WOOD ANATOMY OF THE STYRACACEAE: EVOLUTIONARY AND ECOLOGICAL CONSIDERATIONS

by

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Summary
Woods of over 40 species representing nine genera of Styracaceae were studied. Features present in most taxa include growth rings, diffuse porosity, combinations of both solitary and pore multiples, exclusively scalariform perforation plates, opposite to alternate intervessel pitting, imperforate tracheary elements with indistinctly bordered pits, both uniseriate and multiseriate heterocellular rays, and axial parenchyma distributed as a combination of diffuse, diffuse-in-aggregates, and scanty. Prismatic crystals occur in species of the genera Brunsvinia, Halesia, and Styrax, and silica is present in a few Neotropical species of Styrax. The characteristic solitary pore distribution and high scalariform perforation plate bar number of Huodendron are of potential evolutionary significance. The xylem of Lissocarpa differs from the Styracaceae in possessing more highly evolved vessel elements with both simple and scalariform perforations and prominently banded axial parenchyma. The occurrence of simple perforation plates in the wider, earlywood vessel elements, along with an increased pore frequency and decreased vessel element length, in Styrax plataniolius and S. texanus is documented. Both species inhabit seasonally dry habitats of the southwestern United States, thus supporting similar specialisations observed in other plants growing in xerophytic conditions. The apparent variation in perforation plate condition within different geographic varieties of S. officinalis is discussed. Significant correlations of wood anatomical characters and latitude of provenance are present among species of Styracaceae. Increasing latitude is strongly correlated with increased pore and multiseriate ray frequency, and decreased vessel element length and wall thickness. Increasing latitude is less strongly correlated with an occurrence of decreased pore diameter, increased bar number per perforation plate, increased fibre-tracheid and intervessel pit diameter, and increased frequency of uniseriate rays. Weak correlations are also evident between increasing latitude and shorter ray height and narrower, shorter, and thinner-walled fibre-tracheids.

Key words: Styracaceae, Lissocarpaceae, systematic anatomy, ecological wood anatomy, latitude.

Introduction
The Styracaceae are a woody, dicotyledonous family that is generally described as containing 12 or 13 genera and 150 to 190 species (Wood, 1960; Hutchinson, 1973; Gonsoulis, 1974; Spongberg, 1976). The plants are distributed primarily in eastern Asia to western Malaysia, tropical South America, and the southeastern United States.

The largest genus, Styrax, includes about 120 species and ranges widely in the tropical and warm temperate regions of eastern Asia and America. A conspicuous exception to this distribution pattern is Styrax officinalis L., which is found in the eastern Mediterranean region and in California. In Asia the numerous species extend from the eastern Himalayas to Malaysia, Indochina, Korea, and Japan. The family is absent from Australia, the Philippines, and Sri Lanka. The New World species are widely distributed from Pacific to Atlantic North America, the West Indies, and southward to southern Brazil.

As reviewed by Schadel and Dickison (1979), the Styracaceae have been generally placed in the order Ebenales including, in addition, the families Sapotaceae, Ebenaceae, Sympliacceae, and Lissocarpaceae (Cronquist, 1981, Thorne, 1976; Takhtajan, 1980).

No comparative evolutionary survey of styracaceous wood anatomy has been completed, although there are several descriptive works, often regional in nature, dealing with the xylem structure of various species. The most notable of these are: Chudnoff (1956), Kanehira (1921), Inokuma et al. (1953), Metcalfe & Chalk (1950), Sudo (1959), Versteegh (1968), Moll & Janssonius (1906), Record & Hess (1943), Tang (1932–1934), and Tortorelli (1956). Nevertheless, the wood of this family has neither been fully described nor adequately interpreted ecologically and evolutionarily. A study of the comparative anatomy of the Styr-
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<th>approximate mean fibre-tracheid pit diameter (µm)</th>
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* Immature sample.
** All specimens studied were from Israel. California plants of this species have both simple and scalariform perforation plates.
caceae was undertaken to provide a comprehensive anatomical description of the family, to outline basic trends of anatomical specialisation, and to provide data that may eventually contribute to a better understanding of the evolution and systematics of the group. An earlier paper dealt with leaf anatomy (Schadel & Dickson, 1979).

Materials and Methods

Woods of just over forty species of Styracaceae (s.s.) were studied. Wood samples could not be obtained for the Brazilian genus Pamphila Martius ex A. DeCandolle and only a small twig sample was available of Parastyrax lacei. It should also be noted that many of the wood samples of Chinese origin are apparently without adequate documentation. Nevertheless, most of these specimens currently represent the only available specimens for a few styracaceous genera and species and there is no reason to doubt their authenticity. Xylaria abbreviations follow the suggestions of Stern (1978).

Samples were prepared in the usual manner by boiling and storage in equal parts glycerine and 50% alcohol. Sections were cut at between 15–20 µm and stained with safranin. All statistical data regarding cell length (Table 1) were gathered from macerations prepared using Jeffrey’s macerating fluid. Silica distributions were studied with a combination of scanning electron microscopy (SEM) and light microscopy, using radial sections that were left unstained but bleached with a commercial strength bleach. Both crystals and silica were clearly visible in such preparations.

For each sample twenty-five measurements were made of vessel element length (including ligules), diameter, number of bars per perforation plate, and imperforate element length and diameter. Ten measurements per sample were made of vessel wall thickness, intervessel pit diameter, fibre wall thickness and pit diameter, multiseriate ray height and width, and uniseriate ray height. It should be noted that in some instances fibre pit borders are very reduced which made measurements difficult. The entire ray height was counted or measured. Counts in ten one mm² fields per sample were made to determine pore and ray frequency. Pore frequencies were counted on the transverse section whereas ray frequencies were counted from tangential sections. Rays that were only partially in the field of count were tabulated. Measurements encompassed both early and latewood when present.

Latitude was determined from collection data whenever possible. When such determination was not possible, the latitude assigned represented the mid-point of the latitudinal range estimated from available taxonomic and floristic literature. Although precise collecting data were available for only 15 percent of the samples, the latitudes for 80 percent of the samples were estimable to within a 10° range.

Skewness and kurtosis were assessed for each variable and all statistical calculations were performed using SAS. Data for vessel and ray frequency, vessel element and fibre diameter, vessel wall thickness, number of bars per perforation plate, fibre pit diameter, and ray height and width were log-transformed to reduce skewness. Pearson product-moment correlation coefficients were computed for all pairs of variables.

All variables showing correlation with latitude significant at the 10 percent level were subjected to multiple regression analyses in order to further clarify the relationship between latitude and each of the highly intercorrelated variables. Significance of correlation of each variable with latitude after regression on all other variables is shown in Table 2 (see p. 16).

In the generic descriptions the measurements for vessel element length, pore diameter, scleriform perforation plate bar number, and imperforate tracheary element are listed as three or four separate numbers. The numbers in parentheses are the extremes measured in all the specimens examined and the remaining number or numbers represent the average or range of averages for all species. All measurements have been rounded-off to the nearest whole micron.

Results

Generic wood descriptions

Statistical data of Styracaceae wood anatomy are summarised in Table 1 (data on Parastyrax are not included in the table because of the juvenile nature of the material studied).

Alniphyllum Matsumura

Number of species: 8.

Distribution: Southwest China, Indochina, Formosa.

Material studied: A. fortunei Perk., China: (MAD-SJRw 21904), (MAD-SJRw 21923); Hainan: (MAD-SJRw 29560). — A. pterospermum Matsum., Formosa: (TAIFw s.n.), Kanchehira 46 (MAD-SJRw 6447).

Growth rings distinct, represented by narrow zones of radially flattened fibre-tracheids. Pores distributed in aggregate radial rows isolated from adjacent rows by regions devoid of pores (Fig. 1). Vessels both infrequently solitary and in long radial multiples, angular in outline, tan-
gent diameter (30–)59–72(–100) μm. Vessel element length (858–)1317–1370(–2272) μm. Perforations scalariform with up to 24 narrow bars per plate. Intervessel pits mostly opposite to alternate, round in outline, most frequently 6–8 μm in diameter. Vessel-ray pitting similar but half-bordered. Tyloses absent. Imperforate tracheary elements (1060–)1919–2080(–2696) μm in length, with generally distinct bordered pits equally distributed on both radial and tangential walls. Imperforate element pit diameter ranges between approximately 5–9 μm. Axial parenchyma apotracheal diffuse and diffuse-in-aggregates between 2–6 cells; less frequently also paratracheal scanty. Rays heterocellular; uniseriates composed predominantly of square and upright cells; bi- and triseriate rays with uniseriate marginal extensions of mostly erect cells and a central portion of procumbent cells (Figs. 2, 3). Crystals of calcium oxalate absent. Silica bodies absent.

**Brusinsmia** Boerlage & Koorders

Number of species: 1 or 2.

Distribution: Assam, Burma, Malaysia (excluding Malay Peninsula).

Material studied: *B. styracoides* Boerl. & Koord., Java: (MAD-SJRw 31236); New Guinea: BW 6000 (USw 32003), CSIRO (USw 34785), CSIRO (USw 35256), CSIRO (USw 35289).

Growth rings absent. Vessels solitary and in radial multiples of 2–3, rarely clusters of 3, mostly circular in outline, tangential diameter (67–)158(–212) μm. Vessel element length (747–)1520(–2272) μm. Perforations scalariform with (10–)15(–33) bars per plate. Intervessel pits mostly alternate, some transitional between opposite and alternate, round in outline, mostly 10 μm in diameter. Vessel-ray pitting similar but half-bordered. Tyloses absent. Imperforate tracheary elements (1373–)2469(–3484) μm in length, with indistinctly to distinctly bordered pits that are more abundant on the radial walls. Imperforate element pit diameter ranges between approximately 3–7 μm. Axial parenchyma mostly diffuse and diffuse-in-aggregates between 2–6 cells, also occasionally paratracheal scanty. Rays heterocellular, uniseriates composed of square and upright cells; multiseriates 2–6 cells wide with uniseriate marginal extensions of upright cells and a central portion of procumbent cells. Crystals of calcium oxalate in the form of prisms and small, irregular clusters present in chambered axial parenchyma cells, and also rarely in ray parenchyma. Axial parenchyma cells often with both transverse and vertical septations resulting in multiple crystal chambers. Silica bodies absent.

**Halesia** Ellis ex Linnaeus

Number of species: 3–5.

Distribution: Eastern Asia, southeastern United States.

Material studied: *H. carolina* L., Adcock 75 (MADw 35851), (PRFw 3509). – *H. diptera* Ellis, (MAD-SJRw 43450), (PRFw 12904), Mississippi: Koehler 34 (MADw 2933), Florida: Anderson 99 (MAD-SJRw 45884). – *H. macgregorii* Chun, China: (MAD-SJRw 29811), (MAD-SJRw 29815).

Growth rings distinct, irregularly spaced, represented by zones of radially flattened fibres-tracheids, vessels narrower in diameter at the termination of a growth increment. Vessels solitary and in radial multiples of 2–5 (6), occasionally in clusters of 3–4, angular to circular in outline, tangential diameter (25–)50–55 (–82) μm. Vessel element length (535–)905–963(–1494) μm. Perforations scalariform with up to 20 narrow bars per plate. Intervessel pits mostly opposite, round in outline, diameter most frequently 6–8 μm. Vessel-ray pitting similar but half-bordered. Tyloses absent. Imperforate tracheary elements (949–)1385–1453(–2090) μm in length, with indistinctly to distinctly bordered pits on both radial and tangential walls. Imperforate element pit diameter ranges between approximately 3–7 μm. Axial parenchyma diffuse and diffuse-in-aggregates of 2–5 cells, also occasional paratracheal scanty. Rays heterocellular, uniseriates composed of mostly square and procumbent cells (upright cells common in *H. macgregorii*); multiseriates with uniseriate marginal extensions of square and occasionally upright cells and a central portion of procumbent cells. The heterocellular condition is more pronounced in *H. macgregorii*. Prismatic crystals of calcium oxalate of sporadic and infrequent occurrence in chambered axial parenchyma cells in *H. carolina* and *H. diptera*. Silica bodies absent.

**Huodendron** Rehder

Number of species: 6.

Distribution: Southern China, Thailand, Indochina.


Growth rings distinct, evenly spaced, represented by narrow zones of radially flattened fibre-tracheids. Vessels predominantly solitary (93%), or in infrequent radial multiples of 2–4, rarely in clusters of 3, circular in outline (Fig. 9), tangential diameter (45–)57(–72) μm. Vessel element length (737–)1153(–1494) μm. Per-
Fig. 1–6. Wood anatomy of Styracaceae and Lissocarpaceae. — Fig. 1–3. *Alniphyllum fortunei* (MAD-SJRw 21904). — 1: Transverse section showing radial pattern of vessel distribution. — 2: The same, tangential section. — 3: The same, radial section showing heterocellular ray. — Fig. 4–6. *Lissocarpus guianensis* (PRFw 17105). — 4: Transverse section showing radial pore multiples and prominent narrow-banded distribution of axial parenchyma. — 5: The same, tangential section. — 6: The same, tangential section showing mostly opposite intervessel pitting.
Fig. 7–10. Wood anatomy of Styracaceae. — Fig. 7 & 8. *Sinojackia xylocarpa* (MAD-SJRw 29823). 7: Transverse section illustrating pores distributed in radial zigzag lines. — 8: The same, tangential section. — Fig. 9 & 10. *Huodendron biaristatum var. parviflora* (MAD-SJR 22029). — 9: Transverse section showing solitary pore distribution. — 10: The same, tangential section.
Fig. 11–17. Wood anatomy of *Styrax*. – 11: *S. americanus* (PRFw 12944), TrS showing growth ring and pore multiples. – 12: The same, TgS. – 13: *S. pallidus* (MADw 35861), TrS. – 14: The same, TgS, showing mostly alternate intervessel pitting. – 15: The same, TgS. – 16: *S. odoratissimum* (MAD-SJRw 21921), TrS in the vicinity of a growth ring. – 17: The same, TgS, showing prismatic crystals (arrows) in the ray parenchyma. – TrS: transverse section; TgS: tangential section.
Fig. 18–23. Wood anatomy of *Styrax*. — Fig. 18–20. *S. officinalis* (SJRw 47817). – 18: Transverse section showing semi-ring-porous condition. – 19: The same, tangential section. – 20: The same, radial section showing crystalliferous axial parenchyma strand. — Fig. 21–23. *S. platanifolius* (USw 19556). – 21: Transverse section showing ring-porous condition. – 22: The same, tangential section. – 23: The same, radial section showing simple perforation plate (arrow) next to scalariform plate with two thick bars.
Fig. 24–26. Wood anatomy of *Styrax*. — Fig. 24 & 25. *S. tarapotensis* (MAD-SJRw 39673). — 24: SEM of radial section illustrating solitary silica grains (s) in the upright ray cells, x 800. — 25: The same, light microscopy of radial section showing silica grains (arrows) in the ray parenchyma. — Fig. 26. *S. hypochryseus* (USw 26822), light microscopy of radial section showing prismatic calcium oxalate crystals (c) in axial parenchyma cells and silica grains (arrows) in the ray parenchyma.

forations scalariform with (19–)29(–35) bars per plate. Intervessel pits opposite, round in outline, diameter approximately 4 μm. Vessel-ray pitting similar but half-bordered. Tyloses absent. Imperforate tracheary elements (1242–)1873–2424 μm in length, with indistinctly to distinctly bordered pits on both radial and tangential walls, pitting occasionally bi- and triseriate. Imperforate element pit diameter ranges between approximately 3–6 μm. Axial parenchyma diffuse and diffuse-in-aggregates between 2–3 cells, also paratracheal scantly (Fig. 9).

Rays heterocellular (Fig. 10); uniseriates composed of upright cells; multiseriates up to 7 cells wide, with very long uniseriate marginal extensions of generally upright cells and a central portion of procumbent cells. The central multiserate portion often with enlarged marginal cells, sometimes forming an incomplete sheath. Crystals of calcium oxalate absent. Silica bodies absent.

*Melliodendron* Handel-Mazzetti

Number of species: 3.

Distribution: Southern and southwestern China.


Growth rings distinct, unevenly spaced and often wavy, represented by narrow zones of radially flattened fibre-tracheids. Pores often distributed in zigzag radial lines or aggregations, particularly in *M. xylocarpum*. Vessels solitary and in radial multiples of 2–7 (8) and clusters of 3–5, angular to circular in outline, tangential diameter (27–)64–76(–92) μm. Vessel element length (454–)847–1015(–1323) μm. Perforations scalariform with (5–)11(–21) bars per plate. Intervessel pits transitional between opposite and alternate, round in outline, diameter most frequently 6–8 μm. Vessel-ray pitting similar
but half-bordered. Tyloses absent. Imperforate tracheary elements (1040—1494—1717(—2434) μm in length, with indistinctly distinctly bi-bordered pits more or less equally distributed on both radial and tangential walls. Imperforate element pit diameter ranges between approximately 5—7 μm. Axial parenchyma diffuse and paratracheal scanty, occasionally diffuse-in-aggregates between 2—3 cells. Rays heterocellular of two sizes; uniseriates composed of mostly square and erect cells (infrequently also procumbent); multiseries up to 5 cells wide, with uniseriate marginal extensions of mostly square and erect cells and a central portion of predominantly procumbent cells. Crystals of calcium oxalate absent. Silica bodies absent.

**Parastyrax** W.W. Smith

Number of species: 2.
Distribution: Burma and southern China.
Material studied: *P. lacei* W.W. Smith, Burma: Lace 5340 (E), young stem, diam. 4 mm.

Growth rings not evident in young stem. Vessels solitary and in radial multiples of 2—5 and clusters of 3—6, angular to more commonly circular in outline. Perforations scalariform with up to 17 bars per plate. Intervessel pits opposite to commonly transitional to alternate, round to slightly elongate in outline. Vessel-ray pitting similar. Tyloses absent. Imperforate tracheary elements with generally indistinctly bordered pits primarily on the radial walls. Axial parenchyma diffuse, diffuse-in-aggregates between 2—3 cells, and also occasionally paratracheal scanty. Rays heterocellular; uniseriates composed of erect cells; multiseries with uniseriate marginal extensions of upright cells and a central portion of both erect and procumbent cells. Crystals and silica not observed.

**Pterostyrax** Siebold & Zuccarini

Number of species: 7.
Distribution: Burma to Japan.

Growth rings present, unevenly spaced, represented by a zone of radially flattened fibre-tracheids. Vessels solitary and in radial multiples of 2—5 and clusters of 3—5, mostly circular in outline, tangential diameter (37—)56—64(—100) μm. Vessel element length (484—1968 —1013(—1414) μm. Perforations scalariform with (5—)12—14(—36) bars per plate. Intervessel pits opposite, round in outline, diameter most frequently 6—8 μm. Vessel-ray pitting similar but half-bordered. Tyloses absent. Imperforate tracheary elements (858—1406—1829(—2282) μm in length with indistinctly distinctly bordered pits approximately equally distributed on both radial and tangential walls. Imperforate element pit diameter ranges between approximately 3—7 μm. Axial parenchyma diffuse and diffuse-in-aggregates between 2—4 cells, also paratracheal scanty. Rays weakly heterocellular, uniseriates composed of procumbent and square cells; bi- and triseriate rays with uniseriate marginal extensions of procumbent, square and occasionally erect cells and a central portion of procumbent cells. Crystals of calcium oxalate absent. Silica bodies absent.

**Rehderodendron** Hu

Number of species: 10.
Distribution: China, Indochina.

Growth rings distinct, unevenly spaced and wavy in outline, represented by zones of radially flattened fibre-tracheids. Vessels solitary and in radial multiples of 2—6 and clusters of 3—6, angular to circular in outline, tangential diameter (25—)48—58(—75) μm. Vessel element length (323—)835—1021(—1424) μm. Perforations scalariform with (4—)10—12(—20) bars per plate. Intervessel pits mostly opposite with some transitional to alternate, circular in outline, diameter most frequently 6—7 μm. Vessel-ray pitting similar but half-bordered. Tyloses absent. Imperforate tracheary elements (939—)1346—1577(—2151) μm in length, with indistinctly distinctly bordered pits on both radial and tangential walls. Imperforate element pit diameter ranges between approximately 3—7 μm. Axial parenchyma mostly diffuse and diffuse-in-aggregates with 2—5 (6) cells, also paratracheal scanty. Rays heterocellular; uniseriates composed of square and erect cells, multiseries with uniseriate marginal extensions of square and erect cells and central portion of procumbent cells. Crystals of calcium oxalate absent. Silica bodies absent. Pith flecks scattered in all collections.

**Sinojackia** Hu

Number of species: 3.
Distribution: Southern China.
Material studied: *S. xylocarpa* Hu, China: Tang (MAD-SJRw 29823).

Growth rings distinct, evenly spaced, repre-
presented by narrow zones of radially flattened and thicker-walled fibre-tracheids. Pores frequently distributed in zigzag radial lines (Fig. 7). Vessels solitary and in radial multiples of 2–5 (6) and clusters of 3–6, angular to circular in outline, tangential diameter (25–)45–(60) μm. Vessel element length (606–)894–(1424) μm.

Intervessel pits opposite, circular in outline, diameter mostly 5 μm. Vessel-ray pitting similar but half-bordered. Tyloses absent. Imperforate tracheary elements (858–)1335–(1666) μm in length, with generally distinctly bordered pits on both radial and tangential walls. Imperforate element pit diameter ranges between approximately 5–7 μm. Axial parenchyma mostly diffuse, occasionally also diffuse-in-aggregates between 2–3 cells and paratracheal scanty. Rays heterocellular (Fig. 8); uniseriates composed of both erect and procumbent cells; bi- and triseriates with uniseriate marginal extensions of erect and procumbent cells and a central portion of procumbent cells. Crystals of calcium oxalate absent. Silica bodies absent.

**Styrax** Linnaeus

Number of species: ca. 120.

Distribution: Eastern Asia (primarily in tropical and subtropical areas), West Indies, South and Central America, the Mediterranean region (one species), and North America.


Growth rings absent to distinct, when present represented by narrow to broad zones of radially flattened fibres. The last formed latewood is often devoid of pores (Fig. 11). Wood mostly diffuse-porous, infrequently semi-ring-porous or ring-porous (Figs. 18, 21). Vessels solitary and in radial multiples of 2–7 (8) and clusters of 3–7, mostly circular in outline (Figs. 11, 13, 16), tangential diameter (12–)43–111(–140) μm. Vessel element length (191–)345–1193 (–1727) μm. Perforations scalariform with (1–)3–13(–26) bars per plate; bars comparatively thick and widely spaced in *S. officinalis*, *S. platani­folius*, and *S. texanus*. In the distinctly ring-porous species of *S. platani­folius* and *S. texanus* both simple and scalariform perforation plates occur (Fig. 23). Simple plates are restricted to the wide, earlywood elements whereas scalariform plates occur exclusively in the narrow, latewood vessel elements. This same condition has also been reported in *S. officinalis* var. *califor­nicum* by Copeland (1938) and more recently in *S. officinalis* var. *fulvescens* by Bissing (1976) and Carlquist (1980). Simple plates are
oblique to more commonly transverse in orientation. Intervessel pits either transitional between opposite and alternate or alternate (Fig. 14), mostly round in outline, with a most frequent diameter between 4–8 μm. Vessel-ray pitting similar but half-bordered. Solid, amorphous deposits present in the vessels of a number of species. Imperforate tracheary elements (464–1647–1892–2535) μm in length, with generally very indistinctly to distinctly bordered pits on both radial and tangential walls. Imperforate element pit diameter ranges between approximately 2–7 μm. Axial parenchyma abundant, diffuse, diffuse-in-aggregates between 2–6 (7) cells, and paratracheal scanty. Parenchyma lines mostly uniseriate but sometimes bi- and triseriate. Apotracheal parenchyma occasionally approaches the banded condition (Fig. 16); forming narrow terminal bands in S. suberifolius. Rays heterocellular (Figs. 12, 15, 19, 22); uniseriates composed of erect, square, and procumbent cells; multiseriates generally 2–5 cells wide, with uniseriate marginal extensions of square and erect cells and a central portion of mostly procumbent cells. Marginal cells in S. officinalis sometimes erect forming incomplete sheaths. Crystals of calcium oxalate were observed in all species except S. americanus, S. grandifolius, S. polyanus, S. polyspermum, and S. tarapotensis. Crystal prisms are predominantly restricted to chambered axial parenchyma cells (Figs. 20, 26), infrequently also in ray parenchyma (Fig. 17) as in S. hypargyreus, S. officinalis, and S. suberifolius. Silica bodies are present in the following species: S. argenteus, S. fanthawei, S. glabatus, S. guianensis, S. hypargyreus, S. hypochryseus (Fig. 26), S. leprousus, S. pallidus, and S. tarapotensis (Figs. 24, 25). Silica was not always present in all collections of a species, as in S. argenteus. The grains are small (4–9 μm) and round or irregular in shape with a granular surface, occurring as solitary grains in the ray parenchyma. Although silica bodies may occur in both the procumbent and upright ray cells, they are typically larger and more abundant in the square and upright cells.

Lissocarpa Bentham
(Lissocarpaceae, sensu Gilg, 1924)
Number of species: 2.
Distribution: Tropical South America.
Material studied: L. guianensis Gleason, Guiana: (PRFw 17105).
Growth rings absent. Vessels solitary (24%) and in radial multiples and clusters of 2–9 (Fig. 4), circular in outline, tangential diameter (37–)101(–145) μm. Vessel element length (868–)1148(–1464) μm. Perforations simple and scalariform. Oblique simple perforations predominately, but scalariform plates with up to 25 very fine and closely spaced bars occur sporadically. Some vessel elements have simple and scalariform perforations at opposite ends. No distinction in size can be made between elements possessing simple or scalariform plates. Intervessel pits opposite, or transitional between opposite and alternate, round in outline, small, diameter mostly 4 μm (Fig. 6). Vessel-ray pitting half-bordered, unilaterally compound, mostly opposite. Imperforate tracheary elements of the libriform fibre type, (1434–)2353(–2777) μm in length, with thick walls and sparse pitting. Axial parenchyma distributed in regular uniseriate (occasionally biseriate) bands and as paratracheal scanty (Fig. 21). Rays heterocellular (Fig. 5); uniseriates range between 3–21 cells high and are composed of procumbent and square or upright cells; biseriates range between 11–55 cells in height and are composed of a mixture of procumbent, square, and upright cells. The biseriate condition is often restricted to localised regions along the ray body. Crystals and silica absent.

General summary of xylem anatomy of Styracaceae (s.s.)

Growth rings. – Growth rings occur in all genera except Bruinsmia. Growth rings range from indistinct to prominent, evenly to irregularly spaced, and when present are generally recognisable by the presence of a narrow zone of radially compressed and thicker-walled imperforate tracheary elements of the latewood. Often the last several layers of latewood xylem are distinguished by the absence of pores, or pores of reduced diameter. In some species the occurrence of growth rings is variable among different collections of the same species. Styrax platanifolius and S. texanus are unusual among species examined as a result of their distinctly ring-porous condition (Type IX growth ring of Carlquist, 1980), in which vessels are considerably wider in diameter and more numerous in the early than latewood. A semi-ring-porous condition, in which the earlywood is marked by occasional large vessels, also characterises plants of Halesia and Israeli plants of Styrax officinalis.

Vessels. – Vessel element length ranges between species means of 345 μm in Styrax texanus and 405 μm in S. platanifolius, up to 1520 μm in Bruinsmia styracoides. Most species have vessel elements ranging between 700–1200 μm. Mean pore diameter ranges between 43 μm in Styrax texanus and S. platanifolius and 158 μm in Bruinsmia styracoides. Small diameter vessels
Table 2. Correlation analysis* and regression analysis** significance probability levels in Styracaceae (PR > F).

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* Values on upper right half of table show correlation coefficient significance.
** Values in left vertical column show partial regression coefficient significance.

Explanation of symbols: LAT, latitude; VFR, vessel (pore) frequency; VWT, vessel wall thickness; VED, vessel element diameter; URH, uniseriate ray height; MRH, multiseriate ray height; GR, growth rings; VEL, vessel element length; MRF, multiseriate ray frequency; FD, fibre diameter; FL, fibre length; FPD, fibre pit diameter; BARS, number of bars per perforation plate; IVPD, intervessel pit diameter; FWT, fibre wall thickness; URF, uniseriate ray frequency.
characterise *Sinojackia xylocarpa*, *Styrax americanus*, *S. grandifolius*, *Halesia diptera* and plants of *Rehderodendron*. Generally there is no significant difference in vessel diameter throughout the growth ring, excepting the smaller, very last formed elements. Distinctly ring-porous woods occur only in a small number of *Styrax* species. In *S. plataniolus*, for example, earlywood pores average 67 μm in diameter whereas latewood vessels have an average width of 26 μm. However, little difference in length is evident between early and latewood vessel elements. Wider, earlywood elements with simple perforation plates average 391 μm in length and the narrower latewood elements with scalariform perforation plates average 407 μm in length. These dimensions, and those recorded for fibre-tracheid length, are similar to those reported by Copeland (1938) for *S. officinalis* var. *californicum*.

Pore outline is generally a combination of angular and circular. Predominantly circular pores occur in the genera *Bruinsmia*, *Huodendron* and *Styrax*. Vessel wall thickness is typically thin, ranging between 2 and 3 μm, rarely exceeding 4 μm. Tyloses have not been observed in our material but dark-staining, occluding deposits may occur in the apparently nonfunctional pores. Pore number ranges from moderately few (5–10 mm⁻²) in *Bruinsmia styracoides* to very numerous (over 100 per mm²) in *Halesia diptera*, *Pterostyrax corymbosus*, *Rehderodendron*, and species of *Styrax* such as *S. grandifolius*, *S. plataniolus*, and *S. texanus*.

Intervessel pitting is characteristically opposite transitional to alternate; however, depending upon the species either an opposite or alternate arrangement may predominate. Alternate pitting predominates in *Bruinsmia* and *Styrax*. Intervessel pits are crowded and generally circular in outline. Average species pit diameters range between 4–10 μm, but are mostly 5–8 μm. Vessel-ray pitting is similar except half-bordered.

With very few exceptions, perforation plates are exclusively scalariform. *Pamphilia*, the only genus not examined, also apparently has scalariform perforations (Record & Hess, 1943). Our observations do not support the report of simple perforations in *Bruinsmia* by Metcalfe and Chalk (1950). Mean bar number ranges between 3 and 29. Bars are typically narrow, non-bordered, and closely spaced. Combinations of simple and scalariform plates were observed only in the Texas species *Styrax plataniolus* and *S. texanus*. This condition has also been reported in the two varieties of *S. officinalis* from California (Copeland, 1938; Carlquist, 1980). These species are distinctly ring-porous or semi-ring-porous and simple perforation plates are restricted to the wider, earlywood elements. Narrower latewood vessel elements possess only scalariform perforations. The scalariform plates in these plants possess bars that are generally thicker and more widely spaced than is typical for the genus. All collections that were examined of Israeli plants of *Styrax officinalis* contained only scalariform perforation plates. This observation is in agreement with the recent report of Baas et al. (1983).

The Styaraceae are characterised by vessels that are distributed both as solitary and pore multiples. A distinctive radial pattern of vessel distribution occurs in *Alniphyllum* and vessels distributed in zigzag radial lines distinguishes *Sinojackia xylocarpa*. *Huodendron* is the only genus in which vessels are nearly all solitary. Both pore chains and clusters composed of 2–6, in-frequently up to 8, vessels, as well as solitary vessels, occur in the remaining genera with somewhat varying percentages of each type. The percent solitary pores in all genera ranges mostly between 60–75%.

**Imperforate tracheary elements.**—Imperforate tracheary elements range from fibre-tracheids with distinctly bordered pits to elements having small, indistinctly bordered pits that approach the simple condition. Pit apertures are typically slit-like and crossed. Imperforate tracheary elements are nonseptate and have mean species ranges between 647 μm long and 13 μm wide in *Styrax texanus*, and 2469 μm long and 41 μm wide in *Bruinsmia styracoides*. Imperforate elements mostly fall into the medium to long category between 1300–1800 μm. Cell walls are mostly thin to medium in thickness.

**Rays.**—All genera possess a mixture of both multiseriate and uniseriate heterocellular rays. Multiseriates range in width between 2 and 7 cells and mean height between 14 and 29 cells. Uniseriates range between 3 and 8 cells in mean height. Ray histology conforms to the heterogeneous I and II types of Kribs (1968). Occasional upright marginal cells forming incomplete sheaths occur in the multiseriate rays of *Huodendron*.

**Axial parenchyma.**—Axial parenchyma is rather uniformly distributed as a combination of diffuse, diffuse-in-aggregates with irregularly distributed, mostly uniseriate (rarely bi- or triseriate) tangential lines containing 2–7 cells, and para-tracheal scanty. Parenchyma is most abundant in species of the genus *Styrax* where apotracheal parenchyma occasionally approaches the banded condition.

**Crystals.**—Prismatic calcium oxalate crystals are present in species belonging to the genera *Bruinsmia*, *Halesia*, and *Styrax*. In *Styrax*, pris-
Fig. 27 & 28. Latitude and vessel-frequency in Styraceae. – 27: Relationship of vessel frequency and latitude. – 28: Log values of same data plotted in Figure 27.
matic crystals occur in the majority of species examined; however, crystals are not always present in all samples of a taxon. Reports of the absence of crystals, therefore, may be the result of insufficient sample size. Crystals are generally borne in chambered axial parenchyma cells. *Bruinsmnia styracoides* has crystalliferous parenchymatous strands that are often subdivided both horizontally and vertically. Crystals are also infrequently located in ray parenchyma, as in *Bruinsmnia styracoides*, *Styrax hypargenus*, *S. officinalis*, and *S. suberifolius*. Miller (1976) reported that tropical members of *Styrax* tend to accumulate more crystals than the temperate species.

Silica. — Silica grains occur in combination with calcium oxalate crystals in a number of species of *Styrax*. *Styrax tarapotensis* is the only species examined in which silica is present and calcium oxalate absent. All species that have thus far been confirmed as possessing silica are confined to the Neotropics. Not all collections of a species may possess silica as illustrated by *S. argenteus*, in which a specimen collected in Mexico was positive for silica whereas two collections from Panama were without silica depositions. As reported by Ter Welle (1976), silica is restricted to the ray parenchyma cells.

**Discussion**

Wood anatomy of Styracaceae is qualitatively rather uniform. Features present in almost all species include exclusively scalariform perforation plates, pores occurring as both solitary and pore multiples, intervessel pits arranged in an opposite to alternate manner, fibres with indistinguishably to distinctly bordered pits, both multiseries and uniseriate heterocellular rays, and axial parenchyma distributed as a combination of diffuse, diffuse-in-aggregates and scanty. Prismatic crystals and silica occur in a number of species but are not present in all genera.

In accordance with the widely accepted trends in wood evolution as reviewed by Bailey (1957), Carlquist (1961), and Dickson (1975), the occurrence of more primitive features of predominantly solitary pore distribution and the presence of comparatively high bar number on the scalariform perforation plates in *Huodendron* are of potential evolutionary significance. Any phylogenetic speculation, however, must await study of additional specimens.

Schadel and Dickson (1979) commented upon the unique foliar structure of the genus *Parastyrax*, as compared with other Styracaceae, including a distinctive petiolar vascularisation, actinodromous primary venation, and the presence of crystal sand in the leaf mesophyll. Additional points of difference between *Parastyrax* and other taxa of the Styracaceae include an unusual height of 150 feet or more and drupaceous fruit with a glabrous, fleshy exocarp marked with elongate, whitish lenticels (Smith, 1920). Although only a single twig sample of *Parastyrax* was available for study, qualitative characters of the secondary xylem appear consistent with other members of the family.

Baas (1972) presented abundant evidence for the removal of *Afrystyrax* Perkins & Gilg from the Styracaceae and for its subsequent placement in the family Huaceae. As noted by Baas, significant wood anatomical differences between *Afrystyrax* and Styracaceae include vessel perforations simple in *Afrystyrax*, scalariform in Styracaceae; axial parenchyma multiseries banded in *Afrystyrax*, diffuse-in-aggregates and scanty in Styracaceae; fibres with simple pits in *Afrystyrax*, fibres with indistinctly bordered pits in Styracaceae. Additional features distinguishing these two taxa are presented by Baas (l.c.).

The genus *Lissocarpa*, also removed from the Styracaceae by Perkins (1907), has subsequently been generally regarded as constituting the closely related monogenic family Lissocarpaceae (Gilg, 1924; Hutchinson, 1959; Wagenitz, 1964; Cronquist, 1981). In addition to reproductive characters, Schadel and Dickson (1979) described the following features of foliar anatomy that can be used to separate *Lissocarpa* from Styracaceae: diffuse, branched sclereids in the petiole and mesophyll, petiole vascularisation consisting of an arc with outwardly curving ends, and fimbriate marginal ultimate venation. In addition, the xylem of *Lissocarpa* differs from the Styracaceae by possessing vessel elements with both simple and scalariform perforation plates, and prominently banded axial parenchyma.

An interesting aspect of styracaceous wood structure is the occurrence of simple perforations in a few species of *Styrax* in an otherwise entirely scalariform perforation plate family. This feature was apparently first described by Copeland (1938) in plants of *S. officinalis* var. *californicum*, although for the most part it has been overlooked in subsequent descriptions of the family. Bissing (1976) and Carlquist (1980) reported the presence of simple plates in *S. officinalis* var. *fulvescens* and we are now also documenting the occurrence of simple plates in the wider, early wood vessel elements of *S. plataniifolius* and *S. texanus*. All of these plants occupy seasonally dry habitats in portions of the southwestern and western United States. *Styrax texanus* is found in the plateau region of central Texas where it typically grows on
the sides of steep limestone cliffs. *Styrax platani-folius*, another species from central Texas, also grows on highly calcareous soils in dry, wooded bottomlands and on rocky banks and cliffs (Gonsoulis, 1974).

Our observations are in agreement with Baas et al. (1983) as regards the presence of exclusively scalariform perforation plates in plants of *Styrax officinalis* from Israel, albeit with reduced bar number and thickened bar width. However, California plants presumably belonging to the same species, have evolved both simple and scalariform perforations. Gonsoulis (1974) commented upon the rather confused nomenclatural history of the *S. officinalis* complex and found the differences between the Mediterranean and California material significant only at the varietal level. Accordingly, the differences in perforation plate type within what appears to be varieties of the same species is of special interest. It would be particularly interesting to determine to what extent this character is genetically stable.

The occurrence of reduced scalariform perforation plate bar numbers and even simple perforations in species of *Styrax* from localities with long dry periods correlates with similar specialisations observed in other plants growing in xerophytic conditions (Baas et al., 1983; Carlquist, 1975; Dickison, 1979; Dickison et al., 1978). Van den Oever et al. (1981), however, found that the considerable variation in bar number in *Symphlocos* could not be interpreted in terms of water availability.

Carlquist (1980) speculated that the type of growth ring in which wider vessels from the earlywood possess simple perforation plates is a potential accommodation to the flow of greater volumes of water per unit time earlier in the season. The presence of scalariform perforations in the latewood elements was not regarded as being disadvantageous as a result of slower rates of water movement in latewood. Although these ideas were only offered as hypotheses, the trend from exclusively scalariform to a combination of scalariform and simple perforations in *Styrax* appears clearly to be a response to drier conditions. Additional xerophytic adaptations present in *Styrax* woods include vessels that are overall narrower in diameter, shorter in member length, and more numerous per unit area. Baas et al. (1983) found that the Mediterranean *Styrax officinalis* had a more or less identical vessel member length as the cool temperate species studied by Van der Graaff and Baas (1974); however, in our more extensive materials the xeric species of *Styrax* (*S. officinalis*, *S. platanifolius*, *S. texanus*) show somewhat shorter vessel members than the mesic cool temperate ones (such as *S. americanus*, *S. grandifolius*, *S. japonicus*, and *S. obassia*), indicating that mesic-xeric trends can override latitudinal trends. It is also interesting to note that within the family as a whole, the tall tropical tree species *Bruinsnia styracoides* possesses vessel elements and fibres of the greatest dimensions.

Wood anatomical data were subjected to statistical analysis to determine which, if any, features are correlated with latitude of provenance. A portion of the results of the correlation analysis is included in Table 2. Vessel element frequency as well as multisierate ray frequency show significant positive correlation with increasing latitude, whereas vessel element length, vessel wall thickness, pore diameter, multisierate and uniseriate ray height, and fibre-tracheid length and diameter show significant negative correlation with increasing latitude at the .01% level. Growth rings are also more common in temperate as opposed to tropical species. Fibre-tracheid pit diameter, intervessel pit diameter, and the number of bars per scalariform perforation plate are significantly correlated with increasing latitude at the .005% level, and fibre-tracheid wall thickness and uniseriate ray frequency at the .1% level. Of the variables positively correlated with latitude at the .01% significance level, all show strong (.01% level) correlation with each other with the exception of growth rings and uniseriate ray height and growth rings and multisierate ray frequency.

Of the variables showing correlation with latitude at the .5% or 10% levels, all show strong (.01% level) correlation with at least three of the variables showing a strong correlation (less than or equal to .1% level) with latitude. A multiple regression analysis was performed for each variable in order to clarify the effects of intercorrelation. Table 2 demonstrates significance levels for the partial correlation coefficients of each variable with latitude after regression of all other variables. Eight variables were significant at the 10% or less level. Growth rings and fibre-tracheid pit diameter failed to meet the 5% level of probability in any of the regression models tested in a procedure in which obtaining the maximum $R^2$ (a measure of closeness of fit of a model) was the main criterion (MAXR option of GLM). Remaining variables were significant at the 5% level or less in at least eleven models. It is interesting to note that vessel diameter and uniseriate ray height were also significant at the 5% level in eleven or more models. Even the variables with partial correlation coefficients significant only at the 25% level or more were significant at the 5% or less level in at least one of the models, with the exception of fibre-tracheid length, which like
fibre-tracheid pit diameter, and growth rings, was not significant at the level in any of the models tested.

The above analyses of wood features in Styracaceae indicate that pore frequency, vessel element length and wall thickness, and multisierate ray frequency show the strongest evidence of correlation with latitude. Pore frequency and multisierate ray frequency increase with distance from the equator whereas vessel element length and wall thickness decrease. Figure 27 shows the relationship of vessel frequency and latitude and Figure 28 illustrates the log values of the same data. Similar correlations between pore frequency and vessel element length with latitude have been reported in a number of other taxa (Baas, 1973; Carlquist, 1966, 1982; van den Oever et al., 1981; van der Graaff & Baas, 1974). Van den Oever et al. (1981) demonstrated a decrease in vessel wall thickness with increasing latitude in Symplocos, a situation also present in Styracaceae. It is somewhat surprising that in light of the rather strong correlation between greater multisierate ray frequency with higher latitudes that exists in Styracaceae, a similar condition is apparently not present in the other genera that have been analysed in this manner. Carlquist (1966), however, does mention an inverse correlation between multisierate ray frequency and latitude in the Asteraeae.

Variables for which correlation with latitude is somewhat less strongly indicated include pore diameter, intervessel pit diameter, number of bars per perforation plate, fibre-tracheid pit diameter, and unisierate ray frequency. Values for all but one variable increase with increasing latitude. Only pore diameter decreases at higher latitudes, a correlation that has been frequently reported in other genera (Baas, 1973; Carlquist, 1966, 1982; van den Oever et al., 1981; van der Graaff & Baas, 1974). Our finding of a latitudinal trend toward increased intervessel pit size from the tropics to more temperate regions is opposite of what Miller (1976) reported for Juglans. In the tropical black walnuts intervessel pits are larger in tropical species than temperate ones.

Carlquist (1982) noted an inverse correlation between perforation plate bar number and latitude for Illicium, as did Baas (1973) for Ilex. Van den Oever et al. (1981), however, observed no such condition for Symplocos. Van der Graaff and Baas (1974) list several examples of positive correlation, negative correlation, and no correlation with respect to variation in bar number and latitude, which led them to conclude that there is no general trend in woody plants for this feature.

Weak negative correlation is evident in Styracaceae of latitude with ray height and fibre-tracheid length, diameter, and wall thickness. In all of these features values decrease with increasing latitude. Van den Oever et al. (1981) noted similar weak negative correlations in their data on Symplocos.

The trends reported here for Styracaceae have now been generally confirmed in a large number of diverse groups. As noted by Rury and Dickison (1984), what is now required is a better understanding of the relationship of xylem anatomy to other aspects of plants structure and physiology.

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References


