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WOOD AND BARK ANATOMY OF SCHISANDRACEAE: IMPLICATIONS FOR PHYLOGENY, HABIT, AND VESSEL EVOLUTION

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ABSTRACT

Qualitative and quantitative features are reported for mature wood and bark of two species of *Kadsura* and five species of *Schisandra*. Newly reported for the family are predominance of simple perforation plates (all species); presence of pit membrane remnants in vessels of first-formed secondary xylem; two to three series of pits per facet on tracheids; diffuse axial parenchyma (*Kadsura*); multiseriate rays more than three cells wide at the widest point (all species); ethereal oil cells in axial xylem; and certain details of comparative bark anatomy. Differences in wood anatomy between Illiciaceae and Schisandraceae are nearly all differences of degree. These differences relate to the shrubby to arboreal habit in *Illicium* as opposed to the scandent habits in Schisandraceae. Larger pits on tracheids, wider and shorter vessel elements, and a high figure for conductive area per mm² of transection are features related to the scandent habit of Schisandraceae; opposing character states in *Illicium* relate to the self-supporting nature of growth forms in that genus.

Key words: bark anatomy, comparative wood anatomy, ethereal oil cells, *Illicium*, *Kadsura*, Magnoliidae, mucilage cells, *Schisandra*, vessel evolution, xylem.

INTRODUCTION

Although the materials in the present study (two species of *Kadsura*, five of *Schisandra*) do not represent a large proportion of the two genera of Schisandraceae (which have 22 and 25 species, respectively, according to Smith 1947), the nature of the material offers reasons for presentation of this study.

Unlike the dried materials available to Bailey and Nast (1948) and Metcalfe (1987), all but one of the species in the present investigation are represented by liquid-preserved stems. Thus, phloem, cortical, and pith cells are not collapsed and can be successfully sectioned by a paraffin technique (Carlquist 1982a). Secondly, all of the material is from relatively mature stems 5 mm or more in diameter; thus, mature wood and phloem patterns are present. Bailey and Nast (1948) and Metcalfe (1987) stress that data available to them are based on relatively young stems of few species (the number not documented in those studies), and that their conclusions, accordingly, are limited.

In many of the specimens studied here, however, wood formed during the first year of secondary growth has scalariform perforation plates with numerous bordered bars. Such perforation plates provided opportunities to search for presence of pit membrane remnants as are found in Illiciaceae (Carlquist 1992). Schisandraceae are considered by most authors to be close to Illiciaceae on the basis of macromorphology and anatomy (Metcalfe 1987) as well as on the basis of molecular data (Qiu et al. 1993).

A relatively recent monograph of the woods of *Il-*

licium (Carlquist 1982b) also provides the basis for a comparison between Illiciaceae and Schisandraceae. Woods of Schisandraceae can be used to document the adaptations to the scandent habit by the Illiciales, in both qualitative and quantitative terms. Woody vines and lianas have a number of distinctive anatomical features (Carlquist 1985, 1991). Lianas, however, do not have a single mode of structure in wood or bark. Although there are character states in wood and bark of lianas that are more common than they are in non-scandent relatives of particular scandent taxa, there is no single optimal wood or stem anatomy for a scandent species. The present study, therefore, is a contribution to an appreciation of the diverse ways in which lianas are constructed. Perhaps particular modes of lianoid structure will emerge more clearly as a result of such comparative studies. Despite recent attention paid to wood of lianas, wood anatomy of scandent plants is still more poorly known than that of self-supporting woody plants. Tree species have traditionally formed the preferred objects for study by wood anatomists on account of the economic value of trees.

MATERIALS AND METHODS

Stem samples preserved in 50% aqueous ethanol were available except for *Kadsura scandens* (Blume) Blume; for that species, a xylarium accession was used. The large vessels and, in bark, the intermixture of sclerenchyma and thin-walled cells provide sectioning difficulties not readily solved with a sliding microtome. Therefore, an alternative method (Carlquist

1982a) was used. Sections were stained with a safranin-fast green combination. Some paraffin sections were left unstained, mounted on aluminum stubs, cleansed of paraffin, air-dried, sputter-coated, and examined with scanning electron microscopy (SEM). Macerations of mature wood were prepared with Jeffrey's Fluid and stained with safranin.

Specimens documenting this study are as follows: *Kadsura japonica* (L.) Dunal, coastal forest of Miyajima Island, Japan, *Carlquist 15688* (RSA); *K. scandens*, cultivated at Buitenzorg Botanic Garden from seeds collected in China, *SJRw-19511* (Forest Products Laboratory); *Schisandra glabra* (Brickell) Rehd., about 8 km from Williamston, Martin Co., North Carolina, *Ornduff 7698* (UC), cultivated at the University of California, Berkeley, Botanic Garden, *74.0465*; *S. henryi* Clarke, Chuang Hua Pref., W. Zhejiang Prov., China, from plants grown in Shanghai Botanic Garden, cultivated at the University of California, Berkeley, Botanic Garden, *87.0605*; *S. repanda* (Sieb. & Zucc.) A. C. Smith, cultivated at the Koshikawa Botanic Garden of the University of Tokyo, *Carlquist 15689*; *S. rubriflora* Rehd. & Wils., cultivated at the Huntington Botanic Gardens, San Marino, California, *Carlquist 8055* (RSA); *S. sphenanthera* Rehd. & Wils., cultivated at the Huntington Botanic Gardens, San Marino, California, *Carlquist 8051* (RSA). Nomenclature for the family follows that of Smith (1947).

Terms for wood anatomy follow the IAWA Committee on Nomenclature (1964); the terminology for the imperforate tracheary elements in Schisandraceae used by Lemesle (1932, 1945, 1946) agrees with that reference. Vessel diameter was measured as mean lumen diameter (for an oval vessel, an average between wide and narrow diameter was taken). The definitions of ethereal oil cells and mucilage cells offered by Baas and Gregory (1985) have been followed. These cells were identified in my material by their idioblastic distribution, their larger size and the presence of a thin primary wall, separated from the secondary wall and usually buckled, inside of the secondary wall (Fig. 20, upper right). Freshly cut stems of Schisandraceae have a distinctive scent probably produced by ethereal oils in these cells.

In this paper, as in many papers on comparative wood anatomy by various authors, means are given for quantitative features. These means are based upon 25 measurements. Most workers in wood anatomy find that standard deviation is relatively high with fewer than 20 measurements, but even above 20 measurements, standard deviation is still relatively high compared with other biological features which are commonly subjected to statistical analysis, so that one could question conclusions based upon statistical analysis. Wood cells are more variable than one might expect. Another difficulty involved in statistical analysis

is that large numbers of samples are almost never used in anatomical studies. In the present study, material of mature wood was available for only a minority of species (use of twigs from herbarium specimens would have resulted in mixture of data on juvenile wood and data on mature wood). Main stems differ from branches and roots (the latter not available for this family). Statistical data yield conclusions only about material studied—usually very little in anatomical studies because of demands of collecting and processing numerous stems and roots—and do not yield any information about material not studied. Nevertheless, there is value in offering simple quantitative data where similarities or differences are marked, if one views the limitations of quantitative data in woods carefully.

RESULTS

Growth Rings

The only species in the present study that does not have growth rings is *K. scandens* (Fig. 1). This species is native to areas within 10° of the equator, and the locality where the plant sampled was cultivated, the Java uplands, is a similar distance from the equator. All of the remaining species of Schisandraceae studied come from temperate localities and have growth rings. Growth rings are present in Fig. 11; a single growth ring (with small portions of preceding and succeeding growth rings) is shown in Fig. 13 (earlywood of that ring represented by the large vessel, center; the two smaller vessels above it, right and left, respectively, are latewood vessels). In addition to narrow vessels demarcating latewood, one layer of radially narrow tracheids terminates each growth ring (Fig. 13). Exceptionally well-marked growth rings characterize *S. repanda*; earlywood vessels in material of that species are 180–200 μm in diameter and are localized at the beginning of the ring, whereas the remainder of the ring has latewood vessels 60–150 μm in diameter.

Vessel Elements

Metcalf (1987) describes perforation plates in the family as a whole as, “. . . mostly scalariform, but with fewer bars than in *Illicium*, and also with larger apertures between the bars. Perforations of some of the larger vessels simple.” Certainly scalariform perforation plates with few bars and wide intervening perforations occur in Schisandraceae, but they prove to be much less common than simple perforation plates in all species of the present study. The simple nature of perforation plates of most schisandraceous vessels is well revealed in macerations, which were apparently not used in earlier studies of wood of Schisandraceae.

Scalariform perforation plates with numerous bars are present in late metaxylem and early secondary xy-

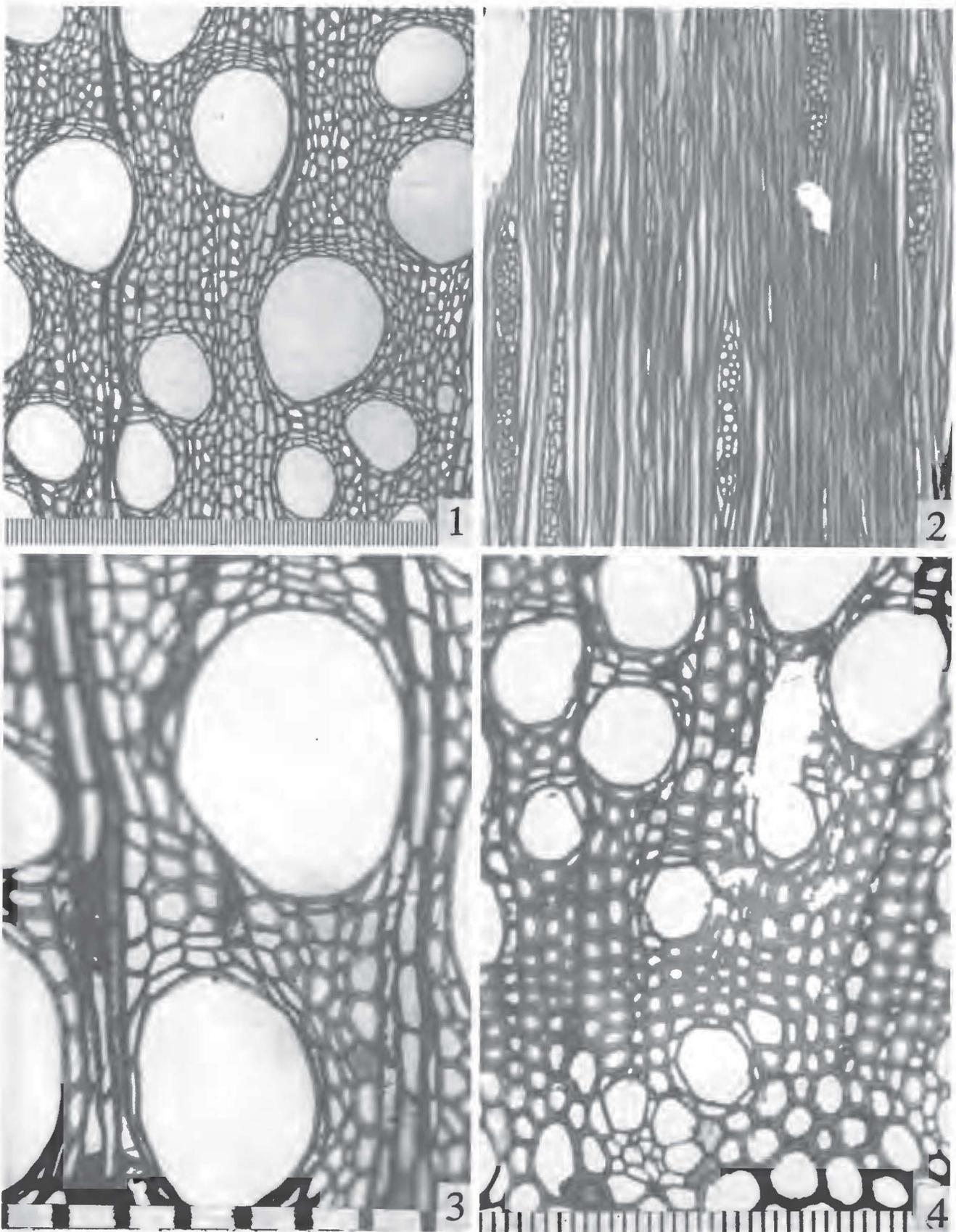


Fig. 1-4. Wood sections of *Kadsura*.—1, 3, 4. *K. scandens*.—1. Transection; vessels exceptionally wide.—2. *K. japonica*. Tangential section; uniseriate rays present on some multiseriate rays, absent on others.—3. Transection portion; several layers of axial parenchyma abaxial to vessels.—4. Pith (bottom) and earlier-formed secondary xylem; vessels sparse in earliest secondary xylem. (Fig. 1-2, magnification scale below Fig. 1 [divisions = 10 μ m]; Fig. 3, scale below Fig. 3 [divisions = 10 μ m]; Fig. 4, scale below Fig. 4 [divisions = 10 μ m].)

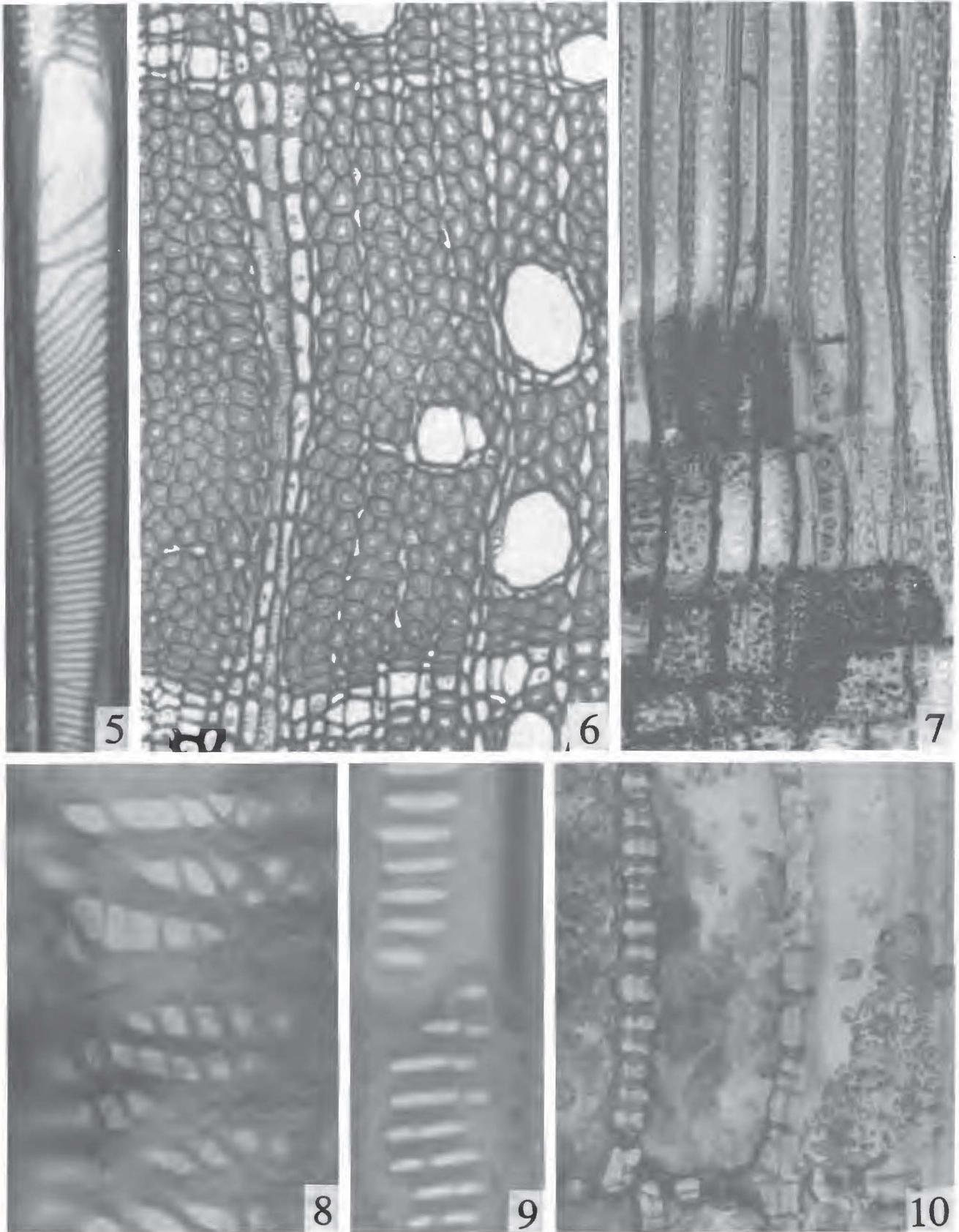


Fig. 5-10. Wood sections of *Kadsura japonica* (Fig. 5, 6, 8, 9) and *K. scandens* (Fig. 7, 10).—5. Perforation plate from radial section.—6. Transverse section; terminal axial parenchyma bands, top (left) and bottom.—7. Radial section; tracheids with 1-2 rows of pits (above) and procumbent to upright cells with dark-staining contents (below).—8. Vessel to ray pitting ("unilaterally compound").—9. Vessel to axial

lem. Such a plate is shown for *K. japonica* in Fig. 5 (absence of bars at top natural). Numerous wide-bordered bars characterize the perforation plate of *S. sphenanthera*, a portion of which is shown in Fig. 14. The perforation plate of Fig. 14, examined carefully at high power with light microscopy, shows irregularities (bits of material adherent or between the bars). Such irregularities are suggestive, in my experience, of remnants of pit membranes. That interpretation is validated by SEM study of perforation plates in early secondary xylem of *S. glabra* (Fig. 15, 16). These photographs show pit membranes that contain elliptical to oval pores of various sizes. Even supposing that the pores are rendered more prominent because air drying rather than critical point drying was used, lysis of pit membranes that ultimately results in their removal from perforations is in progress. Consequently, the presence of porose pit membrane remnants is a valid indicator of an early stage in evolution of a perforation plate.

At the periphery of the pith, primary xylem vessels are evident in all species of *Kadsura* and *Schisandra* (Fig. 4). In some stems, vessels are sparse or absent in the first-formed secondary xylem. Tracheids therefore initially comprise a larger proportion of the secondary xylem.

Because vessels are almost exclusively solitary in Schisandraceae, vessel-to-vessel pitting is not readily seen (it is restricted mostly to caudate tips of vessels). Vessel-to-tracheid pitting is mostly alternate, although it could be interpreted as opposite in places. Vessel-to-ray pitting is scalariform, often with slender strands of secondary wall material subdividing the elliptical pits into smaller units (Fig. 8). McLaughlin (1933) refers to these as unilaterally compound pits. Vessel-to-axial parenchyma pitting is scalariform to transitional (Fig. 9).

Vessels are solitary or nearly so (Fig. 1, 3, 4, 11, 13). If vessels were randomly arranged, there would perhaps be more numerous contacts among vessels; certainly vessel grouping is quite minimal. Consequently, no figure for number of vessels per group is presented in this paper.

Quantitative features of vessels are given in Table 1. Mean vessel lumen diameter (column 1) is relatively uniform. The exceptionally wide vessel diameter of *K. scandens* is evident in measurements (Table 1) as well as in visually (Fig. 1). Likewise, *K. scandens* has a correspondingly much lower number of vessels per mm² of wood transection (column 2) than in the remaining species. *Kadsura scandens* has vessel ele-

ments that are notably longer than those of the remaining species (column 3). Note should be taken that the *K. scandens* stems studied were 5 mm in diameter, and thus not larger in diameter than those of the other Schisandraceae studied; vessels tend to increase in diameter with age in most dicotyledons. Vessel wall thickness is surprisingly uniform in Schisandraceae and notably thin: 2.2–2.4 μm. Vessel pit diameter was recorded only in terms of vessel to tracheid diameter, and mean diameter of pit cavity diameter (as seen in face view) for species studied ranged from 6 μm (*S. repanda*) to 10 μm (*S. rubriflora* and *S. sphenanthera*).

Tracheids

The imperforate tracheary elements of Schisandraceae are all tracheids in the sense of the IAWA Committee on Nomenclature (1964), a term reaffirmed for Schisandraceae by Lemesle (1932, 1945, 1946). Pit size and density are like those of tracheids in gymnosperms. Tracheids have one to three series of alternate circular pits per wall (Fig. 7). Pit apertures are narrowly elliptical. Mean tracheid lengths (Table 1, column 4) range from 761 μm in *S. glabra* to 1774 μm in *K. scandens*. The mean length of tracheids for the species studied, 1214 μm, is much greater than that of vessel elements, 753 μm. Tracheid wall thickness is appreciably more than vessel wall thickness in the species studied. Mean wall thicknesses of tracheids range from 3.5 μm (*S. henryi*) to 5.3 μm (*S. rubriflora*). The latter figure is close to the mean tracheid wall thickness for all species studied (4.8 μm). There are several layers of thin-walled sclereids at the periphery of the pith (Fig. 4). In none of the wood sections were gelatinous walls found on tracheids (gelatinous walls defined as showing at least some fast green in a safranin-fast green stain and as having shrinkage patterns in walls). The narrower sclereids are similar to tracheids, so that the boundary between the two cell types is difficult to determine from transections.

Axial Parenchyma

Axial parenchyma in *Kadsura* is diffuse plus abaxial (= on the abaxial surfaces of vessels). The diffuse parenchyma is scarce (for example, only four diffuse axial parenchyma cells are present in the area shown in Fig. 6). Abaxial parenchyma in *K. scandens* is abundant, mostly 3–4 cells in thickness (Fig. 1, 3), less in vessels of the secondary xylem (Fig. 4). Abaxial parenchyma in both species of *Kadsura* may extend a

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parenchyma pitting, scalariform (above) and transitional (below).—10. Ray cell walls in sectional view from radial section, to show borders on pits. (Fig. 5–7, scale below Fig. 4; Fig. 8–10, scale below Fig. 3).

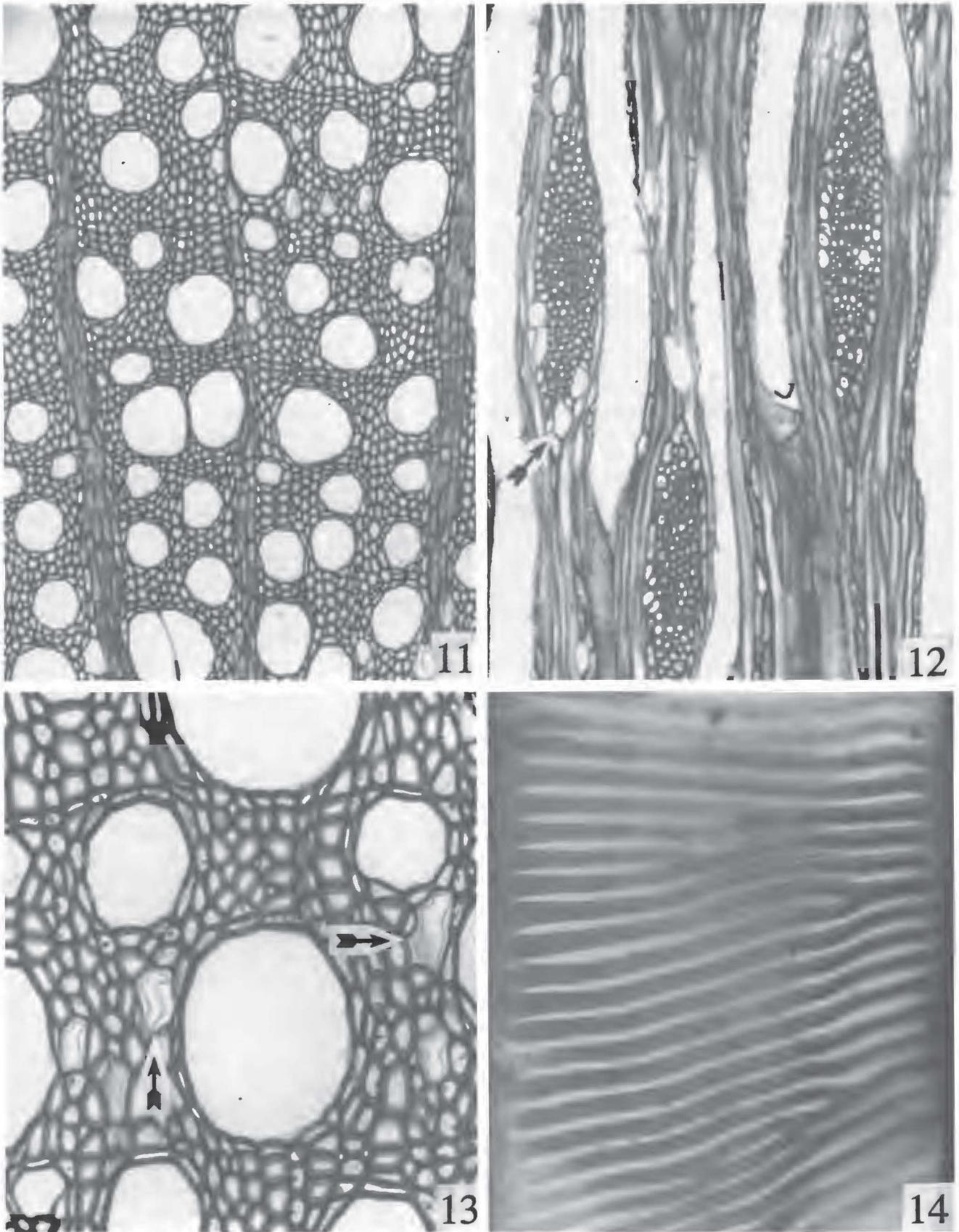


Fig. 11-14. Wood sections of *Schisandra sphenanthera*.—11. Transection; five growth rings are present within the photograph.—12. Tangential section; prominently enlarged cells are oil cells (arrow indicates one of these).—13. Transection; growth ring definable by large earlywood vessel, near center, with latewood vessels to left and right above it; oil cells indicated by arrows.—14. Portion of perforation

little more than halfway around the vessels, as seen in transections (Fig. 1, 3).

In *Schisandra*, diffuse axial parenchyma was not observed. Abaxial parenchyma one cell in thickness is characteristic, with vascentric parenchyma (a sheath around a vessel, rarely more than one cell in thickness) less common. These contrast with the conditions observed in the two *Kadsura* species. The strands of axial parenchyma in both genera consist of four to seven cells each.

Rays

Vascular rays are both multiseriate and uniseriate; multiseriate rays are more abundant except in *S. repanda*, in which the two types are present in approximately equal numbers. In all species, the multiseriate portion of multiseriate rays is composed of procumbent cells except for occasional sheath cells (Fig. 2, 12). The tips of multiseriate rays may lack uniseriate wings or may have uniseriate wings that can be longer than the multiseriate portion of a ray (Fig. 2, 12). Uniseriate wings are composed of upright cells. Quantitative data on rays are shown in Table 1. Multiseriate and uniseriate ray heights (column 5, 7) are not correlated with vessel element length, as they are in many dicotyledons: *K. scandens* has vessel elements longer than those of *K. japonica* and *S. rubriflora*, but multiseriate rays of *K. scandens* are shorter than in those species.

The mean width of multiseriate rays at their widest point (Table 1, column 6) ranges from as little as about three cells (Fig. 2) to more than six cells (Fig. 4). Metcalfe (1987) reports rays one to three cells wide in wood of Schisandraceae. Ray cell walls are lignified and 2.8–3.6 μm in thickness in the species studied. Bordered pits predominate on both tangential walls and on horizontal walls (Fig. 10). As in other dicotyledons, borders on ray cells are best seen in sectional view, although most authors still rely on face views of pits when assessing presence of borders on pits interconnecting ray cells.

Idioblasts and Deposits

Occasional ethereal oil cells were observed in sheath cells of *S. rubriflora* rays. However, in *S. sphenanthera*, oil cells are abundant as sheath cells and wing cells of rays. More importantly, oil cells occur in axial xylem of *S. sphenanthera* (Fig. 13); this mode of occurrence has not been previously reported for the family. Oil cells in rays of Schisandraceae have been re-

Table 1. Wood features of Schisandraceae.

Species	1 VD	2 VM	3 VL	4 TL	5 MH	6 MW	7 UH
<i>Kadsura japonica</i>	92	40	674	1531	1410	3.5	159
<i>K. scandens</i>	137	16	1074	1724	1121	3.3	880
<i>Schisandra glabra</i>	94	33	473	761	990	3.7	221
<i>S. henryi</i>	101	51	762	1106	913	4.2	535
<i>S. repanda</i>	98	52	744	1292	858	3.5	439
<i>S. rubriflora</i>	107	43	738	956	1263	5.7	426
<i>S. sphenanthera</i>	91	51	809	1132	1058	6.2	797
All species averaged	103	41	753	1214	1087	4.3	494

Key to columns: 1 (VD), mean diameter of vessel lumen, μm ; 2 (VM), mean number of vessels per mm^2 transection; 3 (VL), mean vessel element length, μm ; 4 (TL), mean tracheid length, μm ; 5 (MH), mean height of multiseriate rays, μm ; 6 (MW), mean width of multiseriate rays at widest point, cells; 7 (UH), mean height of uniseriate rays, μm . Collection and locality data given in Materials and Methods.

ported by Garratt (1933), McLaughlin (1933), and Baas and Gregory (1985). Brownish droplets and massive deposits of an unidentified compound were observed in ray cells of *K. scandens* (Fig. 7, 10).

Bark

At the outer surface of stems, thin-walled phellem is characteristic for all species. Radially elongate phellem cells were observed in *K. japonica*; phellem cells wider tangentially than radially were observed in the remaining species (Fig. 17). Several layers of thick-walled phelloderm cells are present in all species. The stem cortex persists as bark forms by stretching and division of cortical parenchyma. Within the cortical parenchyma of most species, astrosclereids with calcium oxalate crystals embedded in outer wall surfaces occur commonly (*S. sphenanthera*, Fig. 21). Such sclereids were not observed in *S. glabra* or *S. henryi*. Those same two species have oil cells in secondary phloem rather than mucilage cells (Fig. 17, 19; Fig. 20, upper right). Strands of protophloem fibers occur just inside the cortical parenchyma (Fig. 18). Mucilage cells were observed in secondary phloem of all but those two species. Breakdown of walls between adjacent mucilage cells occurs occasionally in these species, but is characteristic of *S. sphenanthera*. Oil cells and mucilage cells were not reported for bark of Schisandraceae by Baas and Gregory (1985).

Crystalliferous secondary phloem fibers were observed in all species. These fibers have crystals embedded in the walls (Fig. 22). In those species in which the fibers form plates two cells in thickness (e.g., Fig. 18), the crystals are on outward-facing fiber faces rath-

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plate from radial section of earlier-formed secondary xylem. (Fig. 11, 12, scale below Fig. 1; Fig. 13, scale below Fig. 4; Fig. 14, scale below Fig. 3).

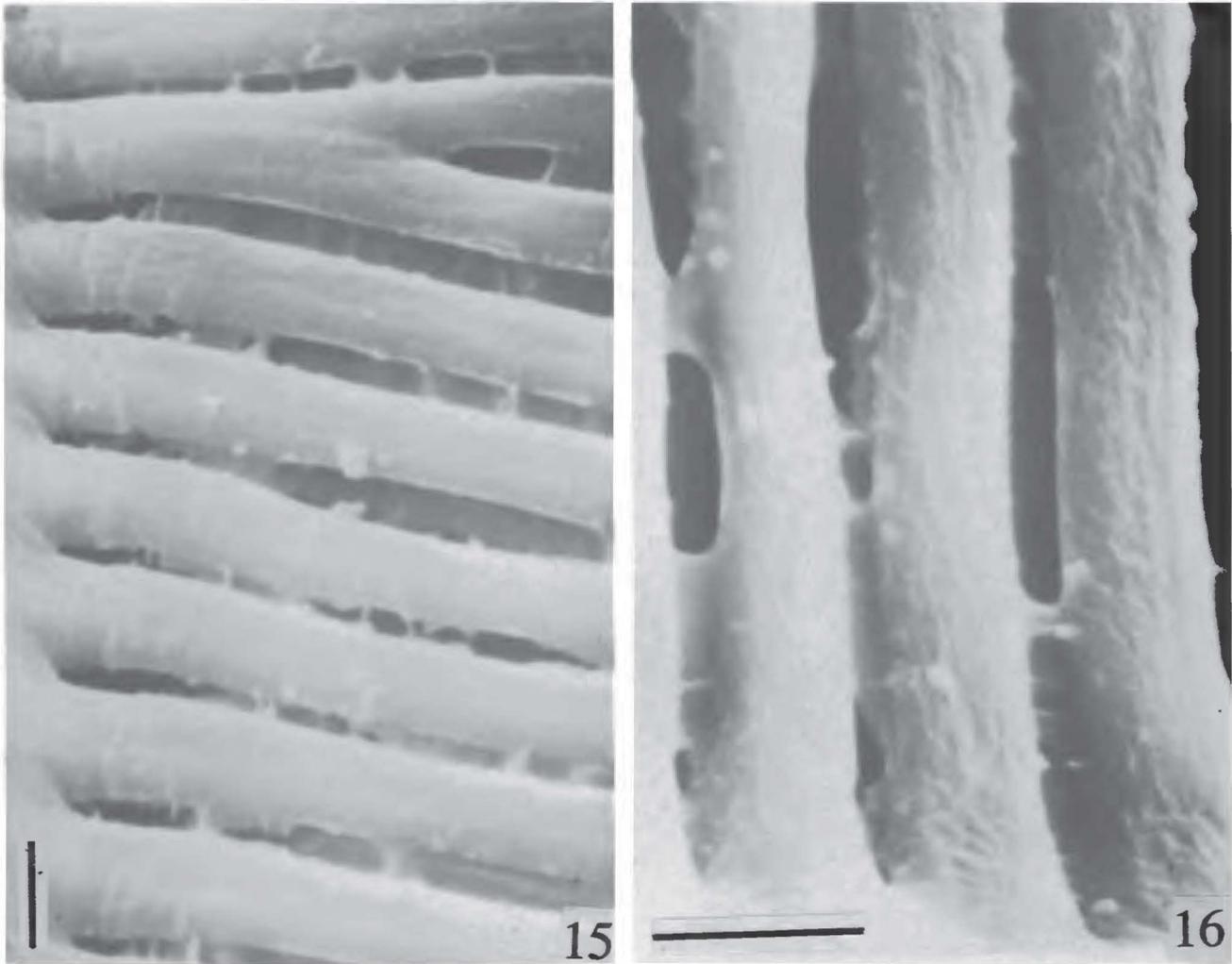


Fig. 15–16. SEM photographs of portions of perforation plates from radial section of earlier-formed secondary xylem of *Schisandra glabra*.—15. Perforation plate portion showing extensive pit membrane remnants containing some oval or elliptical pores.—16. Perforation plate portion with oval to elliptical pores of various sizes in the pit membrane remnants. Scales at lower left in both figures = 5 μ m.

er than on fiber-to-fiber contacts (Fig. 20, 22). Crystalliferous phloem fibers are scarce in *S. glabra*; they occur as isolated cells, not as strands (Fig. 20). In all other species, the fibers are grouped. The groups are cylindrical and composed of several fibers in *K. scandens*, but are in plates in *K. japonica* (plates one cell thick), *S. henryi* (plates one or two cells in thickness: Fig. 17), *S. repanda* (plates two cells thick), *S. rubriflora* (plates one or two cells thick), and *S. sphenanthera* (plates one or two cells thick: Fig. 18).

DISCUSSION AND CONCLUSIONS

Bailey and Nast (1948) contrasted Illiciaceae with Schisandraceae in two respects. They reported that in Schisandraceae rays are both multiseriate and uniseriate at pith margins (uniseriate only in Illiciaceae) and that vessel elements are shorter than in Illiciaceae. The claimed contrast in rays has not been supported by later studies. *Illicium* can have multiseriate rays at pith

margins (Carlquist 1982b). There is overlap between the two families in vessel element length: mean length is 861 μ m in *Illicium parviflorum* Michaux (Carlquist 1982b), whereas mean length is 1074 μ m in *K. scandens*. More significantly, in the earlier-formed secondary xylem of *Schisandra*, there are long vessel elements with highly oblique perforation plates consisting of many bordered bars. These perforation plates bear pit membrane remnants much like those figured for *Illicium* (Carlquist 1992), a feature not previously reported for Schisandraceae. This feature links Schisandraceae closely with Illiciaceae.

There are some points of difference in wood anatomy between the two families that have not been cited previously, however. The majority of perforation plates in Schisandraceae are simple, whereas only scalariform perforation plates have been reported in Illiciaceae. Although there is a small amount of overlap in vessel dimensions between the two families, vessel el-

ements in Illiciaceae as a whole are much longer and narrower than those of Schisandraceae. For example, mean vessel diameter ranges from 91 to 137 μm for species of Schisandraceae, but from 38 to 80 μm in species of Illiciaceae (Carlquist 1982b). Tracheids in *Illicium* have circular pits 5 μm or less in diameter, whereas pits in tracheids of Schisandraceae range from 7 to 9 μm in diameter. Diffuse axial parenchyma cells characterize all species of *Illicium* (Carlquist 1982b), whereas diffuse axial parenchyma is scarce in Schisandraceae and has been reported only from two species of *Kadsura*.

In analyzing the differences between the two families, one finds that they are few in number, and are mainly quantitative differences or differences of degree rather than presence or absence features. Wood anatomy clearly speaks for a close relationship. With few exceptions, the authors cited by Metcalfe (1987) claim on the basis of various lines of evidence that the two families are close. The molecular evidence favoring this concept provided by Qiu et al. (1993) is very persuasive. Noteworthy, however, is the fact that in the cladogram of Qiu et al. (1993) Austrobaileyaceae are basal to Illiciaceae and Schisandraceae, which terminate the illicielean clade.

Given that there are few qualitative differences in wood anatomy between Illiciaceae and Schisandraceae, the quantitative differences should be examined with relation to the marked difference in habit between the two families. *Illicium* consists of shrubs or trees, whereas *Kadsura* and *Schisandra* are all scandent (Smith 1947).

Wide and often relatively short vessel elements characterize vines and lianas (Carlquist 1985, 1991). The vessel dimensions of Schisandraceae fit this pattern. Also, there is little question that Schisandraceae show greater specialization of perforation plates compared to Illiciaceae. The presence of predominantly simple perforation plates in Schisandraceae, newly reported here on the basis of macerations, underlines this difference. Accelerated simplification of perforation plates in lianas and woody vines in families that contain both scandent and nonscandent genera is illustrated by *Tetracera* of the Dilleniaceae (Metcalfe and Chalk 1950) and *Piptocalyx* of the Trimeniaceae (Carlquist 1984a).

The imperforate tracheary elements of Schisandraceae were termed tracheids by Lemesle (1945, 1946), who called them "tracheïdes du type Cycadéen" or "tracheïdes vraies." This is an accurate description, and in a maceration, one probably could not distinguish schisandraceous tracheids from those of cycads. Lemesle (1945, 1946) believed that the tracheids of Schisandraceae mark that family as more primitive than Eupteleaceae, Illiciaceae, Magnoliaceae, etc. However, a functional view of this difference and its

evolutionary significance can be taken. True tracheids and vasicentric tracheids are more common in scandent dicotyledons than in nonscandent ones (Carlquist 1985, 1991). This may provide a greater degree of conductive safety to vines and lianas that have large vessels vulnerable to cavitation. On the other hand, reduction of pit cavity diameter and pit density on walls of imperforate tracheary elements can increase mechanical strength of the cell (see discussion in Carlquist 1975), and thus correlate with evolution into an arboreal habit. If ancestors of Illiciales had tracheid pits like those of Schisandraceae, they would likely be retained during evolution of Schisandraceae, but reduced in size in Illiciaceae. Alternatively, if the tracheids of Illiciaceae were the primitive type in this clade, increase in pit density and diameter could accompany evolution of the scandent habit in Schisandraceae.

Schisandraceae have a very low degree of vessel grouping. This supports the idea that in dicotyledon woods with tracheids, tracheids deter vessel grouping by providing a secondary conductive system that can provide effective translocation in case a large proportion of the vessels experience cavitation (Carlquist 1984b).

Lianas that have great height and tortuous stems tend to have adaptations different from those of Schisandraceae, which are shrubs that climb not by twining but by leaning on stems of shrubs through which they grow. Such features as parenchyma abundance, successive cambia, etc., that characterize lianas are therefore absent in Schisandraceae. However, Schisandraceae do possess one important feature of critical importance where correlation of wood anatomy with scandent habit is concerned. The conductive area (total vessel area per mm^2 of transection) for a selection of woody vines and lianas is 0.359 mm^2 (Carlquist 1975, p. 206). The conductive area for Schisandraceae studied here, averaged, is 0.362 mm^2 , when calculated as in the 1975 selection of vines and lianas (vessel wall thickness included in vessel diameter). The figure for Schisandraceae is thus virtually identical with the 1975 figure for the selection of scandent species. In turn, this figure is much greater than the conductive area figure for any other category of growth form, such as trees, annuals, etc. (Carlquist 1975, p. 206).

Metcalfe (1987) wisely cautioned against premature citation of anatomical features of Schisandraceae as criteria for recognition of species. Only a small portion of the species have been studied in the family. However, the presence of oil cells in secondary phloem and the absence of crystalliferous astrosclereids in bark of two species, *S. glabra* and *S. henryi*, is of potential interest. *Schisandra glabra*, the sole New World species of the family, is placed in the same section (section *Schisandra*) as *S. henryi* (Smith 1947). A larger

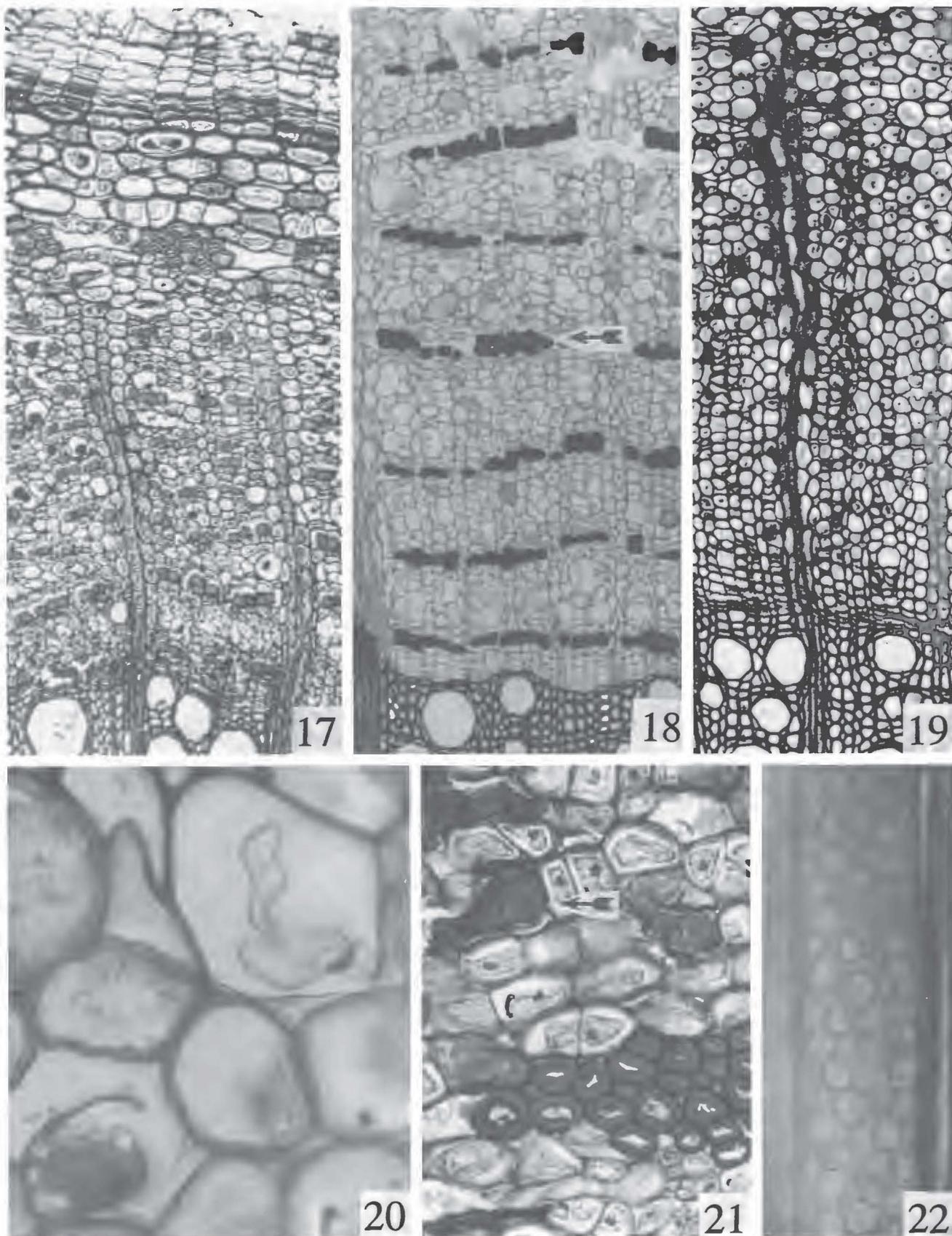


Fig. 17-22. Bark sections of *Schisandra*.—17. *S. henryi* transection, periderm at top, secondary xylem at bottom; arrow indicates a strand of protophloem fibers.—18. *S. sphenanthera* transection with secondary xylem at bottom; bands of dark-staining secondary phloem fibers (arrow) present.—19. *S. glabra* transection, secondary xylem at bottom; phloem fibers absent.—20. *S. glabra* transection portion;

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 single fiber bearing crystals embedded in wall, lower left; oil cell with shrivelled inner wall, upper right.—21. *S. sphenanthera* transection; portions of three astrosclereids, above (arrow points to one of these); protophloem fibers, below.—22. *S. henryi* radial section, showing crystals in face view on surface of secondary phloem fiber. (Fig. 17–19, scale below Fig. 1; Fig. 20, 22, scale below Fig. 3; Fig. 21, scale below Fig. 4).

sampling of Schisandraceae is needed to reveal whether this or any other correlation between anatomy and taxonomy holds within Schisandraceae.

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LITERATURE CITED

- BAAS, P., AND M. GREGORY. 1985. A survey of oil cells in the dicotyledons with comments on their replacement by and joint occurrence with mucilage cells. *Israel J. Bot.* **34**: 167–186.
- BAILEY, I. W., AND C. G. NAST. 1948. Morphology and relationships of *Illicium*, *Schisandra*, and *Kadsura*. *J. Arnold Arbor.* **29**: 77–89.
- CARLQUIST, S. 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley. 259 p.
- . 1982a. The use of ethylene diamine in softening hard plant structures for paraffin sectioning. *Stain Technol.* **57**: 311–317.
- . 1982b. Wood anatomy of *Illicium* (Illiciaceae): phylogenetic, ecological, and functional interpretations. *Amer. J. Bot.* **69**: 1587–1598.
- . 1984a. Wood anatomy of Trimeniaceae. *Pl. Syst. Evol.* **144**: 103–118.
- . 1984b. Vessel grouping in dicotyledon woods: significance and relationship to imperforate tracheary elements. *Aliso* **10**: 505–525.
- . 1985. Observations on functional wood histology of vines and lianas: vessel dimorphism, tracheids, vasicentric tracheids, narrow vessels, and parenchyma. *Aliso* **11**: 139–157.
- . 1991. Anatomy of vine and liana stems: a review and synthesis, pp. 53–71. In F. E. Putz and H. A. Mooney [eds.], *The biology of vines*. Cambridge University Press, Cambridge.
- . 1992. Pit membrane remnants in perforation plates of primitive dicotyledons and their significance. *Amer. J. Bot.* **79**: 660–672.
- GARRATT, G. A. 1933. Bearing of wood anatomy on relationships of the Myristicaceae. *Trop. Woods* **36**: 20–44.
- IAWA COMMITTEE ON NOMENCLATURE. 1964. Multilingual glossary of terms. Verlagsbuchanstalt Konkordia, Winterthur, Switzerland. 186 p.
- LEMESLE, R. 1932. Une particularité structurale chez les diverse espèces de *Kadsura* Juss. *Comp. Rend. Hebd. Séances Acad. Sci.* **194**: 194–196.
- . 1945. Les ponctuations aréolées des fibres des genres *Schisandra* L., *Kadsura* L., *Illicium* L. et leurs rapports avec la phylogénie. *Compt. Rend. Hebd. Séances Acad. Sci.* **221**: 113–115.
- . 1946. Les divers types de fibres à ponctuations aréolées chez les dicotylédones apocarpiques les plus archaïques et leur rôle dans la phylogénie. *Ann. Sci. Nat. Bot. Sér. 11*, **7**: 19–52.
- MCLAUGHLIN, R. P. 1933. Systematic anatomy of the woods of the Magnoliales. *Trop. Woods* **34**: 3–39.
- METCALFE, C. R. 1987. Anatomy of the dicotyledons. Ed. 2, Vol. III. Clarendon Press, Oxford. 224 p.
- , AND L. CHALK. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford. 1500 p.
- QIU, Y.-L., M. W. CHASE, D. H. LES, H. G. HILLE, AND C. R. PARKS. 1993. Molecular phylogenetics of the Magnoliidae; a cladistic analysis of nucleotide sequences of the plastic gene *rbcL*. *Ann. Missouri Bot. Gard.* **80**: 587–606.
- SMITH, A. C. 1947. The families Illiciaceae and Schisandraceae. *Sargentia* **7**: 1–224.