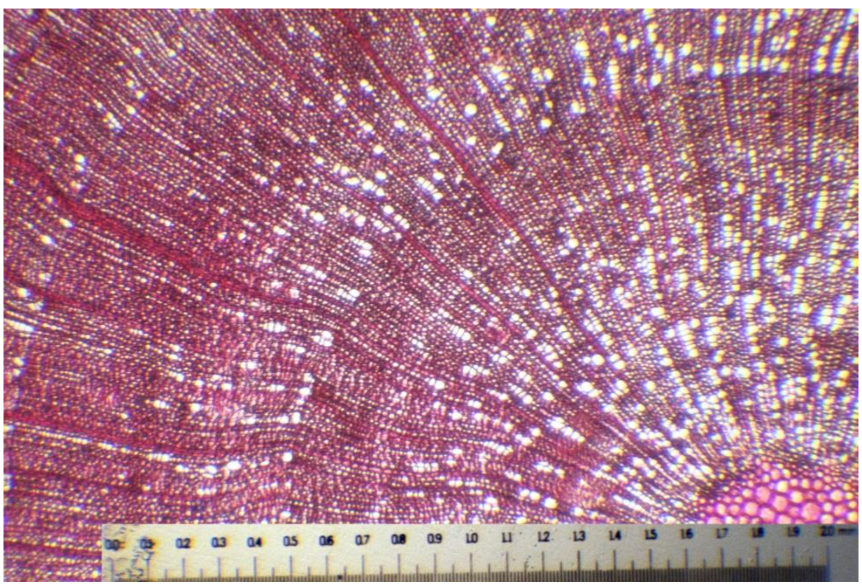

Figure 26 Wood of young stem of *Styrax formosanus* Matsumura (JCR #011483), exhibiting diffuse porous condition in first ring and ring porous condition (Carlquist (1988) Type 1C) in later rings. Stained with 0.5% Safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

When comparing the genus *Styrax* to the outgroup *Sinojackia*, *Sinojackia rehderiana* was diffuse porous, whereas some members of Styrax were ring porous (Carlquist Type 1C). *Sinojackia* differed from *Styrax* in containing wider uniseriate rays (16.90 μm as opposed to 15.17 μm), but more dramatically in reference to its vessel element density of 25.25 per 1.73 mm^2, only 58% of the 43.43 per 1.73 mm^2 in *Styrax*. *Sinojackia rehderiana* also seemed to possess multiples with fewer vessel elements, with a mean of 1.86 as opposed to 2.97 in *Styrax*, as well as a greater number of solitary vessel elements, 6.75 per 1.73 mm^2 (26.25% of vessels) as opposed to 2.10 (5.70% of vessels). Vessel elements also differed in terms of shape and position. Those of *Styrax* contain a tangential wall 1.15 × longer than the radial wall, whereas the vessel tangential walls of *Sinojackia* are 0.92 × longer than the radial wall (radial wall 1.08 × longer than tangential). As there is no significant difference between the vessel element tangential wall length in these two species, this is largely the result of a longer radial walls in *Sinojackia rehderiana*, 29.53 μm as opposed to 21.91 μm.

Species had a significant effect on the density of both uniseriate and multiseriate rays (Table 14). *Styrax americanus* (Figure 27) possessed the highest density of uniseriate rays (10.13 per 1.73 mm^2), separating it from all species except *Styrax formosanus* (8.38 per 1.73 mm^2). On the low end was *Styrax dasyanthus* (3.38 per 1.73 mm^2), separate from all except *Styrax calvescens* and the outgroup, *Sinojackia rehderiana*. As far as ray width, *Styrax confusus* had the widest uniseriate rays at 18.25 μm, though the difference between it, *Styrax dasyanthus*, and the outgroup was not significant. Narrowest rays belonged to *Styrax americanus*, (12.61), *Styrax calvescens* (14.05), and *Styrax formosanus* (13.89). In both characteristics, 50% of the *Styrax* species examined could not be statistically separated from the outgroup.

Table 14 Mean density and width of uniseriate rays observed in cross sections of *Styrax* spp. and an outgroup. Density refers to number of rays observed in a 1.73 mm^2 field of view. Means not connected by the same letter are significantly different according to Student's t-test (α = 0.05).

Taxon	**Uniseriate ray density**		**Uniseriate ray width (µm)**	
<u>*Styrax*</u>				
S. americanus	10.13	A	12.61	E
S. calvescens	4.38	FG	14.05	DE
S. confusus	5.63	DEF	18.25	A
S. dasyanthus	3.38	G	17.14	AB
S. formosanus	8.38	AB	13.89	DE
S. grandifolius	7.38	BCD	15.41	BCD
S. japonicus	5.63	DEF	14.98	D
S. serrulatus	6.38	CDE	15.18	CD
S. tonkinensis	7.75	BC	15.64	BCD
S. wilsonii	7.88	BC	14.54	D
<u>*Sinojackia*</u>				
Si. rehderiana	5.25	EFG	16.90	ABC

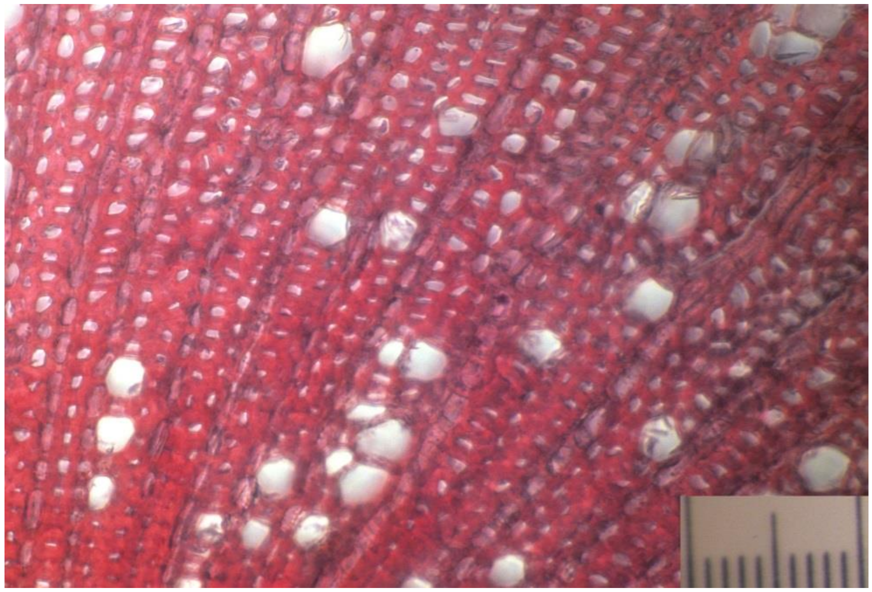

Figure 27 Wood of *Styrax americanus* Lamarck (UDBG #96-15*1) displaying high frequency of uniseriate rays. Stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

The density of multiseriate rays was also significantly affected by species (Table 15). *Styrax confusus* possessed the highest density (2.88 per 1.73 mm^2), separating it from all species examined. All other species (90%) could not be separated from the outgroup. When expressing this as a percentage of the total number of rays, the characteristic was still significant, though resulted in more grouping. *Styrax confusus* (34.35%) could not be separated from *Styrax dasyanthus* (32.29%) and *Styrax japonicus* (24.28%), though one other species, *Styrax americanus* (6.97%), could be separated from the outgroup. Multiseriate rays were usually only biseriate, though triseriate rays were present in some species raising the mean cell number over two. Multiseriate ray width (expressed as number of cells) was also significantly affected by species. *Styrax confusus* (Figure 28) had the greatest tendency towards triseriate rays (Mean number cells per multiseriate ray: 2.35), separating it from all species examined (90%). All species save for *Styrax confusus* clustered with the outgroup. When analyzing the metric width of the ray, clustering was reduced but still significantly affected by species. *Styrax confusus* grouped with four species including the outgroup. In this case, only *Styrax americanus* (18.75 µm) could be separated from the outgroup, though still clustered with 50% of *Styrax* species examined. It appears that while the number of cells per ray can vary in *Styrax confusus,* the actual width of the ray is more aligned with what other species of the genus.

Table 15 Mean density, width, and percentage of total rays multiseriate as observed in cross sections of *Styrax* spp. and an outgroup. Density refers to number of rays observed in a 1.73 mm^2 field of view. Means not connected by the same letter are significantly different according to Student's t-test ($\alpha = 0.05$).

Taxon	**Multi-seriate ray density**		**% Rays Multi-seriate**		**multiseriate ray width (mean cell no.)**		**multiseriate ray width (µm)**	
<u>Styrax</u>								
S. americanus	0.75	C	6.97	D	2	B	18.75	C
S. calvescens	1.13	BC	20.77	BC	2	B	23.66	BC
S. confusus	2.88	A	34.35	A	2.35	A	28.54	A
S. dasyanthus	1.38	BC	32.29	AB	2.14	B	28.7	A
S. formosanus	1.88	B	18.36	CD	2.1	B	23.63	BC
S. grandifolius	1.63	BC	16.4	CD	2.06	B	25.8	AB
S. japonicus	1.63	BC	24.28	ABC	2	B	28.98	AB
S. serrulatus	1	BC	16.11	CD	2	B	22.92	BC
S. tonkinensis	1.63	BC	17.75	CD	2.07	B	23.29	BC
S. wilsonii	1	BC	12.16	CD	2.07	B	23.02	BC
<u>Sinojackia</u>								
Si. rehderiana	1.25	BC	20.25	BC		B	24.39	AB

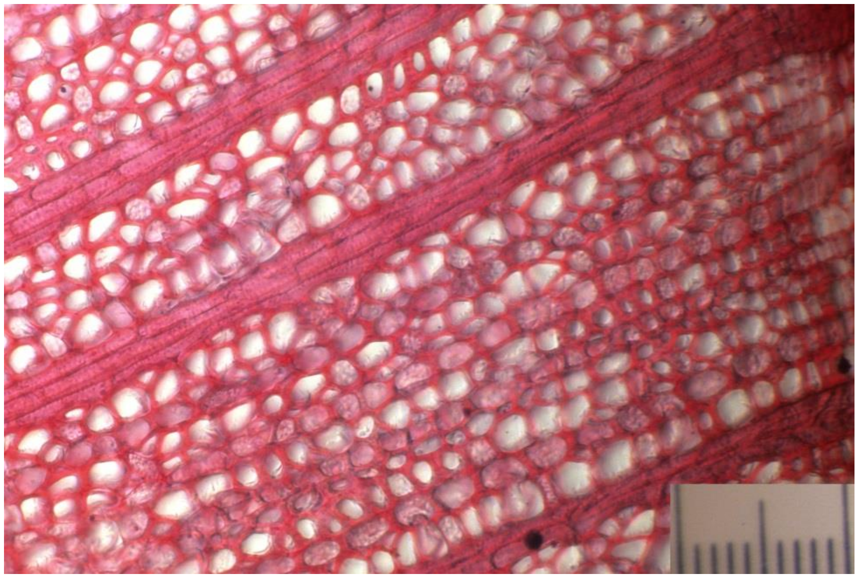

Figure 28 Wood of *Styrax confusus* Hemsley (JCR #001628), displaying two triseriate rays in the first ring of growth. Stained with 0.5% Safranin. 160× Magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

All vessel characteristics examined were significantly affected by species. *Styrax americanus* had the greatest vessel element density (70.75 per 1.73 mm^2), significantly higher than any other species (Table 16). The outgroup contained the lowest density (13.75), though could not be statistically separated from 50% of *Styrax* examined. The density of vessel element multiples was highest in *Styrax americanus* (21.5 per 1.73 mm^2), *Styrax serrulatus* (18.13 per 1.73 mm^2), and *Styrax formosanus* (17.75 per 1.73 mm^2), though the latter species and all others examined (80%) could not be separated from the outgroup. This index of vessel element multiples also included solitary vessel elements. When counting these solitary vessel elements separately, the outgroup contained the highest density (6.75 per 1.73 mm^2), clustering with *Styrax japonicus* (5.25 per 1.73 mm^2). All other species could be separated from the outgroup. This same pattern occurs when examining the mean number of vessel elements per multiple, with the outgroup (1.86 vessels per multiple) distinct from all others save for *Styrax japonicus* (2.37 vessels per multiple). The percentage of solitary vessels also yielded similar results, though in this case *Styrax japonicus* (17.57% of vessels solitary) and the outgroup (26.45% of vessels solitary) were statistically distinct from each other and all other species of *Styrax*. This was one of only two characteristics in which *Sinojackia* did not cluster with at least one species of *Styrax*.

Table 16 Mean density of vessel elements and vessel element multiples observed in cross sections of *Styrax* spp. and an outgroup. Density refers to number of vessel elements and vessel element multiples observed in a 1.73 mm^2 field of view. Means not connected by the same letter are significantly different according to Student's t-test ($\alpha = 0.05$).

	Vessel Element Density		**Vessel Element Multiple Density**		**Mean # Vessel elements per Multiple**		**Solitary Vessel element density**		**% of Vessels solitary**	
Styrax										
S. americanus	70.75	A	21.5	A	3.32	ABC	2.13	B	3.28	C
S. calvescens	36.13	BC	13.63	BC	2.68	D	1.25	B	3.81	C
S. confusus	46.63	B	13.75	BC	3.57	A	2	B	3.91	C
S. dasyanthus	37.5	BC	13.13	C	2.95	BCD	1.5	B	4.16	C
S. formosanus	47.63	B	17.75	AB	2.52	D	2.5	B	7.69	C
S. grandifolius	48.5	B	13.25	C	3.59	A	2.13	B	5.31	C
S. japonicus	30.88	C	13.38	C	2.37	DE	5.25	A	17.57	B
S. serrulatus	47.5	B	18.13	A	2.61	D	1.88	B	3.84	C
S. tonkinensis	29.75	C	11.13	C	2.73	CD	1.38	B	4.62	C
S. wilsonii	39	BC	11.5	C	3.36	AB	1	B	2.79	C
Sinojackia										
Si. rehderiana	25.25	C	13.75	BC	1.86	E	6.75	A	26.45	A

The vessel ratio (length of radial wall to length of tangential wall) was also significant. Four groups seemed to form: radial wall 1.23-1.31 × longer than tangential wall, 1.11-1.23 × longer, 1.03-1.11 × longer, and 0.98-1.03 × longer (Table 17). This latter group contained *Sinojackia rehderiana, Styrax confusus,* and *Styrax dasyanthus,* with all other species distinct from the outgroup. Examination of the vessel ratio alone however does not make clear whether the length of the radial wall or tangential wall may vary more than the other in different species. Analysis of the tangential wall length resulted in the outgroup clustering with those species with the longest tangential walls, though it had been previously deemed significantly different from all those species on the basis of vessel ratio. *Styrax wilsonii* (20.48 µm) and *Styrax formosanus* (17.57 µm) exhibited the shortest tangential walls, distinct from all other species save for each other. The longest tangential walls were those of *Styrax japonicus* (31.36 µm), *Styrax grandifolius* (28.67 µm), and the outgroup (26.77 µm), though the latter two also grouped with three other *Styrax* species. In total, 50% of the species could be separated from the outgroup. The outgroup had the longest radial walls, separate from all species of *Styrax*. All *Styrax* species were largely similar save for *Styrax formosanus* with the shortest radial walls (15.34 µm), distinct from all species save for *Styrax wilsonii* (18.42 µm), which in turn also grouped with *Styrax dasyanthus* (21.48 µm).

Table 17 Mean tangential and radial wall length of vessel elements observed in cross sections of *Styrax* spp. and an outgroup. Vessel Ratio refers to the ratio of the tangential to radial wall length. Means not connected by the same letter are significantly different according to Student's t-test ($\alpha = 0.05$).

Species	**Tangential Wall Length (µm)**		**Radial Wall Length (µm)**		**Vessel Ratio**	
<u>*Styrax*</u>						
S. americanus	26.49	BC	21.73	C	1.23	AB
S. calvescens	26.14	BC	22.63	BC	1.15	B
S. confusus	24.05	C	23.58	BC	1.03	CD
S. dasyanthus	24.8	C	21.48	CD	1.17	B
S. formosanus	17.57	D	15.34	E	1.15	B
S. grandifolius	28.67	AB	23.31	BC	1.23	AB
S. japonicus	31.36	A	24.37	BC	1.31	A
S. serrulatus	26.44	BC	22.58	BC	1.17	B
S. tonkinensis	24.92	C	25.66	B	0.98	D
S. wilsonii	20.48	D	18.42	DE	1.11	BC
<u>*Sinojackia*</u>						
Si. rehderiana	26.77	AB	29.53	A	0.92	D

To summarize all findings, the number of both ray and vessel characteristics in which one species could not be statistically separated from another were tallied together and a percentage of similarity was calculated (Table 18).

Table 18 Similarity of *Styrax* species: percentage of characteristics in which *Styrax species* and outgroup were not significantly different. The following ten characteristics were used for this index: uniseriate ray density, uniseriate ray width, multiseriate ray density, multiseriate ray width (both metric and number of cells wide), vessel element density, vessel element multiple density, the percentage of solitary vessels, vessel tangential wall length, and vessel radial wall length. Significance determined by Student's T-test (α = 0.05).

	S. americanus	***S. calvescens***	***S. confusus***	***S. dasyanthus***	***S. formosanus***	***S. grandifolius***	***S. japonicus***	***S. serrulatus***	***S. tonkinensis***	***S. wilsonii***	**Outgroup**
S. americanus	100	70	30	50	60	50	30	70	50	40	30
S. calvescens	70	100	60	80	70	90	80	80	90	70	70
S. confusus	30	60	100	70	30	60	40	50	40	30	40
S. dasyanthus	50	80	70	100	40	80	60	60	70	60	70
S. formosanus	60	70	30	40	100	70	40	70	60	90	40
S. grandifolius	50	90	60	80	70	100	80	90	80	80	60
S. japonicus	30	80	40	60	40	80	100	60	70	60	70
S. serrulatus	70	80	50	60	70	90	60	100	80	70	60
S. tonkinensis	50	90	40	70	60	80	70	80	100	80	60
S. wilsonii	40	70	30	60	90	80	60	70	80	100	50
Outgroup	30	70	40	70	40	60	70	60	60	50	100

The following pairs of species appeared the most similar, with 90% of the characteristics counted not significantly different: *Styrax japonicus* and *Styrax calvescens*, *Styrax calvescens* and *Styrax tonkinensis*, *Styrax wilsonii* and *Styrax formosanus, Styrax calvescens* and *Styrax grandifolius*, *Styrax grandifolius* and *Styrax serrulatus*. The strongest differences observed were in pairs of species that shared only 30% of their characteristics: *Styrax americanus* and *Styrax confusus*, *Styrax americanus* and *Styrax japonicus*, *Styrax americanus* and *Sinojackia rehderiana*, *Styrax confusus* and *Styrax formosanus*, and *Styrax confusus* and *Styrax wilsonii*.

The outgroup, *Sinojackia rehderiana* was most similar to *Styrax japonicus* and *Styrax calvescens*, differing most greatly from the *Styrax americanus*. In total, 70% of the species examined shared greater than 50% of their characteristics with the outgroup, with *Styrax confusus* and *Styrax formosanus* sharing 50%, and *Styrax americanus* sharing only 25%.

Chromosome Count of *Styrax japonicus*

Though the procedure was attempted several times, the anther squashes produced satisfactory staining only in one preparation. Pollen mother cells of several anthers examined appeared to have already completed their second meiotic division by the time of their harvest, supporting Gonsoulin's (1974) observation that the meiotic window for *Styrax* is rather narrow. In the one preparation chromosomes were visible, the chromosome number was difficult to determine primarily due to the small size, complex arrangement, and uncertainty as to whether the cell exhibiting chromosomes represented a pollen mother cell or a part of the anther wall due to insufficient cell dispersal during squashing (Figure 29). As the former cell would be haploid while the latter would be diploid, the chromosome number of *Styrax japonicus* could not be reliably estimated using this preparation.

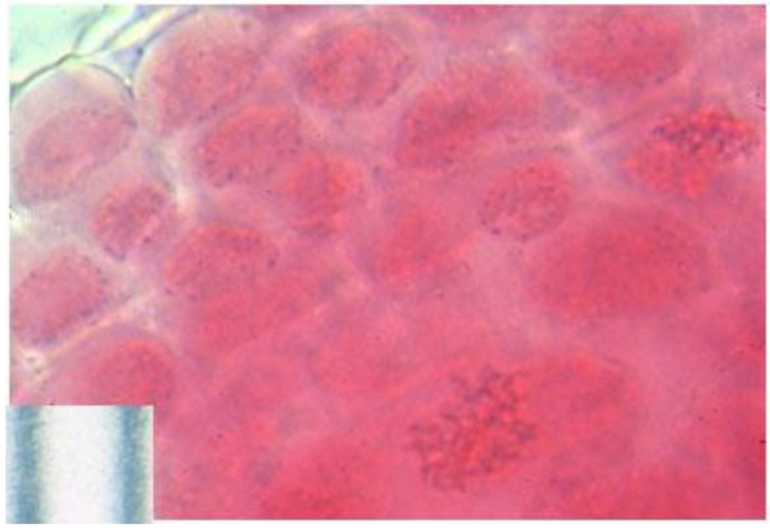

Figure 29 *Styrax japonicus* Siebold & Zuccarini 'Emerald Pagoda' chromosomes as observed in an anther. Stained with acetocarmine, 1000× magnification. Scale bar representing 10 microns. Photograph by the Author & T.D. Pizzolato.

The majority of root tip preparations resulted in little to no staining of the chromosomes, likely due to slow root elongation at time of harvest. Though several techniques were attempted such as pretreatment with *p*-dichlorobenzene or staining with Schiff's reagent or aceto-orecin in place of acetocarmine, none seemed to improve the visibility of the chromosomes.

After several attempts, only one satisfactory preparation was produced (Figure 30), though the chromosome number could not be determined, again due to the small size of the chromosomes. In this case however, since the root tip contained exclusively diploid cells, taking into account the known base number for the species ($x=8$) the specimen's ploidy level (whether $2n=2x$, $2n=5x$, or $2n=6x$) could be estimated. Figure 30 appears to show between 12 and 18 chromosomes one on pole of one cell, which supports a diploid (*2n=2x=16*) level for *Styrax japonicus* ‘Pink Chimes’ as opposed to another ploidy level.

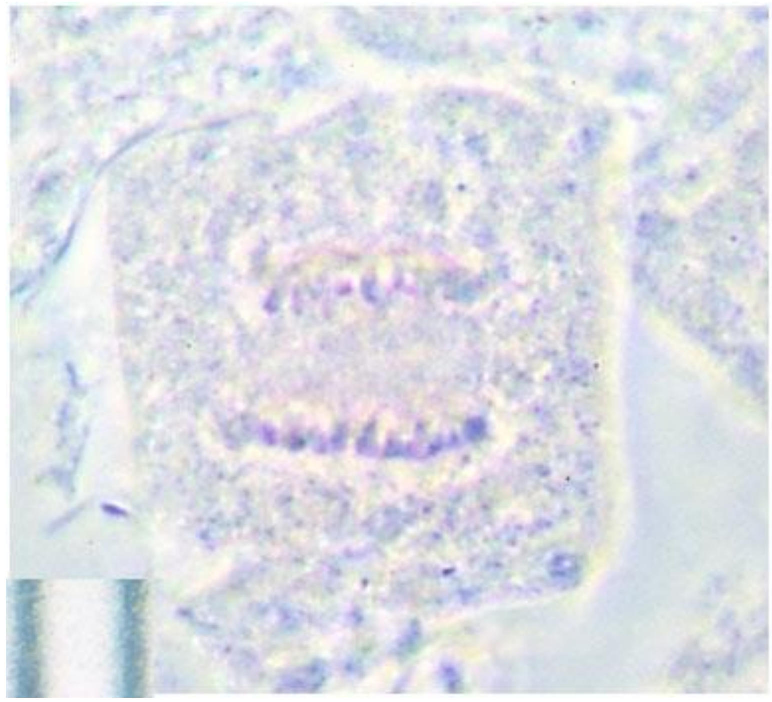

Figure 30 Chromosomes of *Styrax japonicus* Siebold & Zuccarini ‘Pink Chimes’ in a dividing root tip cell. Anaphase. Stained with acetocarmine, 1000× magnification. Scale bar representing 10 microns. Photograph by the Author & T.D. Pizzolato.

The petal squash produced the most effective results, with a satisfactory preparation obtained following several attempts (Figure 31). Chromosomes observed were still minute in size and difficult to count accurately, though were more evident than in the root tip squash. Again ploidy level could be estimated with relative certainty, with Figure 31 showing 7 to 14 chromosomes at each pole, supporting a diploid (*2n=2x=16*) level as opposed to higher ploidy level.

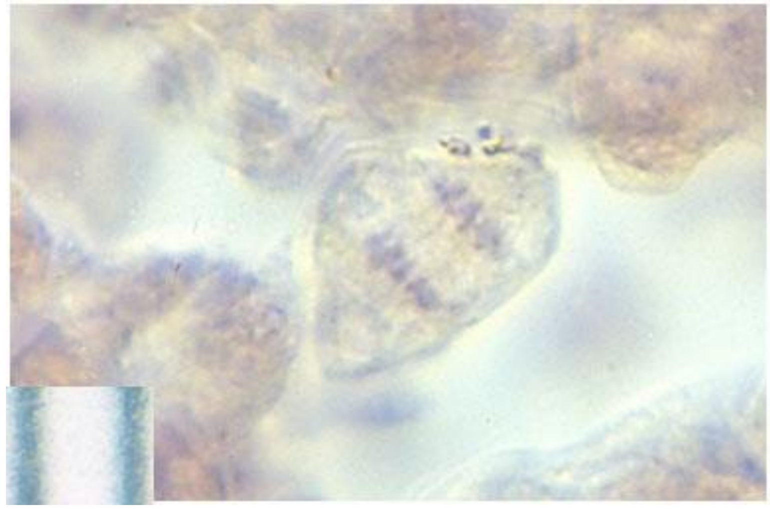

Figure 31 Chromosomes of *Styrax japonicus* Siebold & Zuccarini in dividing cell of an immature petal. Anaphase. Stained with acetocarmine, 1000× magnification. Scale bar representing 10 microns. Photograph by the Author & T.D. Pizzolato.

In the case of all acetocarmine squash techniques, incubating the tissue within the stain for 1-12 hours before squashing and examining failed to produce significantly superior staining. Schiff's reagent did not appear to produce similar staining as compared to acetocarmine. Pretreatment with P-dichlorobenzene also failed to produce preparations in which chromosomes could be more easily counted.

Discussion

Petiole

Vascular patterns on the whole were similar to those described by Schadel & Dickison (1979); recall that they also noted vascular patterns involving a central vascular component, either an arc or a cylinder, accompanied by smaller vascular bundles. All sections observed exhibited at least two vascular bundles, which in virtually all cases were located in the dorsal cortical tissue. Though sections from the basal, medial, and distal portions of the petiole were observed, numerous serial sections would be required to determine the degree to which the path of the vascular bundles weaved throughout the petiole.

Out of the five species examined both by Schadel & Dickison (1979) and in this thesis (*Styrax americanus, Styrax grandifolius, Styrax japonicus, Styrax platanifolius*, *Styrax serrulatus*) only two species (*Styrax japonicus* and *Styrax platanifolius*) displayed similar vascular patterns in all individuals sectioned. A noticeable amount of variability in both the form of the central trace and number and position of additional bundles was evident when observing sections from multiple individuals of the same species, particularly when taken in context of the results of Schadel & Dickison (1979).

Considering first the variability in the shape of the central trace, only *Styrax grandifolius* was observed having different patterns in different individuals. Schadel & Dickison (1979) also examined *Styrax grandifolius*, observing an arc with two invaginated ends. However, the invaginated ends observed in *Styrax grandifolius* PHA# 2009-35*A appeared to exhibit a stronger degree of closure as compared to other petioles sectioned. With a sample size of only three individuals of the species examined, it is difficult to gauge the degree as to which this characteristic varies over the range of the species. It seems likely however, that *Styrax grandifolius* at least shows a greater tendency towards the medullated cylinder condition than other species examined. Additionally, the specimen of *Styrax serrulatus* observed by Schadel & Dickison (1979) exhibited a medullated cylinder, whereas that observed as part of this thesis was an arc with invaginated ends. However, making comparisons between the two individuals of is difficult at this time due to the possibility that the individual sectioned as part of this thesis, JCR# 940340, may be incorrectly identified (Mark Weathington, pers. comm.). Schadel & Dickison (1979) did not examine *Styrax wilsonii*, and without additional context it is difficult to determine whether to interpret its apparently unique central trace form as such, or instead as a modification of the medullated cylinder form. However, as all other individuals sectioned displayed the central trace phloem and xylem much more tightly associated the central trace of *Styrax wilsonii* appears unique at least in the context of this sample.

Variability within individuals of the same species was more pronounced when observing the smaller, accessory bundles. Making direct comparisons to the research of Schadel & Dickison (1979) is difficult as the authors did not separate the bundles into three categories. As they only mention the presence or absence of two dorsal cortical bundles however, it seems likely that the bundles they reference are equivalent to the "accompanying bundles" mentioned above, and that other smaller bundles were not present or deemed irrelevant.

Considering first the larger accompanying bundles, *Styrax serrulatus* was the only species to display none. The petiole observed by Schadel & Dickison (1979) did have such bundles, though a direct comparison again is unwise due to the uncertain identity of the petiole sectioned for this thesis. Though one individual of *Styrax confusus* (PHA #2009-56*A) exhibited only one accompanying bundles, the other three sectioned exhibited two. When examining medial in addition to distal portions however, both PHA #2009-56*A and AA# 1082-89*C had only one, solitary integrated bundle. By the distal portion however, two accompanying and two associated bundles were observed in the latter, but only one accompanying and two integrated bundles in the former. It seems plausible that two accompanying bundles is the standard condition for the species, though if environmental or other conditions prevent them from forming smaller associated or integrated bundles form. Additionally, a section of the main vein of PHA #2009-56*A further into the petiole/lamina continuum may have revealed a second accompanying bundle. A full developmental study would be a necessity for shining more light upon these curiosities.

The petioles of *Styrax americanus* (one of var. *americanus* and one of var. *pulverulentus*) sectioned by Schadel & Dickison (1979) exhibited no bundles, whereas UDBG #96-15*1 displayed two accompanying bundles, and PHA 70-085*A displayed two accompanying and one associated bundles. This could indicate variability within the species as to whether these bundles form, though it also possible they simply sometimes form further towards the lamina as discussed above with *Styrax confusus*.

The most unique characteristics appear to be a stronger tendency towards a medullated cylinder in *Styrax grandifolius*, thick band of accompanying sclerenchyma in *Styrax platanifolius* ssp. *texanus*, extension of the main trace phloem past the main trace xylem in *Styrax wilsonii*, and lack of accompanying bundles in the purported *Styrax serrulatus*. In all cases however, a larger sample size including multiple petioles from multiple plants of differing provenances and growing conditions should be collected in order to better understand the amount these characteristics vary within each species. These characteristics may show promise for field identification were such research completed, though currently identification of *Styrax* species from petiole sections alone is not advised as a reliable technique.

Wood

The stem wood of *Styrax* can be qualitatively described as predominantly diffuse porous with a tendency towards a ring or semi-diffuse porous condition (Carlquist Type 1C) in some species, a radial system comprised mostly of uniserriate rays with some biseriate rays or triserriate rays, and a vascular system of vessel elements generally aggregated into multiples with a relatively low percentage occurring solitarily. The tangential wall is usually somewhat longer than the radial wall, though this difference is insignificant in some species. As compared to *Styrax*, the wood of *Sinojackia rehderiana* appears to contain vessel elements with longer radial walls and has a weaker propensity towards aggregation of these vessels into multiples.

The most unique characteristics of the *Styrax* taxa sampled were the ring or semi-diffuse porous (Carlquist Type 1C) wood of *Styrax dasyanthus* and *Styrax formosanus*, the higher number of solitary vessel elements in *Styrax japonicus* (though still significantly lower than *Sinojackia rehderiana*), the high and low uniserriate ray density in *Styrax americanus* and *Styrax calvescens*, respectively, and the greater percentage of multiseriate rays and stronger disposition towards triseriate rays in *Styrax confusus*. *Styrax tonkinensis* displayed a vessel ratio more similar to *Sinojackia* than other species of *Styrax*, in which the radial walls were as long as or slightly longer than the tangential walls. *Styrax grandifolius* and *Styrax wilsonii* appear to be intermediate for many of these characteristics described above, though the former displays larger vessels with significantly longer tangential walls and radial walls as compared to the former. Recall however that differences in both vessel element width and the percentage of solitary vessel elements may also be explained by cross section size in addition to species. Additional sections of *Styrax japonicus* of varying diameter will likely need to be examined to better quantify the effect of cross section width on percentage of solitary vessel elements and determine if it remains a unique characteristic for that species.

Analysis of wood anatomy reveals the following species have the greatest number of significant similarities, sharing 90% of their characteristics: *Styrax japonicus* and *Styrax calvescens*, *Styrax calvescens* and *Styrax tonkinensis*, *Styrax wilsonii* and *Styrax formosanus, Styrax calvescens* and *Styrax grandifolius*, *Styrax grandifolius* and *Styrax serrulatus*. When putting this in the context of distribution, the similarities between the first two pairs are not entirely unsurprising as they consist of species distributed throughout East Asia, namely China. Comparing *Styrax japonicus* to *Styrax calvescens*, the two samples came from different sources and the former had twice the cross section diameter than the latter. Thus there appear to be few external factors at play that could explain this similarity. Cross sections of *Styrax calvescens* and *Styrax tonkinensis* however did share the same source and only differed in diameter by 1 mm.

The third pair is also between two species in East Asia, though *Styrax wilsonii* is endemic to Baoxing Xian, Sichuan, China, whereas *Styrax formosanus* is distributed in Taiwan. Cross sections of the two were both occurred from the JC Raulston Arboretum and differed in diameter by 2 mm. Considering also differences in habit, *Styrax wilsonii* is a small, multistemmed shrub whereas *Styrax formosanus* is a tree thought to be closely related to *Styrax japonicus* (Huang et al. 2003). In contrast, *Styrax formosanus* and *Styrax japonicus* only shared 40% of their characteristics, though in this case the section of *Styrax japonicus* was from a different source but only 2mm wider in diameter. The latter two pairs sharing 90% similarity are somewhat more surprising as they hint towards heavy relatedness between East Asian taxa and *Styrax grandifolius,* which is a large suckering shrub distributed throughout the southeastern US. *Styrax serrulatus* in particular has a much more subtropical distribution, extending well into India and Myanmar. Additionally *Styrax calvescens* and *Styrax serrulatus* are much more tree-like in terms of habit. The section of *Styrax grandifolius* was obtained from the University of Delaware Botanic Gardens whereas the other two were from the JC Raulston Arboretum, and approximately half the diameter of the section of *Styrax grandifolius*. *Styrax grandifolius* is generally thought to be a close relative of *Styrax americanus* (Fritsch 2001), though analysis of wood anatomy revealed only a 50% similarity between the two.

Conversely, the strongest differences observed were in pairs of species that shared only 30% of their characteristics: *Styrax americanus* and *Styrax confusus*, *Styrax americanus* and *Styrax japonicus*, *Styrax americanus* and *Sinojackia rehderiana*, *Styrax confusus* and *Styrax formosanus*, and *Styrax confusus* and *Styrax wilsonii*. This is less surprising as *Styrax americanus* and *Styrax confusus* are not thought to be closely related to any of these species based on the literature. These differences are in part explained by the uniquely high uniseriate ray density of *Styrax americanus* and disposition of *Styrax confusus* towards triseriate rays as discussed above, which prevented them from clustering tightly with other species based on ray characteristics.

The characteristics chosen for the similarity percentage excluded the percentage of rays multiseriate, mean number of vessel elements per multiple, and vessel ratio as they represent proportions of measurements already included, and would thus overemphasize those characteristics. Similarly, in the case of solitary vessel elements, the percentage of the vessel elements which occurred solitarily was used as opposed to the raw number of solitary vessel elements. This was due to the fact that the total number of vessel element multiples actually includes the solitary vessels as well, so in this case the percentage better isolates the characteristic and avoids double counting of the vessel elements.

The only two characteristics which seemed to differ in relation to whether they occurred in the first ring or later rings were the number of vessel elements and number of vessel element multiples, in both cases decreasing in density in later rings. Since four first and four later rings were examined for each species however, these differences were likely controlled for in the above analysis. There were however, significant differences observed when comparing both the continental distribution and cross section source for each species. In the majority of characteristics, the differences between source and distribution mirrored each other closely, with the same characteristics significantly higher both in species distributed in North America and sections collected from the University of Delaware Botanic Gardens. This likely resulted from the fact that the two North American species examined (*Styrax americanus* and *Styrax grandifolius*) were collected from the University of Delaware Botanic Gardens as opposed to the JC Raulston Arboretum. It seems plausible that differences between species are still responsible for most of this diversity, with characteristics such as higher uniserriate ray density in sections obtained from UDBG and of North American distribution likely only significantly different as the mean is pulled upwards by the unique characteristics of the wood of *Styrax americanus*. Another seemingly unique characteristic, the stronger tendency towards solitary vessel elements, was likely insignificant when considering source as the two species exhibiting the greatest, *Styrax japonicus* and *Sinojackia rehderiana*, were collected from different sources. However, it would be advisable to eliminate source as a variable by collecting all sections from the same location, or to make certain that sections of at least some species are sampled from multiple locations to better understand how much these characteristics vary based on environmental growing conditions.

One significant limitation of the above analysis is the limited sample size. Though multiple fields of view from each cross section were observed, each cross section represented only a single branch from a single plant of a given species. At least two species examined here: *Styrax japonicus* and *Styrax serrulatus*, are known for the great amount of variability they exhibit over their respective ranges (Huang et al. 2003). Though in many cases this limitation is artificially imposed due to the scarcity of several of these taxa in cultivation, sections from plants representing multiple provenances throughout these distributions should be examined in order to determine the uniformity of the wood within those species before further extrapolating as to the differences between species. *Styrax japonicus* is the most commonly cultivated member of the genus, and germplasm representing several different morphological forms and provenances could likely be obtained with relatively little difficulty. In contrast, the second most commonly cultivated species, *Styrax obassia,* shows very little morphologically diversity over its range. Analyzing the diversity of the wood of both of these species would be valuable to determine how unique some of the above mentioned characteristics, such as tendency towards solitary vessel elements in *Styrax* japonicus, truly are. Additionally, the greater availability of source material for these two species should allow for cross sections more uniform in diameter to be collected, controlling for section diameter as a variable.

Better understanding of the wood would likely also be accomplished by additional analysis of tangential and/or radial sections. This would allow for linear oriented axial parenchyma to be distinguished from rays, as well as allowing for measurement and examination of additional characteristics such as ray height. Use of computer software would also allow for better representation of vessel element size, for example by calculating the cross section area of each element in addition to the approximate length of the tangential and radial walls.

Chromosome Count of *Styrax japonicus*

The chromosomes of *Styrax japonicus* are minute, compact, and thus difficult to count using light microscopy methods. The difficulty in obtaining meiotic figures is likely a result of a late harvest of flower buds, confirming Gonsoulin's (1974) suspicion that the meiosis window for the genus is very small. Though this may be somewhat alleviated by repeated, earlier sampling of the flower buds, when considering the difficulty of distinguishing between a meiotic pollen mother cell division and a mitotic anther wall division, less time-sensitive mitotic preparations of purely sporophytic tissues are likely a superior method.

The preparations resulting from the root tip and petal squashes suggest a ploidy level of $2n=16$ for *Styrax japonicus* as reported by Yamasaki (1993). This chromosome count agrees with Shiuchi & Fujita's (2006) conclusion that *Styrax japonicus* displays multiple ploidy levels over its wide distribution, but strongly supports a diploid level in addition to the pentaploid and hexaploid levels recorded in the literature. Additionally, the data for *Styrax japonicus* 'Pink Chimes', combined with Ranney's flow cytometer data (personal communication) strongly suggests cultivars are diploid.

The superior method for determining chromosome numbers of *Styrax japonicus* appears to be the harvesting of a naturally flattened tissue that is very thin facilitating squashes such as a developing petal, or likely also a young leaf, and staining with acetocarmine, for which a long incubation appears largely unnecessary. Though pretreatment with p-dichlorobenzene was not effective, a similar pretreatment using colchicine or another similar substance may be desirable in order to arrest mitosis at metaphase, possibly increasing the number of cells in which chromosomes are stained and counted. Though flow cytometry may be a far less time consuming method for determination of chromosome numbers of the genus, knowledge of the base numbers of widespread species such as *Styrax japonicus* remains important for improved interpretation of those results.

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Appendix A

CHECKLIST OF NAMES

Accepted Names

Styrax acuminatus Pohl, Pl. Bras. Icon. Descr. ii. 58. t. 138.
Accepted (Fritsch 2013)
= *Styrax alutaceus* Seub., Fl. Bras. (Martius) 7: 190. 1868
= *Styrax acuminatu*s Pohl var. *alutaceus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 45. 1907

*Styrax acuminatu*s Pohl var. *alutaceus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 45. 1907
Synonym: ***Styrax acuminatus*** Pohl (Fritsch 2013)

Styrax agrestis (Lour) G. Don, Gen. Hist. 4: 5. 1837
Accepted (Huang et al. 2008)
= Styrax warburgii Perkins, Pflanzenr. (Engler) 4, Fam. 241: 27. 1907
= Styrax ledermannii Perkins, Gatt. Styracac. 20 (1928), in clavi; Perkins in Notizbl. Bot. Gart. Berlin, x.457
= *Styrax subcrenatus* Hand.-Mazz., Oesterr. Bot. Z. 80: 342. 1931
= Styrax rostratus Hosok., Trans. Nat. Hist. Soc. Formosa 28: 65. 1938

Styrax agrestis (Lour.) G. Don var. *curvirostratus* B. Svengsuksa, Fl. Cambodge, Laos & Vietnam 26: 176. 1992
Synonym: ***Styrax curvirostratus*** (Svengs.) Y.L.Huang & P.W.Fritsch (Huang et al. 2003)

Styrax albus Martius ex Spreng., Syst. Veg. (ed. 16) [Sprengel] 2: 285. 1825
Synonym: ***Styrax latifolius*** Pohl (Fritsch 2013)

Styrax alutaceus Seub., Fl. Bras. (Martius) 7: 190. 1868
Synonym: ***Styrax acuminatus*** Pohl (Fritsch 2013)

Styrax ambiguus Seub., Fl. Bras. (Martius) 7: 192. 1868
Synonym: ***Styrax pohlii*** A. DC. (Fritsch 2013)

Styrax ambiguus Seub. var. *apiculatus* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 3: 914. 1903
Synonym: *Styrax pohlii* A. DC. (Fritsch 2013)

Styrax americanus Lam., Encycl. [J. Lamarck & al.] 1(1): 82. 1783
Accepted (Fritsch 2009)
= *Styrax laevis* Walter, Fl. Carol. 140. 1788.
= *Styrax laevigatus* Ait., Hortus Kew. (W. Aiton) 2: 75. 1789
= *Styrax pulverulentus* Michx., Fl. Bor.-Amer. (Michaux) 2: 41. 1803
= *Styrax americanus* Lam. var. *laevis* (Walter) Alph.Wood, Class-book Bot. (ed. 1861). 499. 1861
= *Styrax americanus* Lam. f. *genuinus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
= *Styrax americanus* Lam. f. *glaber* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
= *Styrax americanus* Lam. f. *pulverulentus* (Michx.) Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
= *Styrax americanus* Lam. var. *pulverulentus* (Michx.) Rehder in L.H.Bailey, Stand. Cycl. Hort. 6: 3280. 1917

Styrax americanus Lam. var. *laevis* (Walter) Alph.Wood, Class-book Bot. (ed. 1861). 499. 1861
Synonym: ***Styrax americanus*** Lam. (Fritsch 2009)

Styrax americanus Lam. var. *pulverulentus* (Michx.) Rehder in L.H.Bailey, Stand. Cycl. Hort. 6: 3280. 1917
Synonym: ***Styrax americanus*** Lam. (Fritsch 2009)

Styrax americanus Lam. f. *genuinus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
Synonym: ***Styrax americanus*** Lam. (Fritsch 2009)

Styrax americanus Lam. f. *glaber* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
Synonym: ***Styrax americanus*** Lam. (Fritsch 2009)

Styrax americanus Lam. f. *pulverulentus* (Michx.) Perkins, Pflanzenr. (Engler) 4, Fam. 241: 76. 1907
Synonym: ***Styrax americanus*** Lam. (Fritsch 2009)

Styrax andinus Steyerm., Pittieria 4: 12. 1972
Synonym: ***Styrax pavonii*** A. DC. (Fritsch 2008)

Styrax annamensis Guillaumin, Bull. Soc. Bot. France 70: 882. 1924
Accepted (Svengsuksa & Vidal 1992)

Styrax argenteus C.Presl, Reliq. Haenk. 2: 60. 1835
Accepted (Fritsch 1997)
= *Styrax polyanthus* Perkins, Bot. Jahrb. Syst. 31: 479. 1901
= *Styrax myristicifolius* Perkins, Bot. Jahrb. Syst. 31: 481. 1902

Styrax argenteus C.Presl var. *hintonii* (Bullock) Gonsoulin, Sida 5: 226. 1974
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax argenteus var. *grandiflorus* E. Carranza, Acta Bot. Mex. 36: 15, fig. 1996
Synonym: ***Styrax austromexicanus*** P.W. Fritsch (Fritsch 1997)

Styrax argenteus var. *micranthus* (Perkins) D'Arcy, Ann. Missouri Bot. Gard. 66: 169. 1979
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax argenteus var. *parvifolius*, Acta Bot. Mex. 23: 36, f. 1. 1993
Synonym: ***Styrax lanceolatus*** P.W.Fritsch (Fritsch 1997)

Styrax argenteus var. *ramirezii* (Greenm.) Gonsoulin, Sida 5: 227. 1974
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax argentifolius H.L.Li, J. Arnold Arbor. 24: 371. 1943
Accepted (Hwang & Grimes 1996)

Styrax argyi H.Lév., Repert. Spec. Nov. Regni Veg. 11: 64. 1912
Synonym: ***Styrax dasyanthus*** Perkins (Hwang & Grimes 1996)

Styrax argyrophyllus Perkins, Repert. Spec. Nov. Regni Veg. 2: 18. 1906
Synonym: ***Styrax pavonii*** A.DC. (Jorgensen & Yanez 1999, Fritsch 2008)

Styrax aureus Martius, Reise Bras. (Spix & Martius) 1: 551. 1823
Accepted (Fritsch 2010)

Styrax austromexicanus P.W.Fritsch, Ann. Missouri Bot. Gard. 84(4): 718. 1997
Accepted (Fritsch 1997)
= *Styrax argenteus* var. *grandiflorus* E. Carranza, Acta Bot. Mex. 36: 15, fig. 1996

Styrax barbatus Willd. ex Seub., Fl. Bras. (Martius) 7: 188. 1868
Synonym: ***Styrax sieberi*** Perkins (Perkins 1907)

Styrax benjuiferus Stokes, Bot. Mat. Med. 2: 517. 1812
Synonym: ***Styrax benzoin*** Dryand. (Perkins 1907)

Styrax benzoides Craib, Bull. Misc. Inform. Kew 1912, 267.
Accepted (Hwang & Grimes 1996)

Styrax benzoin Dryand., Phil. Trans. lxxvii. II. 308., t. 12. 1787
Accepted (Svengsuksa & Vidal 1992)
= *Styrax benjuiferus* Stokes, Bot. Mat. Med. 2: 517. 1812
= *Styrax dealbatus* (Miers) Gurke, Nat. Pflanzenfam. [Engler & Prantl] iv. I. (1891) 178.

Styrax betongensis H.R.Fletcher, Bull. Misc. Inform. Kew 1937, 509.
Synonym: ***Styrax porterianus*** G. Don (Huang et al. 2003)

Styrax biaristatus W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 12: 233. 1920
Synonym: ***Huodendron biaristatum*** (W. W. Smith) Rehder (Hwang & Grimes 1996)

Styrax bicolor Ducke, Trop. Woods no. 90: 26. 1947
Accepted (Fritsch 2010)

Styrax bodinieri H.Lév., Repert. Spec. Nov. Regni Veg. 4: 332. 1907
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax bogotensis Perkins, Repert. Spec. Nov. Regni Veg. 2: 19. 1906
Synonym: ***Styrax pohlii*** A. DC. (Fritsch 2013)

Styrax buchananii W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 12: 234. 1920
Accepted (Huang et al. 2003)
= *Styrax serrulatus* var. *latifolius* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 37. 1907

Styrax buchtienii Sleumer, Repert. Spec. Nov. Regni Veg. 41: 125. 1936
Synonym: ***Styrax pentlandianus*** J. Remy (Perkins 1907)

Styrax burchellii Perkins, Pflanzenr. (Engler) 4, Fam. 241: 46. 1907
Synonym: ***Styrax sieberi*** Perkins (Fritsch 2013)

Styrax burchellii Perkins var. *longifolius* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 47. 1907
Synonym: ***Styrax ferrugineus*** Nees & Martius (Fritsch 2013)

Styrax californicus Torr, Smithsonian Contr. Knowl. 6[61]: 4. 1853
Synoymn: ***Styrax redivivus*** (Torrey) L. C. Wheeler (Fritsch 2009)

Styrax californicus var. *fulvescens* Eastw., Bot. Gaz. 41: 286. 1906
Synoymn: ***Styrax redivivus*** (Torrey) L. C. Wheeler (Fritsch 2009)

Styrax caloneurus Perkins, Bot. Jahrb. Syst. 31. 484. 1902
Synonym: ***Styrax suberifolius*** var. ***suberifolius*** (Hwang & Grimes 1996)

Styrax calvescens Perkins, Pflanzenr. (Engler) 4, Fam. 241: 32. 1907
Accepted (Hwang & Grimes 1996)
= *Styrax dasyanthus* var. *cinerascens* Rehder, Pl. Wilson. 1(2): 289. 1912

Styrax camporum Pohl, Pl. Bras. Icon. Descr. ii. 53. t. 136.
Accepted (Zuloaga et al. (eds.) 2008)
= Styrax chrysasterus Pohl, Pl. Bras. Icon. Descr. 2: 59 (t. 139). 1827
= Styrax chrysasterus var. *sellowianus* A.DC., Prodr. (DC.) 8: 264. 1844
= Styrax floridus var. *communis* A.DC., Prodr. (DC.) 8: 263. 1844
= Styrax gardnerianus A.DC., Prodr. (DC) 8: 263. 1844
= Styrax obliquinervius A.DC., Prodr. (DC.) 8: 263. 1844
= *Styrax candollei* Seub., Fl. Bras. (Martius) 7: 189. 1868
= Styrax varians Seub., Fl. Bras. (Martius) 7: 189. 1868
= Styrax gardnerianus A.DC. var. *ovatifolius* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 3: 913. 1903
= Styrax gardnerianus A.DC. var. *pallidior* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 3: 913. 1903
= *Styrax camporum* f. *aureovelutinus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 49. 1907
= *Styrax camporum* f. *gardnerianus* (A.DC.) Perkins, Pflanzenr. (Engler) 4, Fam. 241: 49. 1907
= *Styrax camporum* f. *lanceolatus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 49. 1907
= *Styrax subcordatus* Moric., Pl. Nouv. Am. 117. t. 71.

Styrax camporum f. *aureovelutinus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 49. 1907
Synonym: ***Styrax camporum*** Pohl (Zuloaga et al. (eds.) 2008)

Styrax camporum f. *gardnerianus* (A.DC.) Perkins, Pflanzenr. (Engler) 4, Fam. 241: 49. 1907
Synonym: ***Styrax camporum*** Pohl (Zuloaga et al. (eds.) 2008)

Styrax camporum f. *lanceolatus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 49. 1907
Synonym: ***Styrax camporum*** Pohl (Zuloaga et al. (eds.) 2008)

Styrax candollei Seub., Fl. Bras. (Martius) 7: 189. 1868
Synonym: ***Styrax camporum*** Pohl (Fritsch 2010)

Styrax caudatus Perkins, Pflanzenr. (Engler) 4, Fam. 241: 74. 1907
Synonym: ***Styrax hookeri*** C.B.Clarke (Huang et al. 2003)

Styrax cavaleriei H.Lév., Repert. Spec. Nov. Regni Veg. 9: 447. 1911
Synonym: ***Pterostyrax psilophyllus*** Diels ex Perkins (Hwang & Grimes 1996)

Styrax chinensis Hu & S.Ye Liang, Acta Phytotax. Sin. 18(2): 230. 1980
Accepted (Hwang & Grimes 1996)

Styrax chrysasterus Pohl, Pl. Bras. Icon. Descr. 2: 59 (t. 139). 1827
Synonym: ***Styrax camporum*** Pohl (Fritsch 2010)

Styrax chrysasterus var. *sellowianus* A.DC., Prodr. (DC.) 8: 264. 1844
Synonym: ***Styrax camporum*** Pohl (Fritsch 2010)

Styrax chrysocalyx P.W.Fritsch, Novon 14(1): 43 (-45; fig. 1). 2004
Accepted (Fritsch 2010)

Styrax chrysocarpus H.L.Li, J. Arnold Arbor. 25: 312. 1944
Accepted (Hwang & Grimes 1996)

Styrax cinereus M.F.Silva, Acta Amazonica 1(1): 23 (1971); et in l.c. 1(3): 21 (1971)
Synonym: ***Styrax pallidus*** A.DC. (Fritsch 2010)

Styrax confusus Hemsl., Bull. Misc. Inform. Kew 1906, 162.
Accepted (Hwang & Grimes 1996)

Styrax confusus var. ***confusus***, Autonym
Accepted (Hwang & Grimes 1996)
= *Styrax serrulatus* var. *vestitus* Hemsl., J. Linn. Soc., Bot. 26(173): 77. 1889
= *Styrax philadelphoides* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 32. 1907
= *Styrax mollis* Dunn, Bull. Misc. Inform. Kew 1911, 273.
= *Styrax fukienensis* W.W.Sm. & Jeffrey, Notes Roy. Bot. Gard. Edinburgh 9: 130. 1916
= *Styrax juncudus* Diels, Notizbl. Königl. Bot. Gart. Berlin 9: 198. 1924

Styrax confusus var. ***microphyllus*** Perkins, Das Pflanzenreich 30(IV. 241): 24. 1907
Accepted (Hwang & Grimes 1996)

Styrax confusus Hemsl. var. ***superbus*** (Chun) S.M.Hwang, Acta Phytotax. Sin. 18(2): 161. 1980)
Accepted (Hwang & Grimes 1996)
= *Styrax philadelphoides* var. *superbus* Chun, Sunyatsenia 1(4): 296. 1934

Styrax conterminus Donn.Sm., Bot. Gaz. 18: 5. 1893
Accepted (Fritsch 1997)

Styrax cordatus A.DC., Prodr. (DC.) 8: 267. 1844
Synonym: ***Styrax pavonii*** A. DC. (Fritsch 2008)

Styrax costanus Steyerm., Fieldiana, Bot. 28: 490. 1953
Synonym: ***Styrax glaber*** Sw. (Fritsch 2008)

Styrax crotonoides C.B.Clarke, Fl. Brit. India 3: 589
Accepted (Svengsuksa & Vidal 1992)

Styrax curvirostratus (Svengs.) Y.L.Huang & P.W.Fritsch, Ann. Missouri Bot. Gard. 90(4): 506. 2003
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Styrax cyathocalyx Perkins, Repert. Spec. Nov. Regni Veg. 2: 24. 1906
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax dasyanthus Perkins, Bot. Jahrb. Syst. 31: 485. 1902
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Synonym: ***Styrax calvescens*** Perkins (Hwang & Grimes 1996)

Styrax dasyanthus var. *hypoleucus* Pamp, Nuovo Giorn. Bot. Ital., n.s., 17(4): 688
Synonym: ***Styrax dasyanthus*** Perkins (Hwang & Grimes 1996)

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Styrax dealbatus (Miers) Gurke, Nat. Pflanzenfam. [Engler & Prantl] iv. I. (1891) 178.
Synonym: ***Styrax benzoin*** Dryand.

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Synonym: ***Styrax pohlii*** A. DC. (Zuloaga et al. (eds.) 2008)

Styrax duclouxii Perkins, Repert. Spec. Nov. Regni Veg. 8: 83. 1910
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax duidae Steyerm., Fieldiana, Bot. 28: 491, fig. 110. 1953
Accepted (Fritsch 2008)

Styrax duidae Steyerm. subsp. *paruae* Maguire, Mem. New York Bot. Gard. 29: 213 (-215), fig. 1978
Synonym: ***Styrax neblinae*** (Maguire) P.W. Fritsch (Fritsch 2008)

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Synonym: ***Styrax neblinae*** (Maguire) P.W. Fritsch (Fritsch 2004)

Styrax erymophyllus Pohl, Pl. Bras. Icon. Descr. ii. 57. t. 137.
Synonym: ***Styrax glabratus*** Schott (Fritsch 1997)

Styrax esquirolii H.Lév., Repert. Spec. Nov. Regni Veg. 9: 446. 1911
Synonym: ***Deutzia esquirolii*** (H. L,v.) Rehder (Hwang et al. 2001)

Styrax faberi Perkins, Pflanzenr. (Engler) 4, Fam. 241: 33. 1907
Accepted (Hwang & Grimes 1996)

Styrax faberi var. *acutiserratus*, Pflanzenr. (Engler) 4, Fam. 241: 33. 1907
Synonym: ***Styrax faberi*** var. ***faberi*** (Hwang & Grimes 1996)

Styrax faberi Perkins var. ***amplexifolius*** Chun & F.C.How ex S.M.Hwang, Acta Phytotax. Sin. 18(2): 161. 1980
Accepted (Hwang & Grimes 1996)

Styrax faberi var. ***faberi***, Autonym
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= *Styrax iopilinus* Diels, Notizbl. Königl. Bot. Gart. Berlin 9: 1028. 1926

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Synonym: ***Styrax faberi*** var. ***formosanus*** (Matsum.) S.M. Hwang (Hwang & Grimes 1996)

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Synonym: ***Styrax glaber*** Sw. (Funk et al. 2007)

Styrax ferax J.F.Macbr., Publ. Field Columb. Mus., Bot. Ser. 8: 128. 1930
Synonym: ***Styrax pentlandianus*** J. Rémy (Jørgensen et al. 2013)

Styrax ferrugineus Nees & Martius, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 11(1): 88. 1823
Accepted (Zuloaga et al. (eds.) 2008)
= *Styrax reticulatus* Martius, Reise Bras. (Spix & Martius) 1: 550. 1823
= *Styrax nervosus* A.DC., Prodr. (DC.) 8: 263. 1844
= *Styrax nervosus* A.DC. var. *elongatus* Seub., Fl. Bras. (Martius) 7: 191. 1868
= *Styrax burchellii* Perkins var. *longifolius* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 47. 1907
= *Styrax ferrugineus* Nees & Mart var. *grandifolius* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 51. 1907
= *Styrax floridus* Pohl, Pl. Bras. Icon. Descr. ii. 54. t. 134.
= *Styrax parvifolius* Pohl, Pl. Bras. Icon. Descr. ii. 53. t. 133.

Styrax ferrugineus Nees & Mart var. *grandifolius* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 51. 1907
Synonym: ***Styrax ferrugineus*** Nees & Martius (Jørgensen et al. 2013)

Styrax ferrugineus Pohl, Pl. Bras. Icon. Descr. ii 55. t. 135.
Synonym: ***Styrax pohlii*** A. DC. (Perkins 1907)

Styrax filii Maguire, Mem. New York Bot. Gard. 29: 230 (-231). 1978
Synonym: ***Styrax longipedicellatus*** Steyerm. (Fritsch 2008)

Styrax finlaysonianus Wall. & G.Don, Gen. Hist. 4: 5. 1837
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Styrax floribundus Griff., Not. Pl. Asiat. 4: 287. 1854
Synonym: ***Styrax porterianus*** G. Don (Huang et al. 2003)

Styrax floridus Pohl, Pl. Bras. Icon. Descr. ii. 54. t. 134.
Synonym: ***Styrax ferrugineus*** Nees & Martius (Jørgensen et al. 2013)

Styrax floridus var. *communis* A.DC., Prodr. (DC.) 8: 263. 1844
Synonym: ***Styrax camporum*** Pohl (Fritsch 2013)

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Styrax formosanus var. ***formosanus***, Autonym
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Synonym: ***Styrax suberifolius*** var. ***hayataianus*** (Perkins) K. Mori (Hwang & Grimes 1996)

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Synonym: ***Styrax faberi*** var. ***formosanus*** (Matsum.) S.M. Hwang (Hwang & Grimes 1996)

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Accepted (Jørgensen et al. 2013)

Styrax fukienensis W.W.Sm. & Jeffrey, Notes Roy. Bot. Gard. Edinburgh 9: 130. 1916
Synonym: ***Styrax confusus*** var. ***confusus*** (Hwang & Grimes 1996)

Styrax gardnerianus A.DC., Prodr. [A. P. de Candolle] 8: 263. 1844
Synonym: ***Styrax camporum*** Pohl (Fritsch 2013)

Styrax gardnerianus A.DC. var. *ovatifolius* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 3: 913. 1903
Synonym: ***Styrax camporum*** Pohl (Fritsch 2013)

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Synonym: ***Styrax camporum*** Pohl (Fritsch 2013)

Styrax gentryi P.W.Fritsch, Ann. Missouri Bot. Gard. 84: 723, fig. 1997
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Name Illegitimate, Synonym: ***Styrax americanus*** Lamarck (Gonsoulin 1974)

Styrax glaber Sw., Prodr. 74. 1788
Accepted (Fritsch & Steyermark 2005)
= *Styrax roraimae* Perkins, Bot. Jahrb. Syst. 31: 478. 1901
= *Styrax micrasterus* Perkins, Repert. Spec. Nov. Regni Veg. 2: 24. 1906
= *Styrax glaber* Sw. var. *micranthus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 63. 1907
= *Styrax fanshawei* Sandwith, Kew Bull. 1948: 321.
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= *Styrax tepuiensis* Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 456, fig. 7. 1967

Styrax glaber Sw. var. *micranthus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 63. 1907
Synonym: ***Styrax glaber*** Sw. (Funk et al. 2007)

Styrax glabratus Schott, Syst. Veg. (ed. 16) [Sprengel] 4(2, Cur. Post.): 406. 1827
Accepted (Fritsch 1997)
= *Styrax integerrima* Vell., Fl. Flumin. 183. 1829.
= *Styrax psilophyllus* A.DC., Prodr. (DC.) 8: 266. 1844
= *Styrax lauraceus* Perkins, Bot. Jahrb. Syst. 31: 478. 1901
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= *Styrax erymophyllus* Pohl, Pl. Bras. Icon. Descr. ii. 57. t. 137
= *Styrax leiophyllus* Miers, Lindl. Veg. Kingd. 593a

Styrax glabrescens Bentham, Pl. Hartw. 66.
Accepted (Fritsch 1997)
= *Styrax guatemalensis* Donn.Sm., Bot. Gaz. 15: 27. 1890
= *Styrax glabrescens* var. *pilosus* Perkins, Pflanzenr. IV. 241(Heft 30): 72. 1907
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Synonym: ***Styrax glabrescens*** Bentham (Fritsch 1997)

Styrax grandiflorus Griff., Not. Pl. Asiat. 4: 287. 1854
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax grandifolius Aiton, Hortus Kew. (W. Aiton) 2: 75. 1789
Accepted (Fritsch 2009)
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Styrax guanayanus var. *yutajensis* Maguire, Mem. New York Bot. Gard. 29: 207
Synonym: ***Styrax yutajensis*** (Maguire) P.W. Fritsch (Funk et al. 2007)

Styrax guatemalensis Donn.Sm., Bot. Gaz. 15: 27. 1890
Synonym: ***Styrax glabrescens*** Bentham (Fritsch 1997)

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= *Styrax guyanensis* A.DC. var. *japurensis* A.DC., Fl. Bras. (Martius) 7: 188. 1868
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= *Styrax longifolius* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 166. 1940

Styrax guyanensis A.DC. var. *japurensis* A.DC., Fl. Bras. (Martius) 7: 188. 1868
Synonym: ***Styrax guyanensis*** A. DC. (Jørgensen et al. 2013)

Styrax hainanensis F.C.How, Fl. Hainan. 3: 576 (1974), nom.
Accepted (Hwang & Grimes 1996)

Styrax hainanensis subsp. ***hainanensis***, Autonym
Accepted (Svengsuksa & Vidal 1992)

Styrax hainanensis F.C.How subsp. ***ngokpanensis*** J.E.Vidal, Fl. Cambodge, Laos & Vietnam 26: 170. 1992
Accepted (Svengsuksa & Vidal 1992)

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Synonym: ***Styrax suberifolius*** var. ***hayataianus*** (Perkins) K. Mori (Hwang & Grimes 1996)

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Accepted (Huang et al. 2003)
= *Styrax hemsleyanus* var. *griseus* Rehder, Pl. Wilson. 1(2): 291. 1912
= *Styrax huanus* Rehder, J. Arnold Arbor. 11: 167 (-168). 1930

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Synonym: ***Styrax hemsleyanus*** Diels (Hwang & Grimes 1996)

Styrax heteroclitus J.F.Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 13(5): 230. 1959
Synonym: ***Styrax macrophyllus*** Schott ex Pohl (Jorgensen & Yanez 1999)

Styrax heterotrichus Perkins, Repert. Spec. Nov. Regni Veg. 2: 19. 1906
Accepted (Jorgensen & Yanez 1999)

Styrax hintonii Bullock, Bull. Misc. Inform. Kew 1936: 9.
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax hookeri C.B.Clarke, Fl. Brit. India 3: 589
Accepted (Huang et al. 2003)
= *Styrax macranthus* Perkins, Bot. Jahrb. Syst. 31. 487. 1902
= *Styrax caudatus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 74. 1907
= *Styrax hookeri* var. *yunnanensis* Perkins, Repert. Spec. Nov. Regni Veg. 8: 84. 1910
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= *Styrax perkinsiae* Rehder, Pl. Wilson. 1(2): 292. 1912
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Styrax hookeri var. *yunnanensis* Perkins, Repert. Spec. Nov. Regni Veg. 8: 84. 1910
Synonym: ***Styrax hookeri*** C.B.Clarke (Huang et al. 2003)

Styrax huanus Rehder, J. Arnold Arbor. 11: 167 (-168). 1930
Synonym: ***Styrax hemsleyanus*** Diels (Huang et al. 2003)

Styrax hypargyreus Perkins, Repert. Spec. Nov. Regni Veg. 2: 20. 1906
Accepted (Fritsch 2008)

Styrax hypochryseus Perkins, Bot. Jahrb. Syst. 31: 479. 1901
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Styrax hypoglaucus Perkins, Bot. Jahrb. Syst. 31. 486. 1902
Synonym: ***Styrax tonkinensis*** (Pierre) W. G. Craib ex Hartwich (Hwang & Grimes 1996)

Styrax incarnatus P.W.Fritsch, Ann. Missouri Bot. Gard. 84: 730, fig. 1997
Accepted (Fritsch 1997)

Styrax integerrima Vell., Fl. Flumin. 183. 1829.
Synonym: ***Styrax glabratus*** Schott (Fritsch 1997)

Styrax iopilinus Diels, Notizbl. Königl. Bot. Gart. Berlin 9: 1028. 1926
Synonym: ***Styrax faberi*** var. ***faberi*** (Hwang & Grimes 1996)

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Accepted (Fritsch 1997)
= *Styrax officinalis* L. var. *jaliscanus* (S.Watson) Perkins, Pflanzenr. (Engler) 4, Fam. 241: 82. 1907

Styrax japonicus Siebold & Zucc., Fl. Jap. (Siebold) 1: 53, t. 23. 1838

Accepted (Huang et al. 2003)

= *Styrax grandiflorus* Griff., Not. Pl. Asiat. 4: 287. 1854

= *Styrax seminatus* Farges, Vilm. & Bois, Frutic. Vilm. 181 (1904)

= *Styrax bodinieri* H.Lév., Repert. Spec. Nov. Regni Veg. 4: 332. 1907

= *Styrax duclouxii* Perkins, Repert. Spec. Nov. Regni Veg. 8: 83. 1910

= *Styrax touchanensis* H.Lév., Repert. Spec. Nov. Regni Veg. 11: 64. 1912

= *Styrax kotoensis* Hayata & Hayata, Icon. Pl. Formosan. 9: 68. 1920

= *Styrax japonicus* var. *kotoensis* (Hayata) Masam. & Suzuki, Annual Rep. Taihoku Bot. Gard. 3: 65. 1933

= *Styrax jippei-kawamurai* Yanagita, J. Soc. Forest. 15: 693. 1933

= *Styrax japonicus* var. *iriomotensis* Masam., Masam., Trans. Nat. Hist. Soc. Taiwan 25: 250. 1935

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= *Styrax japonicus* var. *zigzag* Koidz., Acta Phytotax. Geobot. 6: 212. 1937

= *Styrax japonicus* f. *parviflorus* Y. Kimura, J. Jap. Bot. 16: 59. 1940

= *Styrax japonicus* var. *angustifolius*, Acta Phytotax. Geobot. 10: 55. 1941

= *Styrax japonicus* var. *tomentosus* Hatus, J . Jap. Bot. 29: 230. 1954

= *Styrax japonicus* f. *rubicalyx* Satomi, J . Geobot .6: 110. 1957.

= *Styrax japonicus* var. *longipedunculatus* Z.Y.Zhang, F1. Tsinlingensis 1 (4): 395. 1983

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Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

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Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax japonicus var. *tomentosus* Hatus, J . Jap. Bot. 29: 230. 1954
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Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax japonicus f. *jippei-kawakamii* (Yanagita) T.Yamaz., Fl. Jap. (Iwatsuki et al., eds.) 3a: 104. 1993
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax japonicus f. *parviflorus* Y. Kimura, J. Jap. Bot. 16: 59. 1940
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Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

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Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax japonicus f. *tomentosus* (Hatus.) T.Yamaz., Fl. Jap. (Iwatsuki et al., eds.) 3a: 104. 1993
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax jauaensis Steyerm., Bol. Soc. Venez. Ci. Nat. no. 132-133: 390, fig. 1976
Synonym: ***Styrax guanayanus*** Maguire & K.D. Phelps (Fritsch 2008)

Styrax javanicus Blume, Bijdr. Fl. Ned. Ind. 13: 671. 1826
Synonym: ***Alangium chinense*** (Lour.) Harms (Raulston 1992)

Styrax jippei-kawamurai Yanagita, J. Soc. Forest. 15: 693. 1933
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax juncudus Diels, Notizbl. Königl. Bot. Gart. Berlin 9: 198. 1924
Synonym: ***Styrax confusus*** var. ***confusus*** (Hwang & Grimes 1996)

Styrax klotzschii Seub., Fl. Bras. (Martius) 7: 194. 1868
Synonym: ***Styrax latifolius*** Pohl (Fritsch 2010)

Styrax kotoensis Hayata & Hayata, Icon. Pl. Formosan. 9: 68, descr. ampl. 1920
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax lacei W.W.Sm., Bull. Misc. Inform. Kew 1911, 344.
Synonym: ***Parastyrax lacei*** (W.W. Sm.) W.W. Sm. (Hwang & Grimes 1996)

Styrax laevigatus Ait., Hortus Kew. (W. Aiton) 2: 75. 1789
Synonym: ***Styrax americanus*** Lamarck (Gonsoulin 1974)

Styrax laevis Walter, Fl. Carol. 140. 1788.
Synonym: ***Styrax americanus*** Lamarck (Gonsoulin 1974)

Styrax lanceolatus P.W.Fritsch, Ann. Missouri Bot. Gard. 84: 733. 1997
Accepted (Fritsch 1997)
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Styrax lancifolius Klotzsch ex Seub., Fl. Bras. (Martius) 7: 191. 1868
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= *Styrax martii* Seub. var. *gracilius* Warm., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1874: 64. 1875

Styrax langkongensis W.W.Sm. & Hand.-Mazz., Symb. Sin. Pt. vII. 803 (1936), descr. ampl.
Synonym: ***Styrax limprichtii*** Lingelsh. & Borza (Huang et al. 2003)

Styrax latifolius Pohl, Pl. Bras. Icon. Descr. ii. 60. t. 140.
Accepted (Fritsch 2010)
= *Styrax albus* Martius ex Spreng., Syst. Veg. (ed. 16) [Sprengel] 2: 285. 1825
= *Styrax longiflorus* A. DC, Prodr. [A. P. de Candolle] 8: 264. 1844
= *Styrax klotzschii* Seub., Fl. Bras. (Martius) 7: 194. 1868

Styrax lauraceus Perkins, Bot. Jahrb. Syst. 31: 478. 1901
Synonym: ***Styrax glabratus*** Schott (Fritsch 1997)

Styrax ledermannii Perkins, Gatt. Styracac. 20 (1928), in clavi; Perkins in Notizbl. Bot. Gart. Berlin, x.457
Synonym: ***Styrax agrestis*** (Lour.) G. Don (Van Steenis 1949)

Styrax leiophyllus Miers, Lindl. Veg. Kingd. 593a.
Synonym: ***Styrax glabratus*** Schott (Fritsch 1997)

Styrax leprosus Hook. & Arn., J. Bot. (Hooker) 1: 282. 1834
Accepted (Fritsch 2010)
= *Styrax leprosus* Hook. & Arn. f. *latifolius* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 3: 913. 1903

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Synonym: ***Styrax leprosus*** Hook. & Arn. (Fritsch 2010)

Styrax leptactinosus Cuatrec., Fieldiana, Bot. 27: 112. 1950
Synonym: ***Styrax pentlandianus*** J. Rémy (Jorgensen & Yanez 1999)

Styrax limoncillo Miers, J. Linn. Soc., Bot. 17: 292. 1879
Synonym: ***Symplocos limoncillo*** Bonpl. (Kelly & Almeda 2005)

Styrax limprichtii Lingelsh. & Borza, Repert. Spec. Nov. Regni Veg. 13: 386. 1914
Accepted (Huang et al. 2003)
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Styrax litseoides J.E.Vidal, Fl. Cambodge, Laos & Vietnam 26: 159. 1992
Accepted (Svengsuksa & Vidal 1992)

Styrax longiflorus A. DC, Prodr. [A. P. de Candolle] 8: 264. 1844
Synonym: ***Styrax latifolius*** Pohl (Zuloaga et al. (eds.) 2008)

Styrax longifolius Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 166. 1940
Synonym: *Styrax guyanensis* A. DC. (Jorgensen et al. 2013)

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Accepted (Fritsch 2010)
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Styrax loxensis Perkins, Pflanzenr. (Engler) 4, Fam. 241: 41. 1907
Synonym: ***Styrax tomentosus*** Bonpl. (Jorgensen & Yanez 1999)

Styrax macranthus Perkins, Bot. Jahrb. Syst. 31. 487. 1902
Synonym: ***Styrax hookeri*** C.B.Clarke (Huang et al. 2003)

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Accepted (Fritsch 2008)

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Accepted (Fritsch 2010)
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Synonym: ***Styrax tonkinensis*** (Pierre) W. G. Craib ex Hartwich (Hwang & Grimes 1996)

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Synonym: ***Styrax trichocalyx*** Perkins (Fritsch 2008)

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Accepted (Fritsch 2004)
= *Styrax martii* var. *microphyllus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 40. 1907

Styrax martii Seub. var. *gracilius* Warm., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1874: 64. 1875
Synonym: ***Styrax lancifolius*** Klotzsch ex Seub. (Fritsch 2004)

Styrax martii var. *microphyllus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 40. 1907
Synonym: ***Styrax martii*** Seub. (Fritsch 2004)

Styrax martii var. *rotundatus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 40. 1907
Synonym: ***Styrax rotundatus*** (Perkins) P.W.Fritsch (Fritsch 2004)

Styrax mathewsii Perkins, Repert. Spec. Nov. Regni Veg. 2: 17. 1906
Synonym: ***Styrax pavonii*** A.DC. (Jorgensen & Yanez 1999, Fritsch 2008)

Styrax matsumuraei Perkins, Pflanzenr. (Engler) 4, Fam. 241: 34. 1907
Synonym: ***Styrax faberi*** var. ***formosanus*** (Matsum.) S.M. Hwang (Hwang & Grimes 1996)

Styrax micranthus Perkins, Repert. Spec. Nov. Regni Veg. 2: 17. 1906
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax micrasterus Perkins, Repert. Spec. Nov. Regni Veg. 2: 24. 1906
Synonym: ***Styrax glaber*** Sw. (Fritsch 2008)

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Accepted (Idárraga-Piedrahita et al. (eds.) 2011)

Styrax mollis Dunn, Bull. Misc. Inform. Kew 1911, 273.
Synonym: ***Styrax confusus*** var. ***confusus*** (Hwang & Grimes 1996)

Styrax myristicifolius Perkins, Bot. Jahrb. Syst. 31: 481. 1902
Synonym: ***Styrax argenteus*** C. Presl (Fritsch 1997)

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= *Styrax duidae* Steyerm. subsp. *paruae* Maguire, Mem. New York Bot. Gard. 29: 213 (-215), fig. 1978
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Styrax nervosus A.DC., Prodr. (DC.) 8: 263. 1844
Synonym: ***Styrax ferrugineus*** Nees & Martius (Jorgensen et al. 2013)

Styrax nervosus A.DC. var. *elongatus* Seub., Fl. Bras. (Martius) 7: 191. 1868
Synonym: ***Styrax ferrugineus*** Nees & Martius (Jorgensen et al. 2013)

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Accepted (Wallnöfer 1997)

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Accepted (Fuentes et al. 2009)

Styrax obassia Siebold & Zucc., Fl. Jap. (Siebold) 1: 93 (t. 46). 1839
Accepted (Huang et al. 2003)

Styrax obliquinervius A.DC., Prodr. (DC.) 8: 263. 1844
Synonym: ***Styrax camporum*** Pohl (Fritsch 2013)

Styrax oblongus A.DC., Prodr. (DC.) 8: 261. 1844
Accepted (Fritsch 2010)
= *Styrax tarapotensis* Perkins, Bot. Jahrb. Syst. 31: 479. 1901

Styrax obovatus Ridl., J. Straits Branch Roy. Asiat. Soc. 61: 28. 1912
Synoymn: ***Symplocos pendula*** var. ***hirtistylis*** (C.B. Clarke) Noot. (Van Steenis 1949)

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Accepted (Gonsoulin 1974)

Styrax occidentalis Thunb., Styrac. 8. 1813
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Styrax ochraceus Urb., Symb. Antill. (Urban). 7(3): 331. 1912
Accepted (Gonsoulin 1974)

Styrax octandrus L'Hér. ex Ait., Hortus Kew. (W. Aiton) 2: 75. 1789
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Styrax odoratissimus Champ. ex Bentham, Hooker's J. Bot. Kew Gard. Misc. 4: 304. 1852
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Accepted (Tutin 1973)

Styrax officinalis L. var. *californicus* (Torr.) Rehder, Mitt. Deutsch. Dendrol. Ges. 1915: 226.
Synonym: ***Styrax redivivus*** (Torrey) L. C. Wheeler (Fritsch 2006)

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Synonym: ***Styrax redivivus*** (Torrey) L. C. Wheeler (Fritsch 2006)

Styrax officinalis L. var. *jaliscanus* (S.Watson) Perkins, Pflanzenr. (Engler) 4, Fam. 241: 82. 1907
Synonym: ***Styrax jaliscanus*** S. Watson (Fritsch 1997)

Styrax officinalis L. var. *redivivus* (Torr.) R.A.Howard, Sida 5(5): 337. 1975
Synonym: ***Styrax redivivus*** (Torrey) L. C. Wheeler

Styrax officinalis sensu Walt., Fl. Carol. 140. 1788.
Synonym: ***Styrax grandifolius*** Aiton (Gonsoulin 1974)

Styrax oliganthes Steenis, Bull. Jard. Bot. Buitenzorg ser. III, xii. 223, in clavi, 241 (1932)
Synonym: ***Styrax subpaniculatus*** Jungh. & de Vriese (Huang et al. 2003)

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Synonym: ***Styrax suberifolius*** var. ***suberifolius*** (Hwang & Grimes 1996)

Styrax omuk B.Walln., Ann. Naturhist. Mus. Wien 99B: 712. 1997
Accepted (Wallnöfer 1997)

Styrax orizabensis Perkins, Repert. Spec. Nov. Regni Veg. 2: 25. 1906
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax ovatus A.DC., Prodr. (DC.) 8: 267. 1844
Synonym: ***Styrax pavonii*** A. DC. (Fritsch 2008)

Styrax pachyphyllus Mehr. & Chun, Sunyatsenia 2(3?4): 302?303, f. 39. 1935
Name Illegitimate, Synonym: ***Styrax hainanensis*** F.C. How (Hwang & Grimes 1996)

Styrax pachyphyllus Pilg., Bot. Jahrb. Syst. 30(2): 182. 1901
Synonym: ***Styrax pohlii*** A. DC. (Jorgensen et al. 2013)

Styrax pallidus A.DC., Prodr. (DC.) 8: 261. 1844
Accepted (Fritsch 2010)
= *Styrax cinereus* M.F.Silva, Acta Amazonica 1(1): 23 (1971); et in l.c. 1(3): 21 (1971)

Styrax panamensis Standl., Contr. U.S. Natl. Herb. 18: 121. 1916
Accepted (Fritsch 1997)

Styrax paralleloneurus Perkins, Bot. Jahrb. Syst. 31. 484. 1902
Accepted (Svengsuksa & Vidal 1992)

Styrax parviflorus Merr., J. Arnold Arbor. 8: 15. 1927
Synonym: ***Huodendron biaristatum*** var. ***parviflorum*** (Merr.) Rehder (Hwang & Grimes 1996)

Styrax parvifolius Pohl, Pl. Bras. Icon. Descr. ii. 53. t. 133.
Synonym: ***Styrax ferrugineus*** Nees & Martius (Fritsch 2013)

Styrax pauciflorus A.DC., Prodr. (DC.) 8: 265. 1844
Accepted (Fritsch 2010)

Styrax pavonii A.DC., Prodr. (DC.) 8: 266. 1844
Accepted (Fritsch 2008)
= *Styrax cordatus* A.DC., Prodr. (DC.) 8: 267. 1844
= *Styrax ovatus* A.DC., Prodr. (DC.) 8: 267. 1844
= *Styrax argyrophyllus* Perkins, Repert. Spec. Nov. Regni Veg. 2: 18. 1906
= *Styrax mathewsii* Perkins, Repert. Spec. Nov. Regni Veg. 2: 17. 1906
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Synonym: ***Styrax sieberi*** Perkins (Jorgensen et al. 2013)

Styrax pearcei var. *bolivianus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 46. 1907
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= *Styrax subheterotrichus* Herzog, Meded. Rijks-Herb. 40: 31. 1921
= *Styrax ferax* J.F.Macbr., Publ. Field Columb. Mus., Bot. Ser. 8: 128. 1930
= *Styrax socialis* J.F.Macbr., Candollea 5: 398. 1934
= *Styrax buchtienii* Sleumer, Repert. Spec. Nov. Regni Veg. 41: 125. 1936
= *Styrax leptactinosus* Cuatrec., Fieldiana, Bot. 27: 112. 1950

Styrax perkinsiae Rehder, Pl. Wilson. 1(2): 292. 1912
Synonym: ***Styrax hookeri*** C.B.Clarke (Huang et al. 2003)

Styrax peruvianus Zahlbr., Ann. K. K. Naturhist. Hofmus. 7: 4. 1892
Accepted (Fritsch 1997)

Styrax philadelphoides Perkins, Pflanzenr. (Engler) 4, Fam. 241: 32. 1907
Synonym: ***Styrax confusus*** var. ***confusus*** (Hwang & Grimes 1996)

Styrax philadelphoides var. *superbus* Chun, Sunyatsenia 1(4): 296. 1934
Synonym: ***Styrax confusus*** var. ***superbus*** (Chun) S.M. Hwang (Hwang & Grimes 1996)

Styrax philippinensis Merr. & Quisumb., Philipp. J. Sci. 56: 313. 1935
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax pilosus (Perkins) Standl., Contr. U.S. Natl. Herb. 23: 1129. 1924
Synonym: ***Styrax glabrescens*** Bentham (Fritsch 2005)

Styrax platanifolius Engelm. ex Torr., Smithsonian Contr. Knowl. 6[61]: 4. 1853
Accepted (Fritsch 2009)

Styrax platanifolius Engelm. ex Torr. subsp. ***mollis*** P.W.Fritsch, Ann. Missouri Bot. Gard. 84(4): 742, f. 66. 1998
Accepted (Fritsch 1997)
= *Styrax platanifolius* var. *mollis* (P.W.Fritsch) B.L.Turner, Sida 19(2): 261. 2000

Styrax platanifolius subsp. ***platanifolius*** Engelm. ex Torr., Autonym
Accepted (Fritsch 2009)

Styrax platanifolius Engelm. ex Torr. subsp. ***stellatus*** (Cory) P.W.Fritsch, Ann. Missouri Bot. Gard. 84(4): 743. 1998
Accepted (Fritsch 2009)
= *Styrax platanifolius* var. *stellatus* Cory, Madroño 7: 111. 1943

Styrax platanifolius subsp. ***texanus*** (Cory) P.W.Fritsch, Ann. Missouri Bot. Gard. 84: 744. 1998
Accepted (Fritsch 2009)
= Styrax texanus Cory, Madroño 7: 112. 1943
= Styrax platanifolius var. *texanus* (Cory) B.L. Turner, Sida 19(2): 261. 2000

Styrax platanifolius subsp. ***youngiae*** (Cory) P.W.Fritsch, Ann. Missouri Bot. Gard. 84: 744. 1998
Accepted (Fritsch 2009)
= *Styrax youngiae* Cory, Madroño 7(4): 113-115. 1943
= *Styrax platanifolius* var. *youngiae* (Cor) B.L.Turner, Sida 19(2): 261. 2000

Styrax platanifolius var. *mollis* (P.W.Fritsch) B.L.Turner, Sida 19(2): 261. 2000
Synonym: ***Styrax platanifolius*** subsp. ***mollis*** P.W.Fritsch (Fritsch 1997)

Styrax platanifolius var. *stellatus* Cory, Madroño 7: 111. 1943
Synonym: ***Styrax platanifolius*** subsp. ***stellatus*** (Cory) P.W. Fritsch (Fritsch 2009)

Styrax platanifolius var. *texanus* (Cory) B.L. Turner, Sida 19(2): 261. 2000
Synonym: ***Styrax platanifolius*** subsp. ***texanus*** (Cory) P.W. Fritsch (Fritsch 2009)

Styrax platanifolius var. *youngiae* (Cory) B.L.Turner, Sida 19(2): 261. 2000
Synonym: ***Styrax platanifolius*** subsp. ***youngiae*** (Cory) P.W.Fritsch (Fritsch 2009)

Styrax pohlii A.DC., Prodr. (DC.) 8: 264. 1844
Accepted (Fritsch 2010)
= *Styrax ambiguus* Seub., Fl. Bras. (Martius) 7: 192. 1868
= *Styrax punctatus* A.DC., Prodr. (DC.) 8: 264. 1844
= *Styrax pachyphyllus* Pilg., Bot. Jahrb. Syst. 30(2): 182. 1901
= *Styrax ambiguus* Seub. var. *apiculatus* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 3: 914. 1903
= *Styrax bogotensis* Perkins, Repert. Spec. Nov. Regni Veg. 2: 19. 1906
= *Styrax pohlii* f. *calvescens* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 41. 1907
= *Styrax discolor* M.F.Silva, Acta Amazonica 2(1): 17, fig. 1972
= *Styrax tafelbergensis* Maguire, Mem. New York Bot. Gard. 29: 221 (-223). 1978
= *Styrax ferrugineus* Pohl, Pl. Bras. Icon. Descr. ii 55. t. 135.

Styrax pohlii f. *calvescens* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 41. 1907
Synonym: ***Styrax pohlii*** A. DC. (Fritsch 2010)

Styrax poissonianus Perkins, Repert. Spec. Nov. Regni Veg. 2: 18. 1906
Synonym: ***Styrax tomentosus*** Bonpl. (Jorgensen & Yanez 1999)

Styrax polyanthus Perkins, Bot. Jahrb. Syst. 31: 479. 1901
Synonym: ***Styrax argenteus*** C. Presl (Fritsch 1997)

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Synonym: ***Styrax warscewiczii*** Perkins (Fritsch 1997)

Styrax polyspermus C.B.Clarke in Hook.f., Fl. Brit. India 3: 590. 1882
Synonym: ***Bruinsmia polysperma*** (C.B. Clarke) Steenis (Hwang & Grimes 1996)

Styrax porterianus Wall. & G.Don, Gen. Hist. 4: 5. 1837
Accepted (Huang et al. 2003)
= *Styrax floribundus* Griff., Not. Pl. Asiat. 4: 287. 1854
= *Styrax betongensis* H.R.Fletcher, Bull. Misc. Inform. Kew 1937, 509

Styrax portoricensis Krug & Urb., Bot. Jahrb. Syst. 15(3): 337. 1892
Accepted (Gonsoulin 1974)

Styrax prunifolius Perkins, Bot. Jahrb. Syst. 31. 486. 1902
Synonym: ***Styrax odoratissimus*** Champ. ex Bentham (Hwang & Grimes 1996)

Styrax pseudargyrophyllus Sleumer, Repert. Spec. Nov. Regni Veg. 41: 125. 1936
Synonym: ***Styrax pavonii*** A. DC. (Jorgensen & Yanez 1999)

Styrax psilophyllus A.DC., Prodr. (DC.) 8: 266. 1844
Synonym: ***Styrax glabratus*** Schott (Fritsch 1997)

Styrax pulverulentus Michx., Fl. Bor.-Amer. (Michaux) 2: 41. 1803
Synonym: ***Styrax americanus*** Lamarck (Fritsch 2009)

Styrax punctatus A.DC., Prodr. (DC.) 8: 264. 1844
Synonym: ***Styrax pohlii*** A. DC. (Jorgensen et al. 2013)

Styrax punctatus Don.Sm.,
Name Illegitimate, Synonym: ***Styrax argenteus*** (Gonsoulin 1974)

Styrax radians P.W.Fritsch, Ann. Missouri Bot. Gard. 84: 745, fig. 1997
Accepted (Fritsch 1997)

Styrax ramirezii Greenm., Proc. Amer. Acad. Arts 34: 568. 1899
Accepted (Fritsch 1997)
= *Styrax cyathocalyx* Perkins, Repert. Spec. Nov. Regni Veg. 2: 24. 1906
= *Styrax micranthus* Perkins, Repert. Spec. Nov. Regni Veg. 2: 17. 1906
= *Styrax orizabensis* Perkins, Repert. Spec. Nov. Regni Veg. 2: 25. 1906
= *Styrax ramirezii* var. *micranthus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 54. 1907
= *Styrax ramirezii* var. *orizabensis* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 54. 1907
= *Styrax hintonii* Bullock, Bull. Misc. Inform. Kew 1936: 9
= *Styrax argenteus* C.Presl var. *hintonii* (Bullock) Gonsoulin, Sida 5: 226. 1974
= *Styrax ramirezii* var. *hintonii* (Bullock) Gonsoulin, Sida 5: 226. 1974
= Styrax argenteus var. *micranthus* (Perkins) D'Arcy, Ann. Missouri Bot. Gard. 66: 169. 1979
= Styrax argenteus var. *ramirezii* (Greenm.) Gonsoulin, Sida 5: 227. 1974

Styrax ramirezii var. *hintonii* (Bullock) Gonsoulin, Sida 5: 226. 1974.
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax ramirezii var. *micranthus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 54. 1907
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax ramirezii var. *orizabensis* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 54. 1907
Synonym: ***Styrax ramirezii*** Greenm. (Fritsch 1997)

Styrax redivivus (Torr.) L.C.Wheeler, Bull. S. Calif. Acad. Sci. 44: 94. 1946
Accepted (Fritsch 2009)
= Styrax officinalis Linnaeus var. *californicus* (Torr.) Rehder, Mitt. Deutsch. Dendrol. Ges. 1915: 226.
= Styrax officinalis Linnaeus var. *fulvescens* (Eastw.) Munz & I.M.Johnst., Bull. Torrey Bot. Club 51: 297. 1924
= Styrax officinalis Linnaeus var. *redivivus* (Torr.) R.A.Howard, Sida 5(5): 337. 1975

Styrax reticulatus Martius, Reise Bras. (Spix & Martius) 1: 550. 1823
Synonym: ***Styrax ferrugineus*** Nees & Martius (Jorgensen et al. 2013)

Styrax rigidifolius Idrobo & R.E.Schult. Bot. Mus. Leafl. 13: 328. 1949.
Uncertain

Styrax rigidifolius var. *yapobodensis* Idrobo & R.E. Schult., Bot. Mus. Leafl. 13: 332, tab. 38, G & H. 1949
Synonym: ***Styrax yapobodensis*** (Idrobo & R.E.Schult.) Steyerm. (Steyermark 1953)

Styrax roraimae Perkins, Bot. Jahrb. Syst. 31: 478. 1901
Synonym: ***Styrax glaber*** Sw. (Zuloaga et al. (eds.) 2008)

Styrax roseus Dunn, Bull. Misc. Inform. Kew 1911, 273.
Synonym: ***Styrax hookeri*** C.B.Clarke (Huang et al. 2003)

Styrax rossamala Reinw. ex Steud., Nomencl. Bot. [Steudel], ed. 2. ii. 651, nomen.
Synonym: ***Alangium chinense*** (Lour.) Harms (Raulston 1992)

Styrax rostratus Hosok., Trans. Nat. Hist. Soc. Formosa 28: 65. 1938
Synonym: ***Styrax agrestis*** (Lour.) G. Don (Hwang & Grimes 1996)

Styrax rotundatus (Perkins) P.W.Fritsch, Novon 14(1): 52. 2004
Accepted (Fritsch 2010)
= *Styrax martii* var. *rotundatus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 40. 1907

Styrax rubifolius Guillaumin, Bull. Soc. Bot. France 70: 884. 1924
Synonym: ***Styrax dasyanthus*** Perkins (Hwang & Grimes 1996)

Styrax rufopilosus Svengs., Fl. Cambodge, Laos & Vietnam 26: 154. 1992
Accepted (Svengsuksa & Vidal 1992)

Styrax rugosus Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40(1): 61. 1871
Accepted (Hwang & Grimes 1996)

Styrax rugosus var. *formosanus* Matsum., Bot. Mag. (Tokyo) 15(172): 76. 1901
Synonym: ***Styrax faberi*** var. ***formosanus*** (Matsum.) S.M. Hwang (Hwang & Grimes 1996)

Styrax schultzei Perkins, Notizbl. Bot. Gart. Berlin-Dahlem 10: 458. 1928
Accepted (Renner et al. 1990)

Styrax seminatus Farges, Vilm. & Bois, Frutic. Vilm. 181 (1904); Perkins in Engl. Pflanzenr. Styracac.73 (1907)
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Perkins 1907)

Styrax serrulatus Roxb., Fl. Ind. (Roxburgh) 2: 415 (-416). 1832
Accepted (Hwang & Grimes 1996)

Styrax serrulatus var. *latifolius* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 37. 1907
Synonym: ***Styrax buchanii*** W.W. Smith (Huang et al. 2003)

Styrax serrulatus var. *vestitus* Hemsl., J. Linn. Soc., Bot. 26(173): 77. 1889
Synonym: ***Styrax confusus*** var. ***confusus*** (Hwang & Grimes 1996)

Styrax shiraianus Makino, Bot. Mag. (Tokyo) 12: 50. 1868
Accepted (Huang et al. 2003)
= *Styrax shiraianus* var. *discolor* Nakai, J . Jap. Bot. 14: 6 31. 1938

Styrax shiraianus var. *discolor* Nakai, J . Jap. Bot. 14: 6 31. 1938
Synonym: ***Styrax shiraianus*** Makino (Huang et al. 2003)

Styrax shweliensis W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 12: 236. 1920
Synonym: ***Styrax hookeri*** C.B.Clarke (Huang et al. 2003)

Styrax sieberi Perkins, Pflanzenr. (Engler) 4, Fam. 241: 44. 1907
Accepted (Fritsch 2010)
= *Styrax barbatus* Willd. ex Seub., Fl. Bras. (Martius) 7: 188. 1868
= *Styrax burchellii* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 46. 1907
= *Styrax pearcei* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 46. 1907
= *Styrax pearcei* var. *bolivianus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 46. 1907

Styrax sipapoanus Maguire, Mem. New York Bot. Gard. 29: 215, figs. 1978
Accepted (Fritsch & Steyermark 2005)

Styrax socialis J.F.Macbr., Candollea 5: 398. 1934
Synonym: ***Styrax pentlandianus*** J. Rémy (Jorgensen et al. 2013)

Styrax squamulosus M.F.Silva, Acta Amazonica 1(1): 23. 1971 Acta Amazonica 1(3): 23, f. 2. 1971
Synonym: ***Styrax glabratus*** Schott (Fritsch 1997)

Styrax steyermarkii P.W.Fritsch, Ann. Missouri Bot. Gard. 84: 751, fig. 1997
Accepted (Fritsch 1997)

Styrax subargenteus Sleumer, Repert. Spec. Nov. Regni Veg. 41: 126. 1936
Accepted (Zuloaga et al. (eds.) 2008)

Styrax subcordatus Moric., Pl. Nouv. Am. 117. t. 71.
Synonym: ***Styrax camporum*** Pohl (Zuloaga et al. (eds.) 2008)

Styrax subcrenatus Hand.-Mazz., Oesterr. Bot. Z. 80: 342. 1931
Synonym: ***Styrax agrestis*** (Lour.) G. Don (Hwang & Grimes 1996)

Styrax subdenticulatus Miq., Fl. Ned. Ind., Eerste Bijv. 3: 474. 1861 [Dec 1861] Fl. Ind. Bat. Suppl. 474. 1861
Synonym: ***Styrax subpaniculatus*** Jungh. & de Vriese (Huang et al. 2003)

Styrax suberifolius Hook. & Arn., Bot. Beechey Voy. 196 (t. 40). 1837
Accepted (Hwang & Grimes 1996)

Styrax suberifolius var. *caloneurus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 61. 1907
Synonym: ***Styrax suberifolius*** var. ***suberifolius*** (Hwang & Grimes 1996)

Styrax suberifolius var. *fargesii* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 61. 1907
Synonym: ***Styrax suberifolius*** var. ***suberifolius*** (Hwang & Grimes 1996)

Styrax suberifolius var. ***hayataianus*** (Perkins) K. Mori, Trans. Nat. Hist. Soc. Taiwan 25: 418. 1935
Accepted (Hwang & Grimes 1996)
= *Styrax hayataianus* Perkins, Repert. Spec. Nov. Regni Veg. 8: 82. 1910
= *Styrax formosanus* var. *hayataianus* (Perkins) H.L. Li, Woody Fl. Taiwan 753. 1963

Styrax suberifolius var. ***suberifolius***, Autonym
Accepted (Hwang & Grimes 1996)
= *Styrax caloneurus* Perkins, Bot. Jahrb. Syst. 31. 484. 1902
= *Styrax suberifolius* var. *caloneurus* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 61. 1907
= *Styrax suberifolius* var. *fargesii* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 61. 1907
= *Styrax oligophlebius* Merr. ex H.L.Li, J. Arnold Arbor. 24: 451. 1943

Styrax subheterotrichus Herzog, Meded. Rijks-Herb. 40: 31. 1921
Synonym: ***Styrax pentlandianus*** J. Rémy (Jorgensen et al. 2013)

Styrax subleprosum Klotzsch, Fl. Brit. Guian. 3: 1087. 1848.
Name Invalid, Synonym: ***Styrax glaber*** Sw. (Fritsch 2008)

Styrax subniveus Merr. & Chun, Sunyatsenia 1: 78. 1930
Synonym: ***Styrax tonkinensis*** (Pierre) W. G. Craib ex Hartwich (Huang et al. 2003)

Styrax subpaniculatus Jungh. & de Vriese, Pl. Nov. Ind. Bat. 1: 9 (t. 3). 1845
Accepted (Huang et al. 2003)
= *Styrax subdenticulatus* Miq., Fl. Ned. Ind., Eerste Bijv. 3: 474. 1861 [Dec 1861] Fl. Ind. Bat. Suppl. 474. 1861
= *Styrax oliganthes* Steenis, Bull. Jard. Bot. Buitenzorg ser. III, xii. 223, in clavi, 241 (1932)

Styrax supaii Chun & F.Chun, Sunyatsenia 3: 34. 1935
Accepted (Huang et al. 2003)

Styrax tafelbergensis Maguire, Mem. New York Bot. Gard. 29: 221 (-223). 1978
Synonym: ***Styrax pohlii*** A. DC. (Jorgensen et al. 2013)

Styrax tarapotensis Perkins, Bot. Jahrb. Syst. 31: 479. 1901
Synonym: ***Styrax oblongus*** (Ruiz & Pav.) A. DC. (Jorgensen et al. 2013)

Styrax tepuiensis Steyerm. & Maguire, Mem. New York Bot. Gard. 17(1): 456, fig. 7. 1967
Synonym: ***Styrax glaber*** Sw. (Zuloaga et al. (eds.) 2008)

Styrax tepuiensis subsp. *guaiquinimae* Steyerm. & Maguire, Mem. New York Bot. Gard. 29: 218. 1978
Synonym: ***Styrax guaiquinimae*** (Steyerm. & Maguire) P.W. Fritsch (Funk et al. 2007)

Styrax tepuiensis subsp. *huachamacarii* Maguire & Steyerm., Mem. New York Bot. Gard. 29: 218-220. 1978
Synonym: ***Styrax longipedicellatus*** Steyerm. (Fritsch 2008)

Styrax tessmannii Perkins, Notizbl. Bot. Gart. Berlin-Dahlem 10: 459. 1928
Synonym: ***Styrax guyanensis*** A. DC. (Jorgensen et al. 2013)

Styrax texanus Cory, Madroño 7: 112. 1943
Synonym: ***Styrax platanifolius*** subsp. ***texanus*** (Cory) P.W. Fritsch (Fritsch 2009)

Styrax tibeticus J.Anthony, Notes Roy. Bot. Gard. Edinburgh 15: 245. 1927
Synonym: ***Huodendron tibeticum*** (J. Anthony) Rehder (Hwang & Grimes 1996)

Styrax tinifolius G.Don, Gen. Hist. 4: 5. 1837
Synonym: ***Clethra occidentalis*** (L.) Kuntze (Sleumer 1967)

Styrax tomentosus Bonpl., Nov. Gen. Sp. (quarto ed.) 3: 261. 1818
Accepted (Jorgensen & Yanez 1999)
= *Styrax poissonianus* Perkins, Repert. Spec. Nov. Regni Veg. 2: 18. 1906
= *Styrax loxensis* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 41. 1907

Styrax tomentosus Kunth., Pl. Aequinoct. 2: 72, t. 101. 1799
Name Illegitimate (Tropicos.org)

Styrax tonkinensis Craib ex Hartwich, Apotheker-Zeitung xxviii. 698. 1913
Accepted (Huang et al. 2003)
= *Styrax hypoglaucus* Perkins, Bot. Jahrb. Syst. 31. 486. 1902
= *Styrax macrothyrsus* Perkins, Bot. Jahrb. Syst. 31. 485. 1902
= *Styrax subniveus* Merr. & Chun, Sunyatsenia 1: 78. 1930

Styrax touchanensis H.Lév., Repert. Spec. Nov. Regni Veg. 11: 64. 1912
Synonym: ***Styrax japonicus*** Siebold & Zucc. (Huang et al. 2003)

Styrax trichocalyx Perkins, Repert. Spec. Nov. Regni Veg. 2: 22. 1906
Accepted (Fritsch 2008)
= Styrax macrotrichus Perkins, Repert. Spec. Nov. Regni Veg. 2: 23. 1906

Styrax trichostemon P.W.Fritsch, Novon 14(1): 53 (-56; figs. 3-4). 2004
Accepted (Ulloa Ulloa & Neill 2005)

Styrax tuxtlensis P.W.Fritsch, Ann. Missouri Bot. Gard. 84: 753, fig. 1997
Accepted (Fritsch 1997)

Styrax uxpanapensis P.W.Fritsch, Novon 15(3): 421 (-424; fig. 1). 2005
Accepted (Fritsch 1997)

Styrax varians Seub., Fl. Bras. (Martius) 7: 189. 1868
Synonym: ***Styrax camporum*** Pohl (Fritsch 2013)

Styrax veitchiorum Hemsl. & E.H.Wilson, Bull. Misc. Inform. Kew 1906, 161.
Synonym: ***Styrax odoratissimus*** Champ. ex Bentham (Huang et al. 2003)

Styrax vestitus Lundell, Wrightia 4: 121. 1969
Synonym: ***Styrax glabrescens*** Bentham (Fritsch 1997)

Styrax vidalianus Sleumer in Burret, Notizbl. Bot. Gart. Berlin-Dahlem 13: 499. 1937
Synonym: ***Styrax pavonii*** A. DC. (Jorgensen & Yanez 1999)

Styrax vilcabambae (D.R.Simpson) B.Walln., Ann. Naturhist. Mus. Wien 99B: 715. 1997
Accepted (Wallnöfer 1997)

Styrax villosus Blume, Bijdr. Fl. Ned. Ind. 13: 671. 1826
Synonym: ***Alangium villosum*** (Blume) Wangerin (Perkins 1907)

Styrax vulcanicola Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 264. 1940
Synonym: ***Styrax magnus*** Lundell (Fritsch 1997)

Styrax warburgii Perkins, Pflanzenr. (Engler) 4, Fam. 241: 27. 1907
Synonym: ***Styrax agrestis*** (Lour.) G. Don (Van Steenis (1949))

Styrax warscewiczii Perkins, Bot. Jahrb. Syst. 31: 480. 1901
Accepted (Fritsch 1997)
= *Styrax polyneurus* Perkins, Bot. Gaz. 35: 5. 1903

Styrax weberbaueri Perkins, Repert. Spec. Nov. Regni Veg. 2: 16. 1906
Synonym: ***Styrax pavonii*** A. DC. (Jorgensen & Yanez 1999)

Styrax wilsonii Rehder, Pl. Wilson. 1(2): 293. 1912
Accepted (Huang et al. 2003)

Styrax wurdackiorum Steyerm., Acta Bot. Venez. 10: 240 (-241). 1975
Accepted (Fritsch 2008)

Styrax wuyuanensis S.M.Hwang, Acta Phytotax. Sin. 18(2): 160. 1980
Accepted (Hwang & Grimes 1996)

Styrax yapobodensis (Idrobo & R.E.Schult.) Steyerm., Fieldiana, Bot. 28: 492. 1953
Accepted (Steyermark 1953)
= *Styrax rigidifolius* var. *yapobodensis* Idrobo & R.E. Schult., Bot. Mus. Leafl. 13: 332, tab. 38, G & H. 1949

Styrax youngiae Cory, Madroño 7(4): 113-115. 1943
Synonym: ***Styrax platanifolius*** subsp. ***youngiae*** (Cory) P.W. Fritsch (Fritsch 1997)

Styrax yutajensis (Maguire) P.W.Fritsch, Novon 14(1): 56. 2004
Accepted (Fritsch 2008)
= *Styrax guanayanus* var. *yutajensis* Maguire, Mem. New York Bot. Gard. 29: 207

Styrax zhejiangensis S.M.Hwang & L.L.Yu, Acta Bot. Austro Sin. 1: 75. 1983
Synonym: ***Styrax macrocarpus*** Cheng (Huang et al. 2003)

Uncertain Names

Styrax angustifolius Buc'hoz, Herb. Am. t. 26.

Styrax anomalus Sleumer, Repert. Spec. Nov. Regni Veg. 41: 124. 1936

Styrax apricus H.R.Fletcher, Bull. Misc. Inform. Kew 1937, 508.

Styrax barbarossa Gilg, Bull. Soc. Bot. France 57(Mém. 3e): 446. 1910

Styrax bashanensis S.Z.Qu & K.Y.Wang, Bull. Bot. Res., Harbin 9(1): 27. 1989.
Note: Huang et al. (2003) found no authentic material, though suggest this species is a possible synonym of *Styrax hookeri*.

Styrax bracteolatus Guillaumin, Bull. Soc. Bot. France 70: 883. 1923

Styrax camporum f. *viridescens* Hassl., Addenda Pl. Hassl. 8. 1917

Styrax casearifolius Craib, Bull. Misc. Inform. Kew 1920, 304.

Styrax ceramensis Warb., Bot. Jahrb. Syst. 13(3-4): 402, 454. 1891.
Note: Perkins (1907) lists this species as *Maba ceramensis*. *Maba* is currently considered a synonym of *Diospyros* (Flora of China Editorial Committee, 1996). Thus, this name likely refers to a species of *Diospyros*. Specimen SI 00588803 is annotated as *Diospyros ellipticifolia* f. *moluccensis* Bakh., though the validity of this name is also unclear.

Styrax cespedesii Perkins, Repert. Spec. Nov. Regni Veg. 2: 21. 1906

Styrax cotinifolius Salisb., Prodr. Stirp. Chap. Allerton 286. 1796

Styrax crotonoides C.B.Clarke subsp. *fraserensis* (Putz & Ng) Steenis, Fl. Males., Ser. 1, Spermat. 9(3): 568. 1983

Styrax crymophyllus G.Don, Gen. Hist. 4: 5. 1837

Styrax diplotrichus Diels, Notizbl. Bot. Gart. Berlin-Dahlem 13: 508. 1937
Fritsch (1997) could find no authentic material, though suggested possibility this is a synonym of *Styrax ramirezii*

Styrax ellipticus Jungh. & de Vriese, Pl. Nov. Ind. Batav. fasc. i. (1845) 10.

Styrax fortunei Hance, J. Bot. 20: 36. 1882
Note: Perkins (1907) suggests similarity to *Cyrta* (*Styrax*) *agrestis* Miers, though doubts it is synonymous with *Styrax agrestis* (Lour)

Styrax fraserensis Putz & Ng, Malaysian Forester 40(4): 249. 1977
Note: Van Steenis (1982) lists as *Styrax crotonoides* Clark ssp. *fraserensis*, though this name (listed above) is also absent from recent literature.

Styrax fulvus Klotzsch ex A.DC., Prodr. (DC.) 8: 264. 1844

Styrax funkikensis Mori, Trans. Nat. Hist. Soc. Formosa 25: 416. 1935

Styrax glabratus Warb., Bot. Jahrb. Syst. 13(3-4): 402. 189

Styrax grandiflorus J.F.Gmel., Syst. Nat., ed. 13[bis]. 2(2): 1633, sphalm. 1792

Styrax grandifolius var. *grandidentatus* Feay ex Alph.Wood, Class-book Bot. (ed. 1861). 499. 1861

Styrax guineensis G.Don, Gen. Hist. 4: 5. 1837

Styrax henryi Perkins, Pflanzenr. (Engler) 4, Fam. 241: 33. 1907
Note: Native to Taiwan. Treated in Perkins 1908 but conspicuously absent from other treatments of the region

Styrax henryi var. *microcalyx* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 33. 1907

Styrax japonicus Siebold & Zucc. var. *calycothrix* Gilg, Bot. Jahrb. Syst. 34: 58. 1904
Note: Only lower taxon of the species accepted by Hwang & Grimes (1996). However, this name is not listed in Huang et al. (2003)

Styrax japurensis Martius ex Seub., Fl. Bras. (Martius) 7: 188. 1868

Styrax kuhlmannii Condorcet, Atas Soc. Biol. Rio de Janeiro xiii. 81. 1970

Styrax laevigatus Sims, Bot. Mag. 23: t. 921. 1806

Styrax lasiocalyx Perkins, Bot. Jahrb. Syst. 31: 481. 1902

Styrax latifolius f. *klotzschii* Perkins, Pflanzenr. (Engler) 4, Fam. 241: 39. 1907

Styrax latifolius f. *longiflorus* (A.DC.) Perkins, Pflanzenr. (Engler) 4, Fam. 241: 39. 1907

Styrax latifolius L. ex B.D.Jacks., Index Linn. Herb. 142 (1912)

Styrax leveillei Fedde ex H. L,v., Flore du Kouy-Tch,ou 407. 1915.
Note: This is likely a species of *Pterostyrax*, published as *Pterostyrax leveillei* (Fedde ex H. Lév.) Chun in Icones Plantarum 32: , pl. 3161. 1932. and *Pterostyrax psilophyllus* var. *leveillei* (Fedde ex H. Lév.) H. Hara in Journal of Japanese Botany 15(7): 457. 1939. *Pterostyrax psilophyllus* is accepted by Hwang & Grimes (1996) with no mention of var. *leveillei* as a lower taxon.

Styrax lojaensis Perkins, Specimen based record

Styrax lundellii P.W.Fritsch, ined.
Note: Listed on Tropicos as an illegitimate name. Image of type referenced with *Styrax incarnatus*. Uncertain as to whether this name is considered synonymous with *Styrax incarnatus*.

Styrax macrospermus C.Y.Wu, Fl. Yunnan. 3: 427. 1983

Styrax mallotifolius C.Y.Wu, Fl. Yunnan. 3: 420. 1983

Styrax officinarum Crantz, Inst. Rei Herb. 2: 382. 1766

Styrax ovalis Klotzsch ex Seub., Fl. Bras. (Martius) 7: 194. 1868

Styrax parvifolius Herb.Berol. ex A.DC., Prodr. (DC.) 8: 263. 1844

Styrax racemosus A.DC., Prodr. (DC.) 8: 265. 1844

Styrax ridleyanus Perkins, Pflanzenr. (Engler) 4, Fam. 241: 61. 1907

Styrax rigidifolius Idrobo & R.E.Schult., Bot. Mus. Leafl. 13: 328, tab. 38, A-F. 1949

Styrax rigidus Salisb., Prodr. Stirp. Chap. Allerton 286. 1796

Styrax siamensis H.R.Fletcher, Bull. Misc. Inform. Kew 1937, 510.

Styrax siamensis Rordorf, Schweiz. Apoth. Zeitung 1916, 585

Styrax sumatranus J.J.Sm., Tectona x. 205 (1917).

Styrax suzukii Mori, Trans. Nat. Hist. Soc. Formosa 25: 417. 1935

Styrax tomentosus Spreng., Syst. Veg. (ed. 16) [Sprengel] 4(2, Cur. Post.): 405. 1827

Styrax urophyllus Gilg ex Glaz., Bull. Soc. Bot. France 57(M,m. 3e): 446. 1910

Styrax virgatus Wall. & G.Don, Gen. Hist. 4: 5. 1837

Styrax yapacanensis Steyerm., Acta Bot. Venez. 10: 242 (-243). 1975

Appendix B

PHOTOGRAPHS OF STYRAX SPP. SECTIONED PETIOLES AND INTERPRETIVE DIAGRAMS

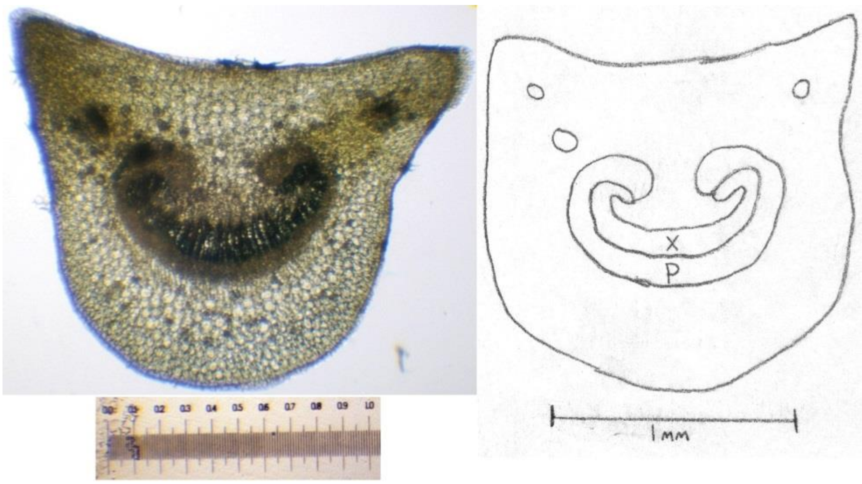

Figure 32 Cross section of distal portion of petiole of *Styrax americanus* Lamarck (PHA 70-085*A), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Bundles within which xylem and phloem were indistinguishable are left blank. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

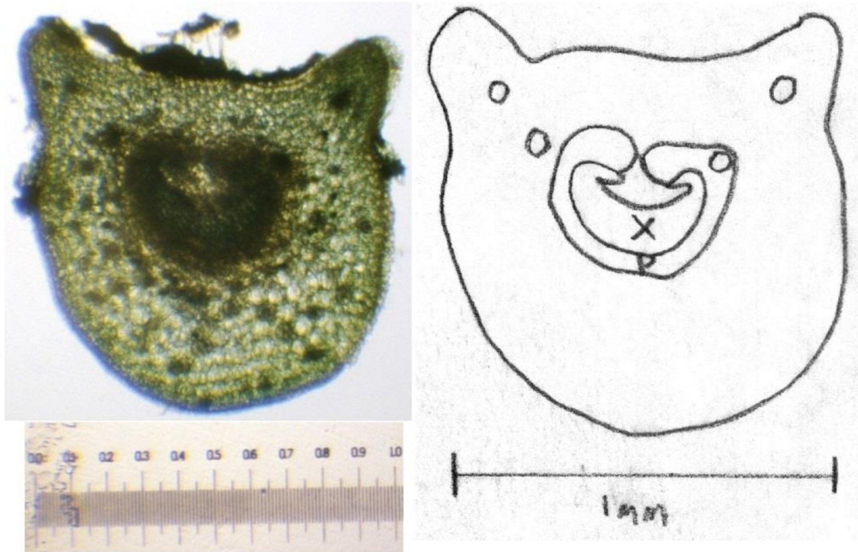

Figure 33 Cross section of distal portion of petiole of *Styrax calvescens* Perkins (Source: JC Raulston Arboretum), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Bundles within which xylem and phloem were indistinguishable are left blank. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

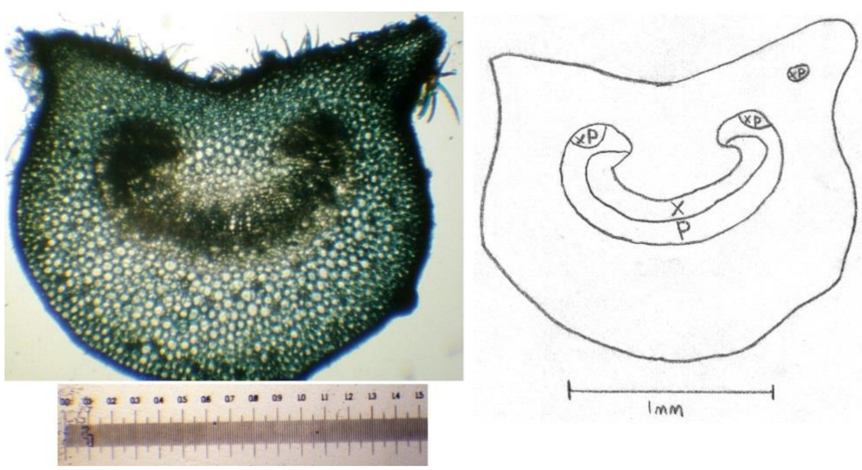

Figure 34 Cross section of distal portion of petiole of *Styrax confusus* Hemsley (PHA #2009-56*A), stained with 0.1% Toluidine Blue O, 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

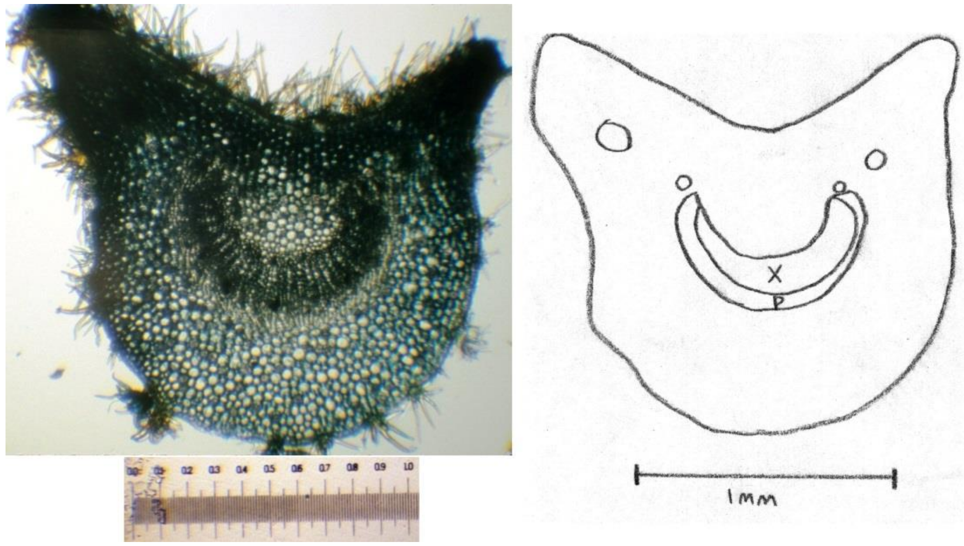

Figure 35 Cross section of distal portion of petiole of *Styrax confusus* Hemsley (AA# 1082-89*D), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Bundles within which xylem and phloem were indistinguishable are left blank. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

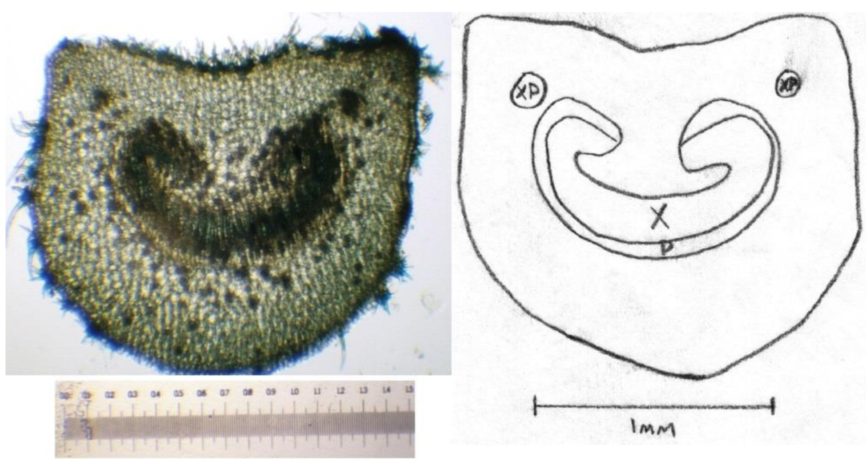

Figure 36 Cross section of distal portion of petiole of *Styrax dasyanthus* Perkins (AA# 164-2008), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

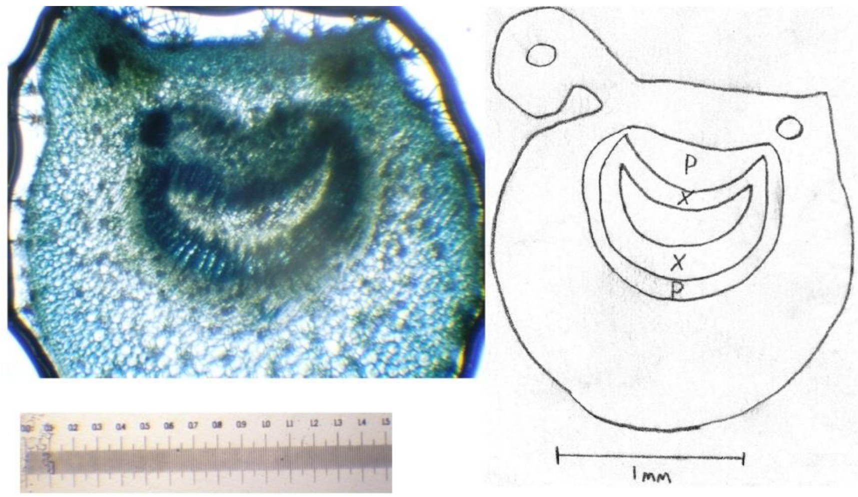

Figure 37 Cross section of distal portion of petiole of Styrax grandifolius Aiton (UDBG# 06-95*1), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Bundles within which xylem and phloem were indistinguishable are left blank. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

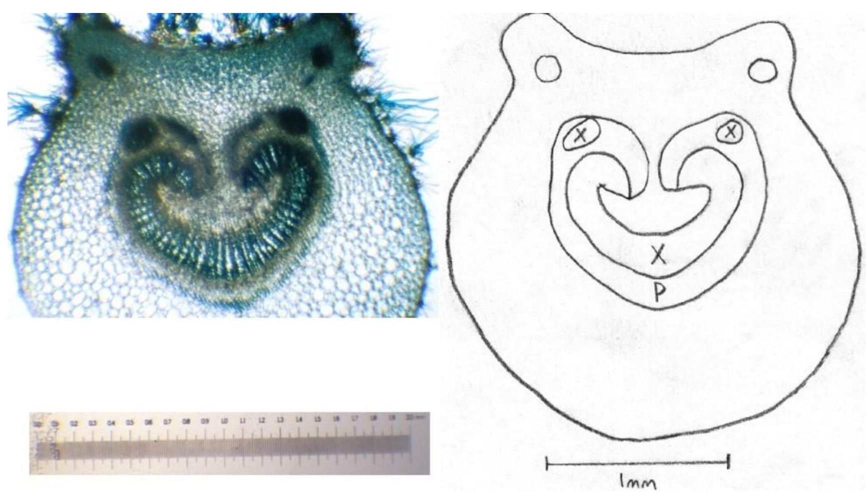

Figure 38 Cross section of distal portion of petiole of *Styrax grandifolius* Aiton (PHA# 2009-35*B), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Bundles within which xylem and phloem were indistinguishable are left blank. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

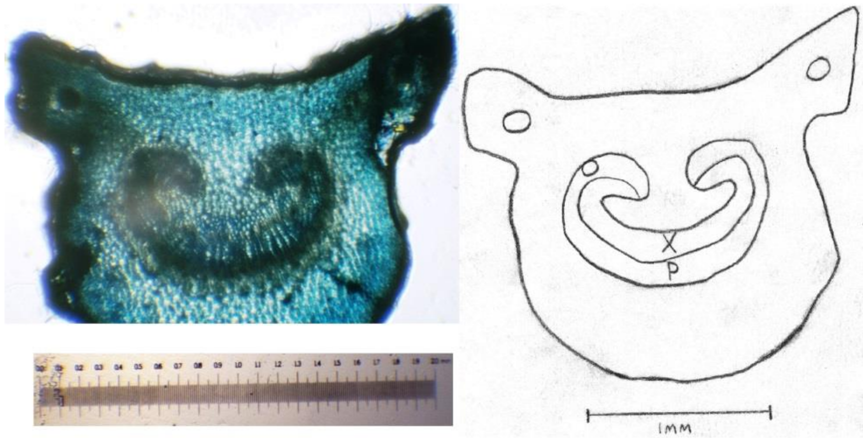

Figure 39 Cross section of distal portion of petiole of *Styrax hemsleyanus* Diels (PHA# 2003-70*A), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Bundles within which xylem and phloem were indistinguishable are left blank. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

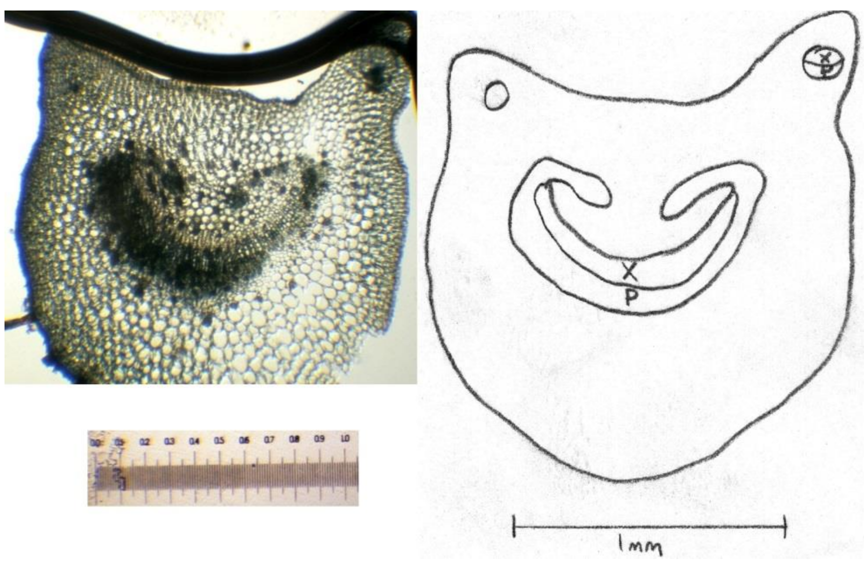

Figure 40 Cross section of distal portion of petiole of *Styrax hemsleyanus* Diels (UDBG# 99-104*1), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Bundles within which xylem and phloem were indistinguishable are left blank. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

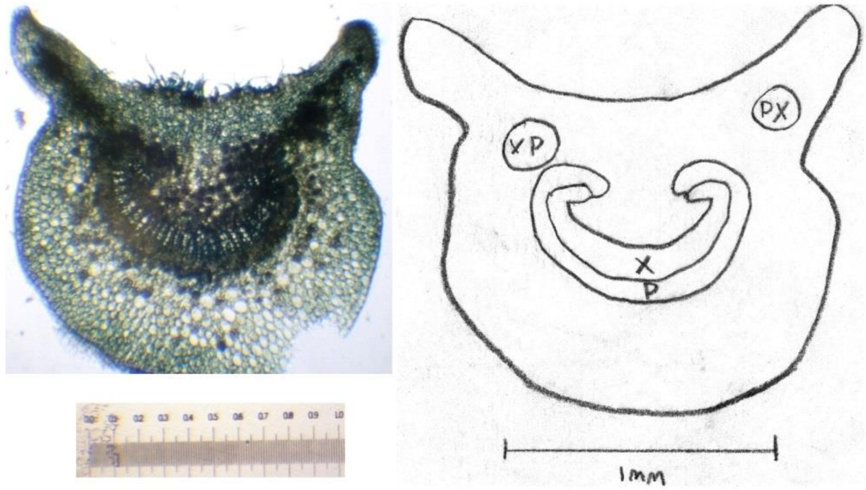

Figure 41 Cross section of distal portion of petiole of *Styrax japonicus* Siebold & Zuccarini (UDBG# 88-83*1), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

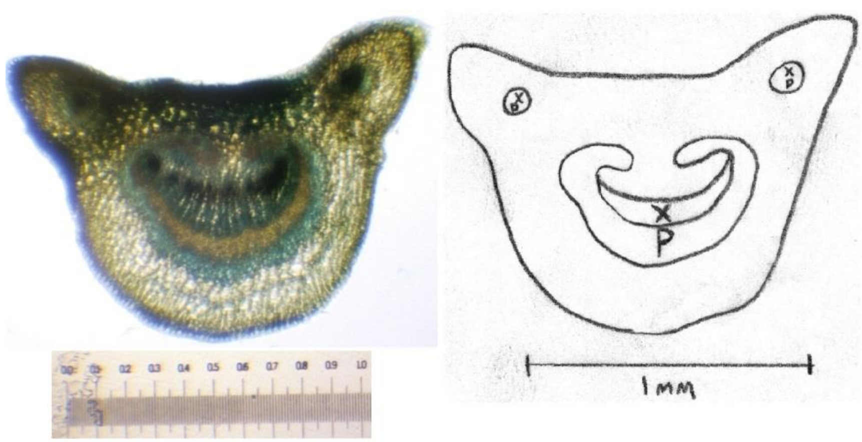

Figure 42 Cross section of distal portion of petiole of *Styrax platanifolius* Engelmann ex Torrey ssp. *texanus* (Cory) P.W.Fritsch (PHA# 2009-90*A), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

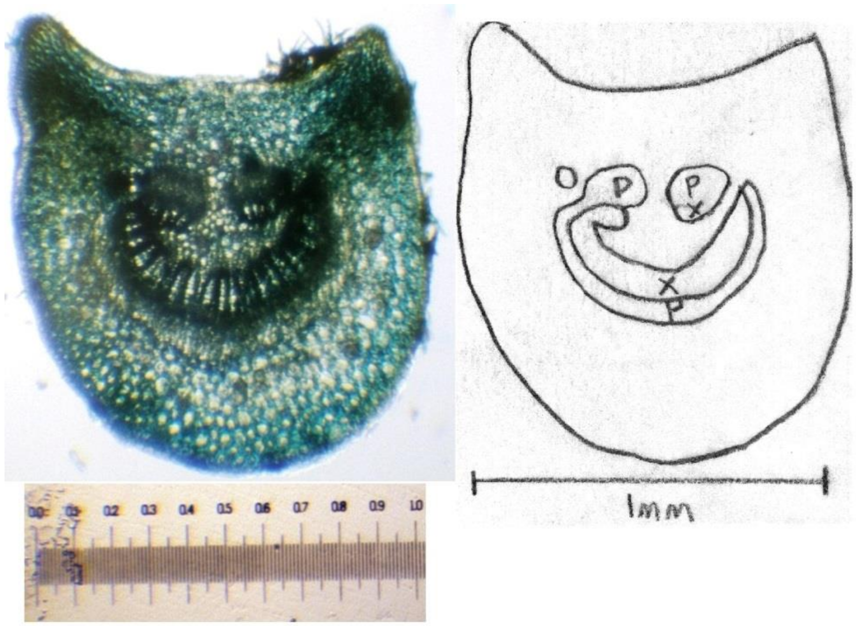

Figure 43 Cross section of distal portion of petiole of *Styrax serrulatus* Roxburgh (JCR# 940340), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Bundles within which xylem and phloem were indistinguishable are left blank. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

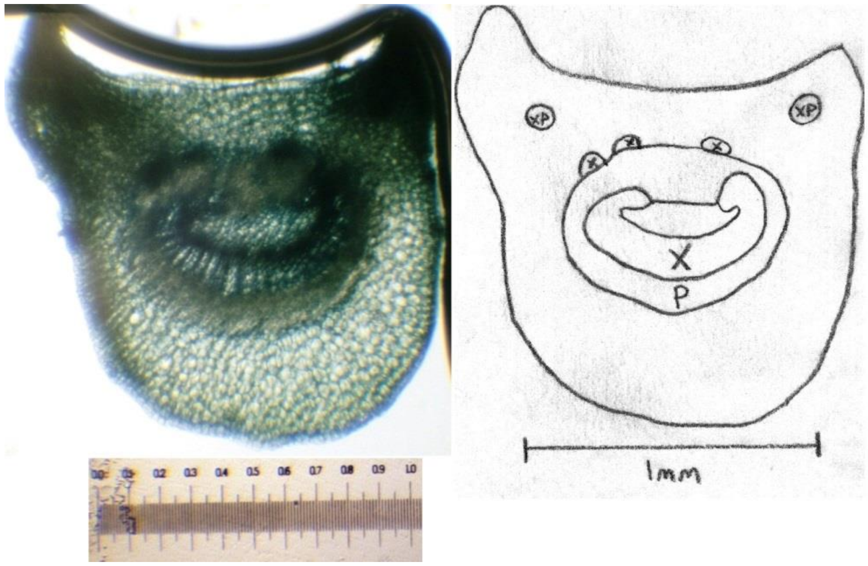

Figure 44 Cross section of distal portion of petiole of *Styrax wilsonii* Rehder (PHA# 2007-30*A), stained with 0.1% Toluidine Blue O. 35× magnification. Interpretive drawing depicting relative location of xylem (X), phloem (P), and vascular bundles. Photograph by the Author & T.D. Pizzolato, drawing by the Author.

Appendix C

PHOTOGRAPHS OF *STYRAX* STEM WOOD CROSS SECTIONS (INCLUDING OUTGROUP *SINOJACKIA REHDERIANA)*

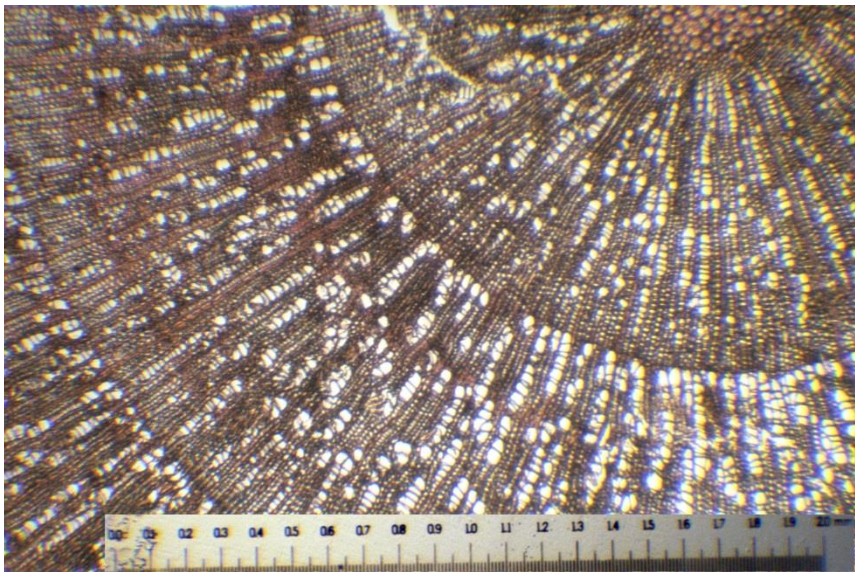

Figure 45 Stem cross section of *Styrax americanus* Lamarck (UDBG #96-15*1) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

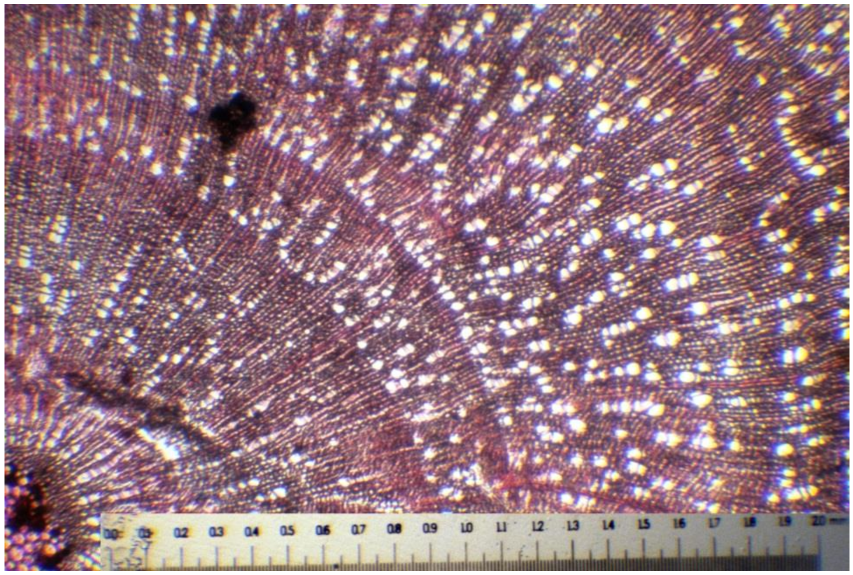

Figure 46 Stem cross section of *Styrax calvescens* Perkins (Source: JC Raulston Arboretum) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

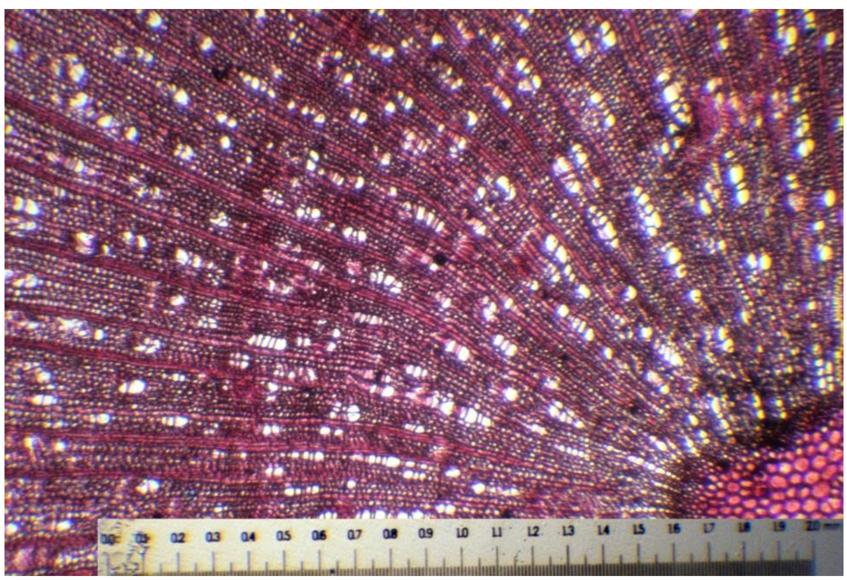

Figure 47 Stem cross section of *Styrax confusus* Hemsley (JCR #001628) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

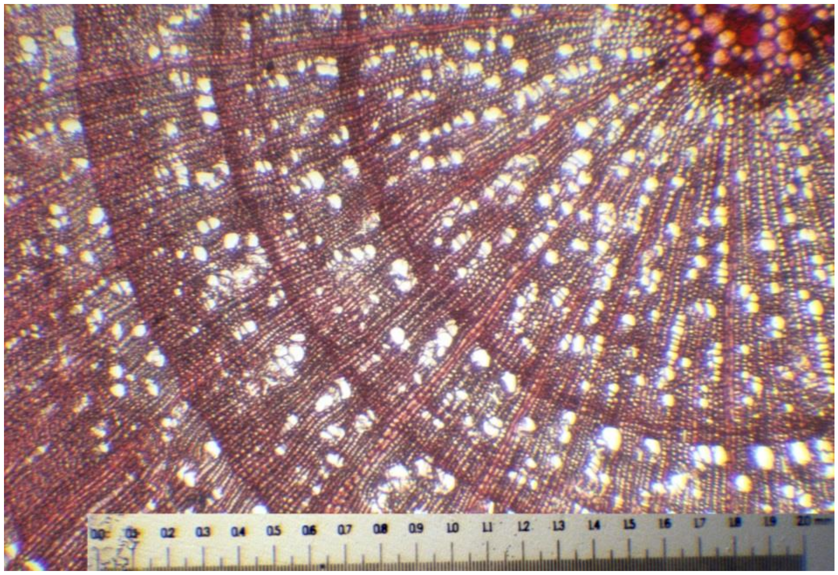

Figure 48 Stem cross section of *Styrax dasyanthus* Perkins (JCR #930409) exhibiting ring porous wood (Carlquist Type 1C). Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

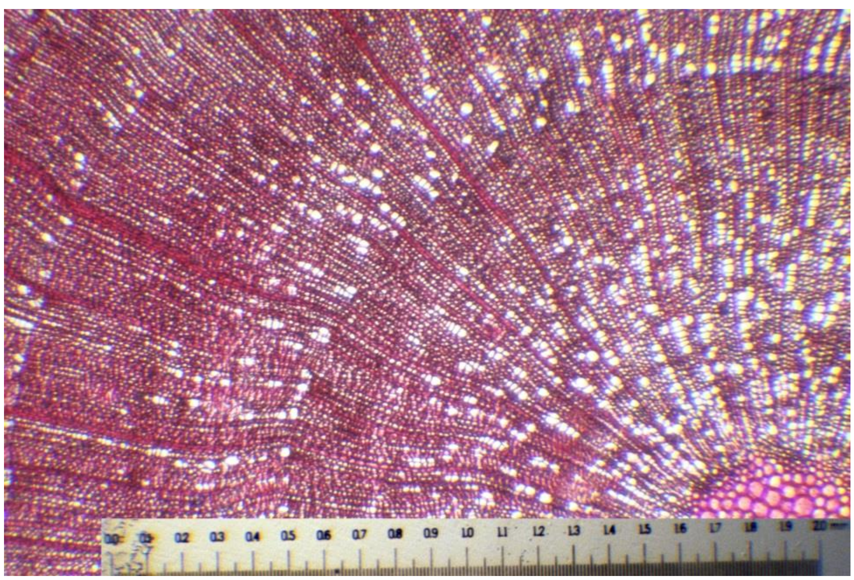

Figure 49 Stem cross section of *Styrax formosanus* Matsumura (JCR #011483) exhibiting ring porous wood (Carlquist Type 1C). Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

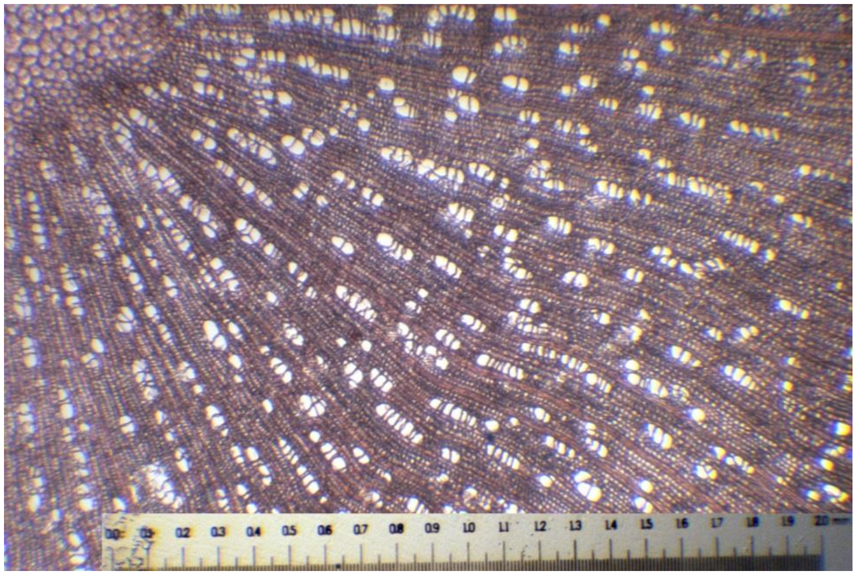

Figure 50 Stem cross section of *Styrax grandifolius* Aiton (UDBG #06-95*1) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

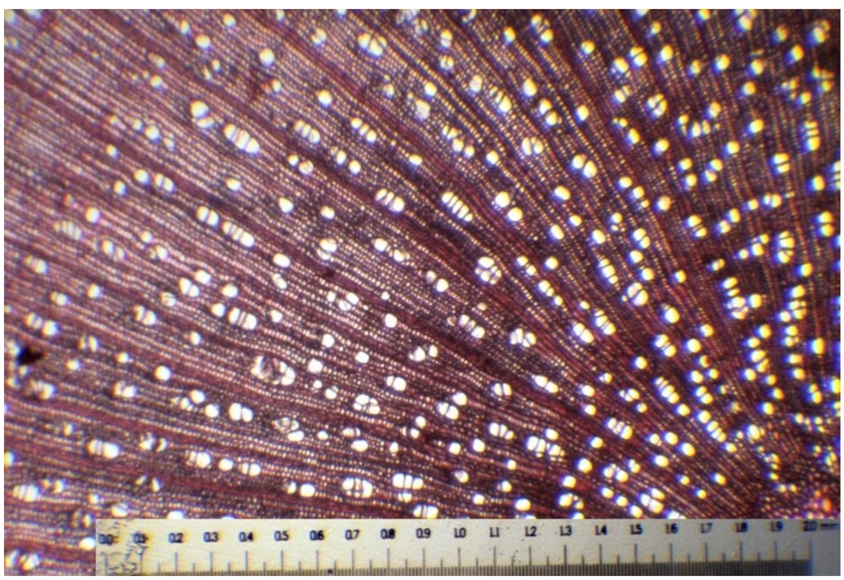

Figure 51 Stem cross section of *Styrax japonicus* Siebold & Zuccarini (UDBG #88-83*1) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

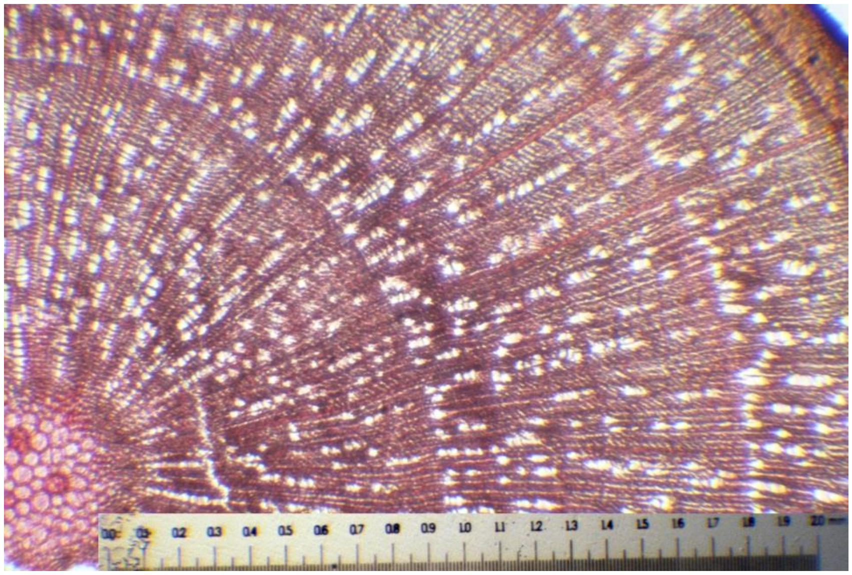

Figure 52 Stem cross section of *Styrax serrulatus* Roxburgh (JCR #940340) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

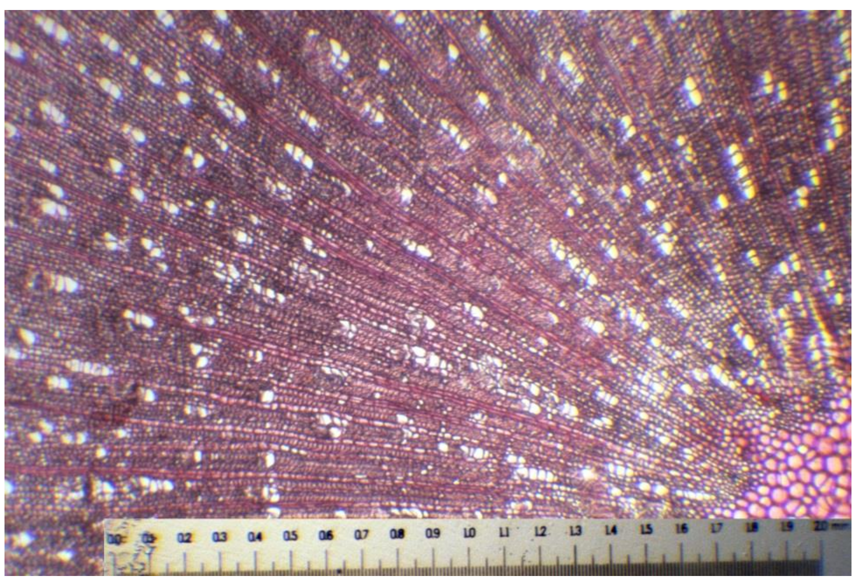

Figure 53 Stem cross section of *Styrax tonkinensis* (Pierre) Craib ex Hartwich (JCR #960302) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

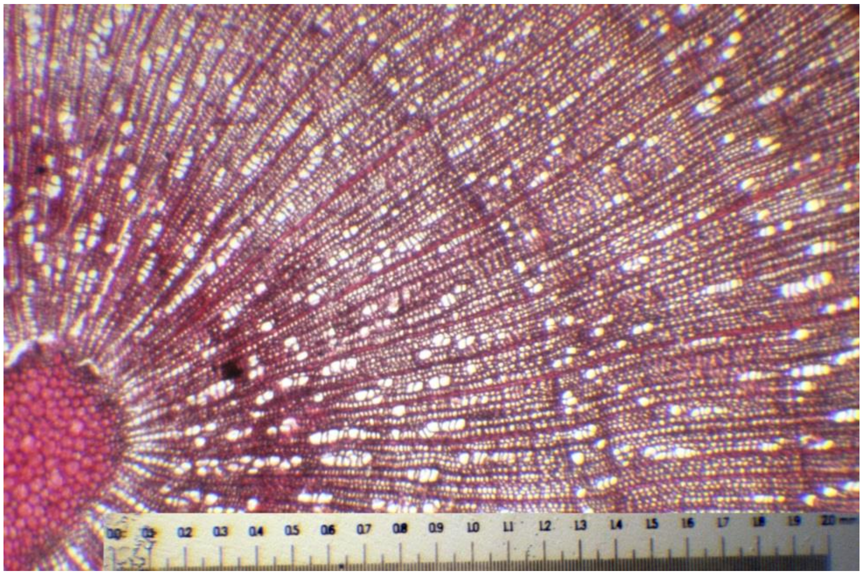

Figure 54 Stem cross section of *Styrax wilsonii* Rehder (JCR #001612) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

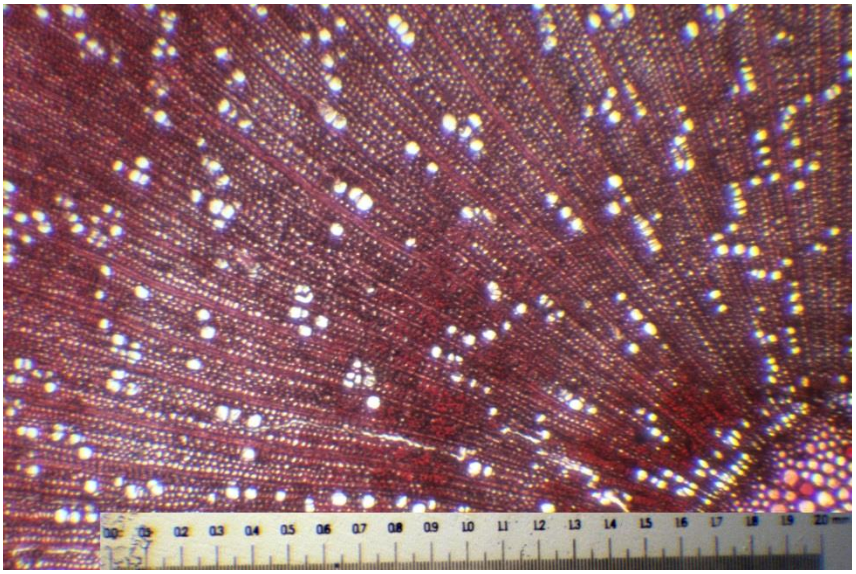

Figure 55 Stem cross section of *Sinojackia rehderiana* Hu (JCR #880421) exhibiting diffuse porous wood. Stained with 0.5% safranin. 35× magnification. Photograph by the Author & T.D. Pizzolato.

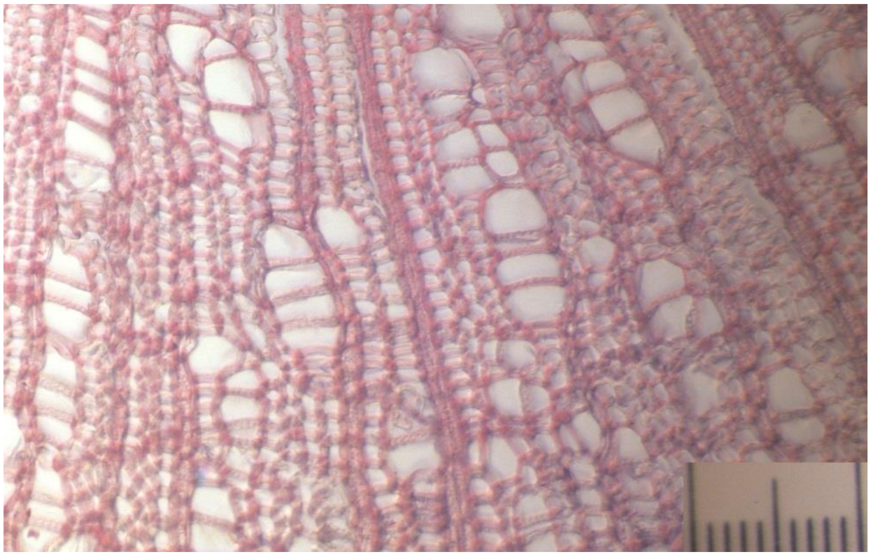

Figure 56 Stem cross section of *Styrax americanus* Lamarck (UDBG #96-15*1) stained with 0.5% safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

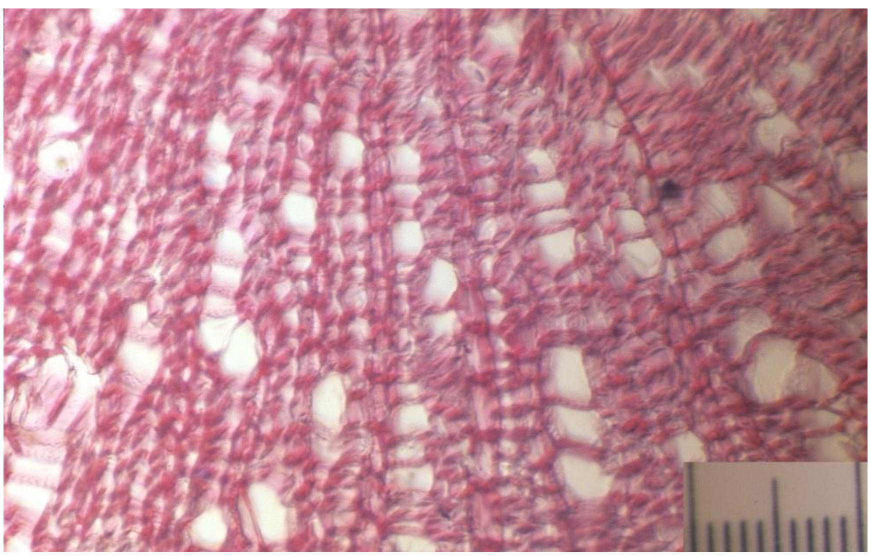

Figure 57 Stem cross section of *Styrax calvescens* Perkins (Source: JC Raulston Arboretum) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

Figure 58 Stem cross section of *Styrax confusus* Hemsley (JCR #001628) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

Figure 59 Stem cross section of *Styrax dasyanthus* Perkins (JCR #930409) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

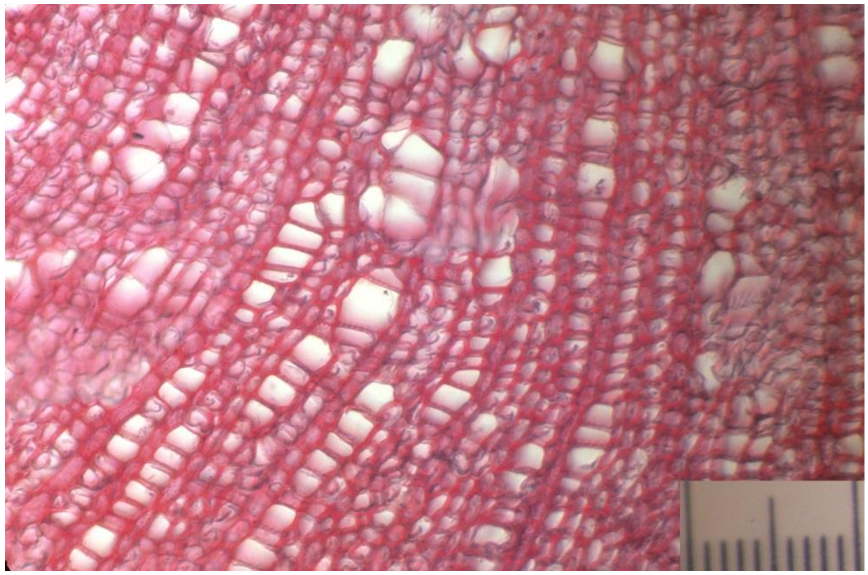

Figure 60 Stem cross section of *Styrax formosanus* Matsumura (JCR #011483) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

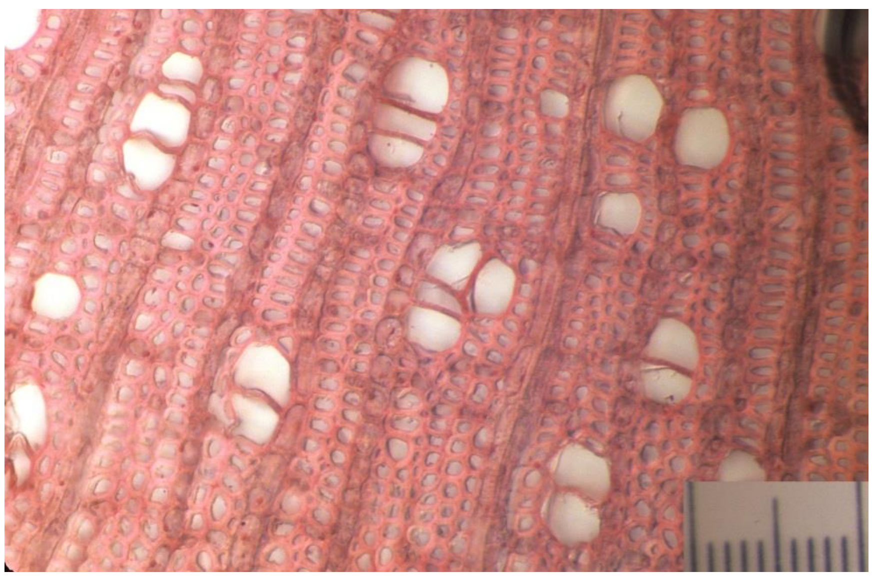

Figure 61 Stem cross section of *Styrax grandifolius* Aiton (UDBG #06-95*1) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

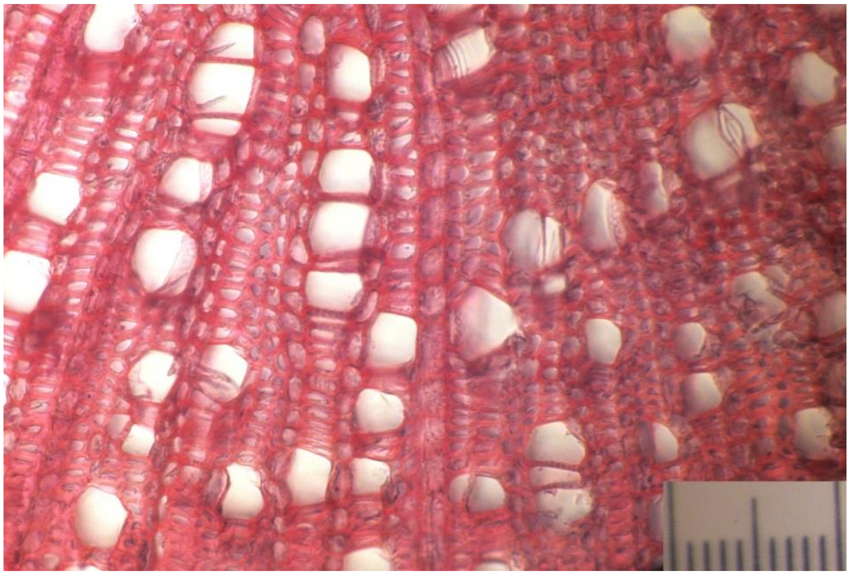

Figure 62	Stem cross section of *Styrax japonicus* Siebold & Zuccarini (UDBG #88-83*1) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

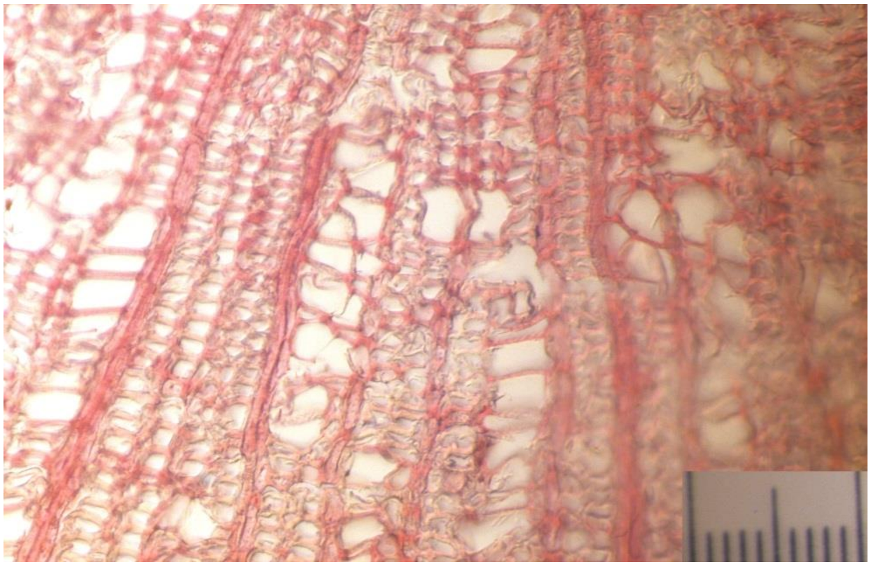

Figure 63	Stem cross section of *Styrax serrulatus* Roxburgh (JCR #940340) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

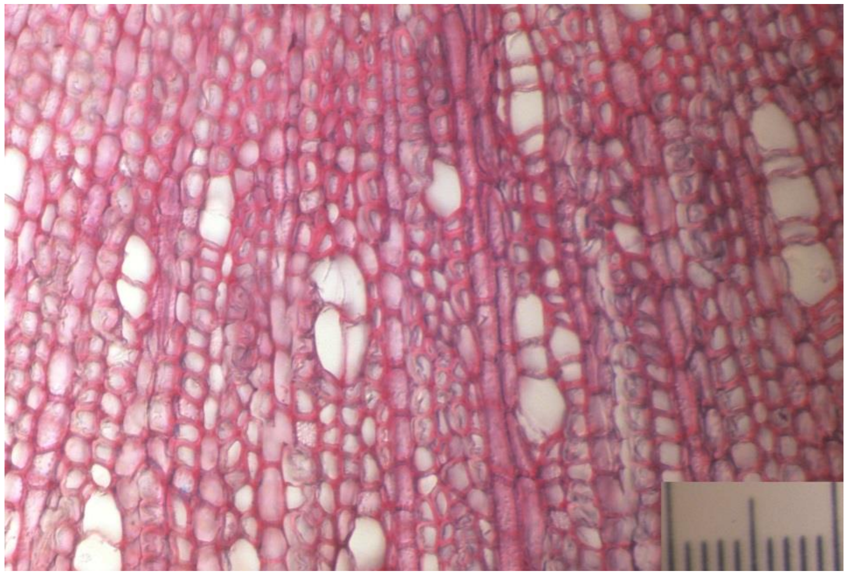

Figure 64 Stem cross section of *Styrax tonkinensis* (Pierre) Craib ex Hartwich (JCR #960302) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

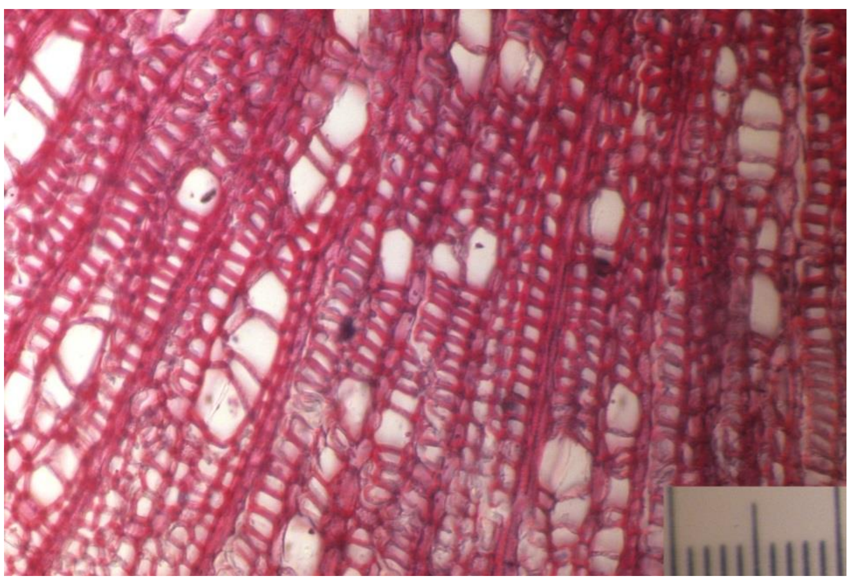

Figure 65 Stem cross section of *Styrax wilsonii* Rehder (JCR #001612) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

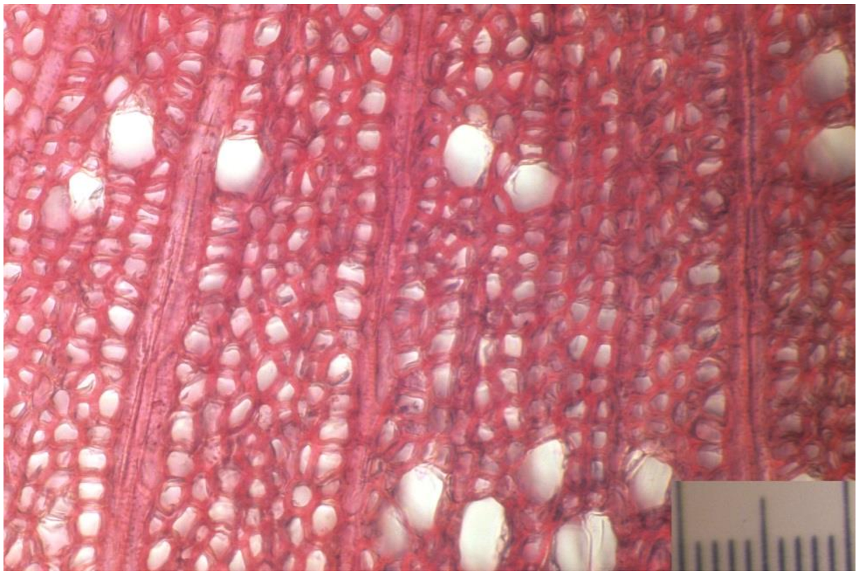

Figure 66 Stem cross section of *Sinojackia rehderiana* Hu (JCR #880421) stained with 0.5% Safranin. 160× magnification. Scale bar representing 0.1 mm. Photograph by the Author & T.D. Pizzolato.

Appendix D

TENTATIVE KEY TO CULTIVATED *STYRAX* SPP.

The key to series and sections is reproduced from Fritsch (1999). The subkey for series *Styrax* is reproduced from Fritsch (2009), with the keying difference between *Styrax officinalis* and *Styrax redivivus* based on provenance due to a lack of effective characteristics to separate the two taxa. The series *Cyrta* subkey is truncated from that of Hwang & Grimes (1996) and Huang et al. (2003), whereas the keys for series *Benzoin* and *Valvatae* are vastly truncated from Hwang & Grimes (1996) and Gonsoulin (1974) and Fritsch (1997), respectively.

Key to Sections & Series: Reproduced from Fritsch (1999)

1a. Plant deciduous; bases of young shoots with scattered stalked ferrugineous or rarely fulvous stellate hairs distinct from the rest of the vesture; sides of the corolla convex in bud; corolla lobes membranous…………………………………….....*Styrax* sect. *Styrax*

  2a. Inflorescences strictly terminal; leaf margins entire, lobed, or coarsely toothed, but never glandular denticulate or glandular serrate………………………………………… Key 1: *Styrax* ser. *Styrax*

  2b. Inflorescences produced laterally (as well as terminally) on at least some shoots (often reduced to 1-2 flowers, the subtending leaves often reduced); leaf margins of at least some leaves on sterile shoots (and often of fertile shoots) glandular-denticulate to glandular-serrate, rarely also lobed......................................Key 2: *Styrax* ser. *Cyrta*

1b. Plant evergreen; bases of young shoots without stalked ferrugineous or fulvous stellate hairs unless these accompanied by a dense tomentum consisting of hairs of the same general color and type; sides of the corolla straight or nearly so in bud; corolla lobes subcoriaceous……….. *Styrax* sect. *Valvatae*

  3a. Mesocarp dry; endocarp at maturity adherent to the mesocarp, not the seed; seeds depressed-globose; seed coat crackled..Key 3: *Styrax* ser. *Benzoin*

3b. Mesocarp juicy, endocarp at maturity adherent to the seed, not the mesocarp; seeds ellipsoid; seed coat not crackled………………………………………….Key 4: *Styrax* ser. *Valvatae*

Key 1: *Styrax* sect. *Styrax* ser. *Styrax*: From Fritsch (2009)

1a. Capsules 7-10mm, grayish white stellate-pubescent; pedicels 1.3-2.3x as long as calyx…………………………………………………………………..*S. platanifolius*
1b. Capsules 11-15mm, tawny or fulvous stellate-pubescent; pedicels 0.5-1.4x as long as calyx……………………………………………….…….2
2a. Native to Middle East, Mediterranean…………………………....*S. officinalis*
2b. Native to Western United States (California)………………………..*S. redivivus*

Key 2: *Styrax* sect. *Styrax* ser. *Cyrta*: 1a Truncated from Hwang & Grimes (1996), 1b from Huang et al. (2003)

1a. Corolla lobe margin usually narrowly involute, valvate, or induplicate
2a. Calyx, pedicel glabrous………………………………..………*S. wuyuanensis*
2b. Calyx, pedicel densely scaly or stellate pubescent……......................................3
3a. Leaf blade abaxially densely stellate tomentose………………………………...................................*S. calvescens*
3b. Leaf blade abaxially glabrous or sparsely stellate pubescent……………………………………………………………….......4
4a. Fruit cylindric to oblique ovoid or ellipsoid to ellipsoid-ovoid; filaments flexuous………………………………………….5
5a. Fruit cylindric to oblique ovoid, 1.2-3 x 8-16mm, apex rostrate to short pointed; leaf blade elliptic, oblong, or elliptic lanceolate, margin entire or irregularly denticulate…………………..……………………...*S. agrestis*
5b. Fruit ellipsoid to ellipsoid-ovoid, 8-16 x 6-8mm, apex acute or apiculate; lamina ovate, oblong, or ovate -lanceolate, margin serrate or rarely entire……………………*S. serrulatus*
4b. Fruit subglobose, globose, ovoid, or obovoid; filaments straight………..6
6a. Trees; lamina leathery or subleathery; inflorescences (3-)5-flowered or more…………………………………………...…7
7a. Inflorescences racemose; fruit 8-15mm in diameter……………………………………………..........*S. confusus*

7b. Inflorescences panculate; fruit 5-7mm in diameter…………………………………..…………….*S. dasyanthus*

6b. Shrubs; lamina papery; inflorescences to 5-flowered……………………………………………….……….…….8

8a. Calyx 2.5-3 mm; fruit irregularly rugose …………………………..
………………………………………………………….*S. formosanus*

8b. Calyx 4-5 mm; fruit smooth…………………………..........*S. faberi*

1b. Corolla lobe margin plane, imbricate

9a. Pseudoterminal inflorescences ≥ 7 cm long, often 8-20(23)-flowered

10a. Two most proximal leaves on each shoot of the current year subopposite to opposite………………………………………………………………….....11

11a. Petiole of larger leaves dilated at base and covering bud……………......................……………………………………*S. obassia*

11b. Petiole of larger leaves not dilated at base and not covering bud……………………………………………………………………..12

12a. Vegetative end buds ≤ 3 mm long; calyx campanulate or broadly cupuliform; fruit globose, indehiscento rarely dehiscent, not longitudinally rugose……………………………………………..………………..13

13a. Tree to 30 m, not suckering from roots; leaves membranaceous; corolla lobes 11-23 x 6-10 mm; fruit 10-17 x 9-19mm……………………………….………*S. glabrescens*

13b. Tree to 6 m, often suckering extensively from roots; leaves chartaceous; corolla lobes 8-16 x 3-7 mm; fruit 8-12 x 6-8 mm……………………………..…*S. grandifolius*

12b. Vegetative end buds 4-6 mm long; calyx narrow -cupuliform; fruit globose to ovoid, dehiscent, slightly longitudinally rugose………………………...………….*S. hemsleyanus*

10b. Two most proximal leaves on each shoot of the current year alternate……………………………………………………………...14

14a. 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, s raight seeds densely tuberculate, sometimes the tubercles arranged in stellate formations ……………………………………………………*S. tonkinensis*

14b. Abaxial surface of the lamina visible through the pubescence, if present; calyx truncate, undulate, or irregularly lobed, the teeth not contiguous if present; filaments narrowing distally, flexuous at middle; seeds usually appressed stellate pubescent, or lepidote…...………. *S. odoratissimus*

9b. Pseudoterminal inflorescences < 7 cm long, ≤ 7-flowered (3-ll-flowered in *S. shiraianus*)…………………………………………….....15

15a. Petiole of larger leaves dilated at base, covering the bud…………………………………………………..…………....*S. shiraianus*

15b. Petiole of larger leaves not dilated at base, not covering the bud………………………………………………………………………16

16a. Calyx teeth 4-5 mm long; calyx abaxially with simple or 2-armed trichomes ca. 1-1.5 mm long………………….………....*S. supaii*

16b. Calyx truncate or teeth < 3 mm long; calyx abaxially with stellate trichomes averaging <1 mm long or glabrous…………………17

17a. Distalmost leaves on sterile shoots usually > 7 cm wide; fruit indehiscent (rarely dehiscent by 3 valves) with corolla 10-28 mm long; North America………………………....18

18a. Tree to 30 m, not suckering from roots; leaves membranaceous; corolla lobes 11-23 x 6-10 mm; fruit 10-17 x 9-19 mm; Mexico and Mesoamerica……………………………..……………*S. glabrescens*

18b. Tree to 6 m, often suckering extensively from roots; leaves chartaceous; corolla lobes 8-16 x 3-7 mm; fruit 8 -12 x 6-8 mm; southeastern United States……………………………………………….…………*S. grandifolius*

17b. Distalmost leaves usually< 7 cm wide (occasionally > 7 cm wide in *S. odoratissimus*, and *S. tonkinensis*); fruit dehiscent or if indehiscent, then corolla 5-9 mm long; Asia…………………………………………………….………..19

19a. 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……………..……..20

20a. Longer pedicels on each twig 15-50 mm long, usually equal to or longer than subtended flower……………………………………….………. *S. japonicus*

20b. Longer pedicels on each twig 2-10(-13) mm long, usually shorter than subtended flower……………………..…..21

21a. 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……………………..……..*S.macrocarpus*

21b. 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…………………………………...22

22a. 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*

22b. 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……………………………………………..23

23a. Flowers (1.3)1.5-2.5 cm long; corolla lobes (11)12-18 mm long; calyx (3.5)5-7(9) x 4-7(11) mm; filaments 4-7 mm long; pericarp at least faintly longitudinally striate……………………………..*S. hookeri*

23b. Flowers < 1.5 cm long; corolla lobes 9-11 mm long; calyx 3-4(5) x 3-4 mm; filaments 1.5-4 mm long; pericarp not longitudinally striate………...*S. odoratissimus*

19b. 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…………………………………………….……..24

24a. 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………………………..*S. tonkinensis*

24b. 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……………………………………………….………..25

25a. Lamina 1-2.5(4) x 0.7-2(2.5) cm; fruit 0.4-0.6 cm wide………………………………………..*S. wilsonii*

25b. Lamina 3-13 x 2-8 cm; fruit ≥ 0.7 cm wide………..…….26

26a. 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……………………………….*S. rugosus*

26b. Only the tertiary veins of lamina abaxially prominent and raised in young leaves; rachis without stalked trichomes; fruit 1.0-1.5 cm wide……………………………………..…….*S. limprichtii*

Key 3: *Styrax* sect. *Benzoin* ser. *Benzoin*: Based on Hwang & Grimes (1996)

1a. Petiole 6-12mm; lamina abaxially gray-yellow or brown yellow stellate pubescent (though veins glabrous)………………………………….*S. benzoin*

1b. Petiole 10-30mm, quadrangular or nearly so; leaf blade abaxially densely brown or brownish stellate tomentose………………………………………..2

2a. Calyx teeth ovate-deltate, ca. 2mm; leaf blade abaxially densely stellate tomentose but stellate pubescent on veins……………...*S. chinensis*

2b. Calyx teeth ± rudimentary, limb undulate, truncate, or subtruncate and led than 2mm; leaf blade abaxially stellate tomentose………………………………………………………..*S. suberifolius*

Key 4: *Styrax* sect. *Benzoin* ser. *Valvatae*: Truncated from Gonsoulin (1974) and Fritsch (1997)

1a. Abaxial surface of the leaves covered with a lepidote pubescence imparting a crusty appearance…………………………….……*S. glaber*

1b. Abaxial surface of the leaves covered with long spreading stellate trichomes or dense, matted, or otherwise tomentose pubescence……………………………………………………………………..2

2a. Arms of the hairs nearest the distal end of the ventral side of the distinct portion of the stamen filaments predominantly pointing upward, some of these up to (0.8)1-2mm long; connectives distinctly prolonged beyond the tapered anther sacs…………………………………………………………………...*S. argenteus*

2b. Arms of the hairs nearest the distal end of the ventral side of the distinct portion of the stamen filaments not predominantly pointing upward, typically not exceeding 0.5(0.7) mm long;

connectives not or only slightly prolonged beyond the non-tapered anther sacs……………………………………………………………….3

3a. Vesture just below mid-calyx of radiate scales……………..…….*S. ramirezii*

3b. Vesture just below mid-calyx predominantly of stellate hairs, sometimes also with a few scale-like hairs scattered around the stellate ones………4

4a. Abaxial surface of the secondary and tertiary veins obscured by the tomemtum; ± evenly scattered, orange-brown hairs (in addition to whitish pubescence) present on the abaxial surface of most or all fully expanded leaves…………………………………………….……….*S. lanceolatus*

4b. Abaxial surface of the secondary and tertiary veins evident; orange-brown hairs on the abaxial surface of fully expanded leaves at most sporadically present on some of the veins, otherwise nearly always absent……………..….*S. ramirezii*

Appendix E

PERMISSIONS

The following correspondence serves as permission to include the following scanned images from J.C. Raulston's slide collection (owned by the JC Raulston Arboretum).

- Slide 105-0328 in Figure 2 (Page 46)
- Slide 122-0241 in Figure 5 (Page 55)
- Slide 097-0284 in Figure 10 (Page 69)
- Slide 100-0341 in Figure 15 (Page 84)
- Slide 095-0017 in Figure 16 (Page 94)
- Slide 116-0187 in Figure 18 (Page 99)
- Slide 031-1036 in Figure 19 (Page 100)
- Slide 105-0298 in Figure 20 (Page 108)

Matthew Lobdell (lobdell@udel.edu)
To: chris_glenn@ncsu.edu
Wed, Apr 10, 2013 at 5:52 PM

Mr. Glenn,

Thanks for allowing me to include some of these slides in my thesis. It's been very interesting learning about JC Raulston's work with the genus over the course of the project and I'm looking forward to including these as figures.

These were the slides I was particularly interested in using:

031-1036 (S. platanifolius ssp. texanus)
095-0017 (S. officinalis)
097-0284 (S. japonicus 'Crystal')
100-0341 (No species listed but this looks like S. shiraianus
105-0298 (S. argenteus)
105-0328 (S. calvescens)
116-0187 (S. platanifolius ssp. youngiae)
122-0241 (S. glabrescens)

Thanks again!
-Matt

Christopher Todd Glenn chris_glenn@ncsu.edu
To: Matthew Lobdell lobdell@udel.edu
Wed, Apr 10, 2013 at 6:32 PM

Matt,

The photographs you've requested are available on our server at the URL below. Please note the photographs were taken by J. C. Raulston and were provided by the JC Raulston Arboretum. There's a slight spelling difference between the two names. Please credit them accordingly.

Chris