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## WOOD ANATOMY OF SCYTOPETALACEAE

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### ABSTRACT

Eight wood samples representing six species in two genera of Scytopetalaceae are examined with respect to qualitative and quantitative features. *Rhaptopetalum* differs from *Scytopetalum* by having scalariform perforation plates, fiber-tracheids, longer vessel elements, and a series of features probably related to the understory status of *Rhaptopetalum* is compared to the emergent nature of *Scytopetalum*. Features of Scytopetalaceae relevant to relationships of the family include (1) scalariform perforation plates; (2) alternate medium-sized intervacular pits; (3) scalariform vessel-parenchyma pitting; (4) diffuse-in-aggregates and scanty vasicentric axial parenchyma; (5) axial parenchyma strands subdivided in places into chains of chambered crystals; and (6) rays that are high, wide, heterogeneous, and with erect cells comprising uniseriate rays. These features are compared for a number of families alleged by recent phylogenists to be related to Scytopetalaceae. Scytopetalaceae appears best placed in Theales, nearest to such families as Caryocaraceae, Lecythidaceae, Ochnaceae, Quinaceae, and Theaceae, although Rosales (e.g., Cunoniaceae) must be cited also on account of numerous resemblances in wood anatomy.

Key words: ecological wood anatomy, Malvales, *Rhaptopetalum*, Rosales, Scytopetalaceae, *Scytopetalum*, Theales, Tiliales, wood anatomy.

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### INTRODUCTION

Scytopetalaceae are a family of West African wet forest trees or shrubs with five genera (*Brazzeia*, *Oubangia*, *Pierrina*, *Rhaptopetalum*, and *Scytopetalum*) containing about 20 species (Cronquist 1981). Some details of wood anatomy have been reported for *Scytopetalum* (no species given) by Metcalfe and Chalk (1950). The present study is motivated in part by the availability of eight wood collections representing six species in two genera. These collections were made available by the Centre de Technique Forestier Tropical in Nogent-sur-Marne, France (CTFw in Stern 1978) through the kindness of M. Pierre Detienne. Although these specimens represent only about a third of the family, the variation described here probably accounts for most features likely to be discovered in the family. Because wood of the shrubby species is not included, quantitative features reported here may not be representative for the entire family.

Even if the sampling of Scytopetalaceae is less than optimal (but good in view of the difficulties in collecting wood of this family), the features reported here are adequate for consideration of the relationships of the family. In earlier systems the relationships were thought to be with Olacaceae (Oliver 1868) or in Tiliales, (Hutchinson 1973). Takhtajan (1987) places Scytopetalaceae in a theoid order, Ochnales, along with Ochnaceae, Lophiraceae, Sauvagesiaceae, Diegodendraceae, Strasburgeriaceae, and Quiinaceae (Takhtajan's orders are less inclusive than those of other authors, comparable to suborders of many authors). Cronquist (1981),

Dahlgren (1980), and Thorne (1976) assign Scytopetalaceae to Theales. The scheme of Thorne (1976) is noteworthy because he aligns Scytopetalaceae with Ochnaceae and Quiinaceae. This has the merit of bringing together three families known to have an unusual feature, cristarque cells, in the leaves. Although earlier literature suggested that only these three families possessed cristarque cells, they now are known to occur much more widely, and have been reported in Balanopaceae (Carlquist 1980) and Celastraceae (Jansen and Baas 1973), as well as in Bom-bacaceae, Huaceae, Ixonanthaceae, Melastomaceae, and Pandaceae (Baas 1972). Although the systems of Cronquist, Dahlgren, and Thorne differ in the sequences in which Scytopetalaceae precedes or follows particular families, stress should not be laid on these relatively minor differences, because the three treatments agree in general. Although earlier workers placed Scytopetalaceae in Malvales (e.g., Takhtajan 1980), that view is not represented in the most recent systems. Families other than thealean families have similarities to Scytopetalaceae with respect to wood anatomy (e.g., Cunoniaceae of the order Rosales), and are worthy of mention.

The ecology of Scytopetalaceae—wet tropical forest—presents an opportunity for relating wood anatomy to ecology. We have implicitly regarded woods of tropical wet forest dicotyledons as a kind of background to which other kinds of woods were to be compared, almost as though wet tropical woods were devoid of adaptations, whereas woods of dry areas represent modifications. In fact, wood of a tropical wet-forest emergent such as *Scytopetalum* represents a series of specializations to conduction of larger volumes of water or more rapid conduction of water, or both, relative to the high transpiration rates characteristic of trees such as *Scytopetalum*.

Wood anatomy of *Rhaptopetalum* differs from that of *Scytopetalum*. Although this difference can be described in terms of a taxonomic difference, the possibility is examined here that many of the differences in wood anatomy are related to differences in ecology. Aubréville (1959) describes *Rhaptopetalum beguei* Mang. as a shrub of marshy coastal forest regions. Oliver (1868) says that *Rhaptopetalum coriaceum* Oliver reaches 30 feet. However, it is an understory tree by comparison to *Scytopetalum tieghemii* Hutch. & Dalz., which reaches 25 m according to Aubréville (1959), 80 feet according to Irvine (1961). Unfortunately, little or no data are available on ecology of most species in the family.

#### MATERIALS AND METHODS

All of the specimens provided were available as dried stem portions from trees of presumably mature size. The geographical sources of these specimens is as follows: *Rhaptopetalum breteleri* Letouzey (CTFw-25572), Cameroons; *R. roseum* Engler (CTFw-19792), Congo Republic; *R. sessiliflorum* Engler (CTFw-20906), Cameroons; *Scytopetalum klaineum* Pierre (CTFw-5186), Gabon; *S. klaineum* (CTFw-16745); *S. pierreanum* van Tieghem (CTFw-18822), Congo Republic; *S. tieghemii* (CTFw-1010), Ivory Coast; *S. tieghemii* (CTFw-20537), Ivory Coast.

Wood samples were boiled in water, stored in aqueous 50% ethyl alcohol, and sectioned on a sliding microtome. Sections were stained with safranin and lightly counterstained with fast green. Macerations were prepared with Jeffrey's Fluid and stained with safranin. All quantitative data are presented in the form of means derived from 25 measurements, except for vessel wall thickness, imperforate

Table 1. Generic comparison of wood features (figures shown are means).

<i>Rhaptopetalum</i>	<i>Scytopetalum</i>
Most perforation plates scalariform	Perforation plates simple
Vessels narrow (107 $\mu\text{m}$ )	Vessels wider (170 $\mu\text{m}$ )
Vessel elements longer (1168 $\mu\text{m}$ )	Vessel elements shorter (848 $\mu\text{m}$ )
Fiber/vessel element ratio lower: 2.23	Fiber/vessel element ratio 2.86
Multiseriate rays narrower (3.46 cells)	Multiseriate rays wider (5.55 cells)
No. multiseriate rays $\approx$ uniseriates	No. multiseriate rays $>$ uniseriates
Multiseriates taller (2526 $\mu\text{m}$ )	Multiseriates shorter 866 $\mu\text{m}$
Multiseriates: long procumbent cells	Multiseriates: short procumbents
Fiber-tracheids	Libriform fibers
Mesomorphy ratio 6,000–7,000	Mesomorphy ratio 20,000–60,000

Mesomorphy ratio = vessel diameter times vessel element length divided by vessels per  $\text{mm}^2$ .

tracheary element diameter, imperforate tracheary element wall thickness, and pit diameter; for these features, a few typical conditions were selected and averaged. Vessel diameter was measured at widest point, as seen in transection, but the lumen diameter rather than outside measurement was taken. Mean number of vessels per group is derived on the basis that a solitary vessel = 1.0, a pair of vessels in contact = 2.0, etc. For number of vessels per  $\text{mm}^2$ , number of vessels (not number of vessel groups) per unit area was counted. Terminology follows the IAWA Committee on Nomenclature (1964). Herbarium specimens documenting the wood samples are cited below and are located in the Musée National d'Histoire Naturelle, Paris.

#### ANATOMICAL DESCRIPTIONS

At present, one cannot give a meaningful summary of wood features of the family in detail because so few species are known. Some features that can be cited as characteristic are given in the Abstract and in Table 2. The characteristics of the two genera studied are summarized in Table 1.

**RHAPTOPETALUM BRETILERI** (*CTFW-25572*, *Breteler 2754*) (Fig. 1–6).—Growth rings absent (Fig. 1). Mean number of vessels per group, 2.13. Mean vessel diameter, 119  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 19.7. Mean vessel element length, 1007  $\mu\text{m}$ . Mean vessel wall thickness, 3.5  $\mu\text{m}$ . Perforation plates all scalariform; mean number of bars per plate, 9.4. Most bars slender, nonbordered, but a few thick and with borders as shown in Fig. 3. Vessel-vessel lateral wall pitting of alternate pits, oval to circular in outline, and about 7  $\mu\text{m}$  in diameter (aperture 1–2  $\mu\text{m}$  in diameter). Vessel-axial parenchyma and vessel-ray pits scalariform, about 7  $\mu\text{m}$  in vertical dimension, borders slender (1–2  $\mu\text{m}$  wide) with apertures correspondingly wide (Fig. 4). All imperforate tracheary elements fiber-tracheids because borders (about 4  $\mu\text{m}$  in diameter) traversed by narrowly elliptical pit apertures. Mean fiber-tracheid length, 2624  $\mu\text{m}$ . Mean diameter fiber-tracheids at widest point, 24  $\mu\text{m}$ . Mean thickness fiber-tracheid walls, 5.8  $\mu\text{m}$ . Axial parenchyma present as diffuse-in-aggregates; parenchyma around vessels little more than could be accounted for by contact of vessels with diffuse-in-aggregates chains (Fig. 1). Number of cells per parenchyma strand 5–10; a chain of 2–3 chambered crystal-bearing cells may substitute for 1–2 cells of the strand (Fig. 5). Crystals

Table 2. Presence (+) or absence (0) of wood features all of which are present in Scytopetalaceae.

Scytopetalaceae	Ochnaceae	Quiinaceae	Lecythidaceae	Theaceae	Cunoniaceae
Plates scalariform	+	0	+	+	+
Plates simple	+	+	+	0	+
Fiber tracheids and/or libriform fibers	+	+	+	0	+
Scalariform vessel-parenchyma pits	0	0	+	+	+
Diffuse-in-aggregates	+	0	+	+	+
Vasicentric scanty parenchyma	+	0	+	+	+
Chambered crystals	+	0	+	+	+
Multiseriate rays heterogeneous	+	+	+	+	+
Multiseriates wide	+	+	+	+	+
Multiseriates tall	+	+	+	+	+
Cells of uniseriates erect	+	+	+	+	+

rhomboidal, solitary, often encapsulated (Fig. 6). Rays both multiseriate and uniseriate, the uniseriate rays somewhat more common (Fig. 2). Mean height multiseriate rays, 2404  $\mu\text{m}$ . Mean height uniseriate rays, 740  $\mu\text{m}$ . Mean width multiseriate rays at widest point, 6.7 cells. Procumbent cells confined to multiseriate portions of multiseriate rays (Fig. 2). Erect cells present in uniseriate rays, uniseriate wings on multiseriate rays (Fig. 5), and as occasional sheath cells on multiseriate rays. Ray cell wall lignified, about 1.5  $\mu\text{m}$  thick. Most pits among ray cells bordered, borders best revealed in sectional view on radial sections. Brownish amorphous deposits observed in axial and ray parenchyma. Wood nonstoried.

*RHAPTOPETALUM ROSEUM* (CTFw-19792, Congo Collection 1264) (Fig. 7).—Growth rings absent. Paired and solitary vessels about equally abundant; mean number of vessels per group, 1.44. Mean vessel diameter, 103  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 19.3. Mean vessel element length, 1141  $\mu\text{m}$ . Mean vessel wall thickness, 2.2  $\mu\text{m}$ . Perforation plates predominantly scalariform (approximately 20% of plates simple); mean number of bars per plate including simple plates, 6.1; mean number of bars per plate excluding simple plates, 7.8. Most bars thick, bordered. Occasional meshworklike plates observed (Fig. 7). Lateral vessel wall pits alternate, circular to oval, about 7  $\mu\text{m}$  in diameter (pit apertures 1–2  $\mu\text{m}$  in diameter) on vessel-vessel contacts (Fig. 7). Vessel-axial parenchyma and vessel-ray pits scalariform, about 8  $\mu\text{m}$  in vertical dimension, with borders 1–2  $\mu\text{m}$  wide and apertures correspondingly larger than in vessel-vessel pits. Imperforate tracheary elements all fiber-tracheids, the pits with borders about 4  $\mu\text{m}$  in diameter traversed by narrowly elliptical pit apertures. Mean fiber-tracheid length, 2428  $\mu\text{m}$ . Mean fiber-tracheid diameter at widest point, 29  $\mu\text{m}$ . Mean fiber-tracheid wall thickness, 4.7  $\mu\text{m}$ . Axial parenchyma diffuse-in-aggregates, with some tendency toward aggregation of parenchyma around vessels as vasicentric scanty. Fiber-tracheid to ray and fiber-tracheid to axial parenchyma bordered, about 3  $\mu\text{m}$  in diameter. Strands of axial parenchyma about 12–15 cells in length. Crystals absent in axial parenchyma. Both multiseriate and uniseriate rays present, the former more abundant. Mean multiseriate ray height, 2733  $\mu\text{m}$ . Mean uniseriate ray height, 797  $\mu\text{m}$ . Mean width multiseriate rays at widest point, 5.2 cells. Procumbent cells

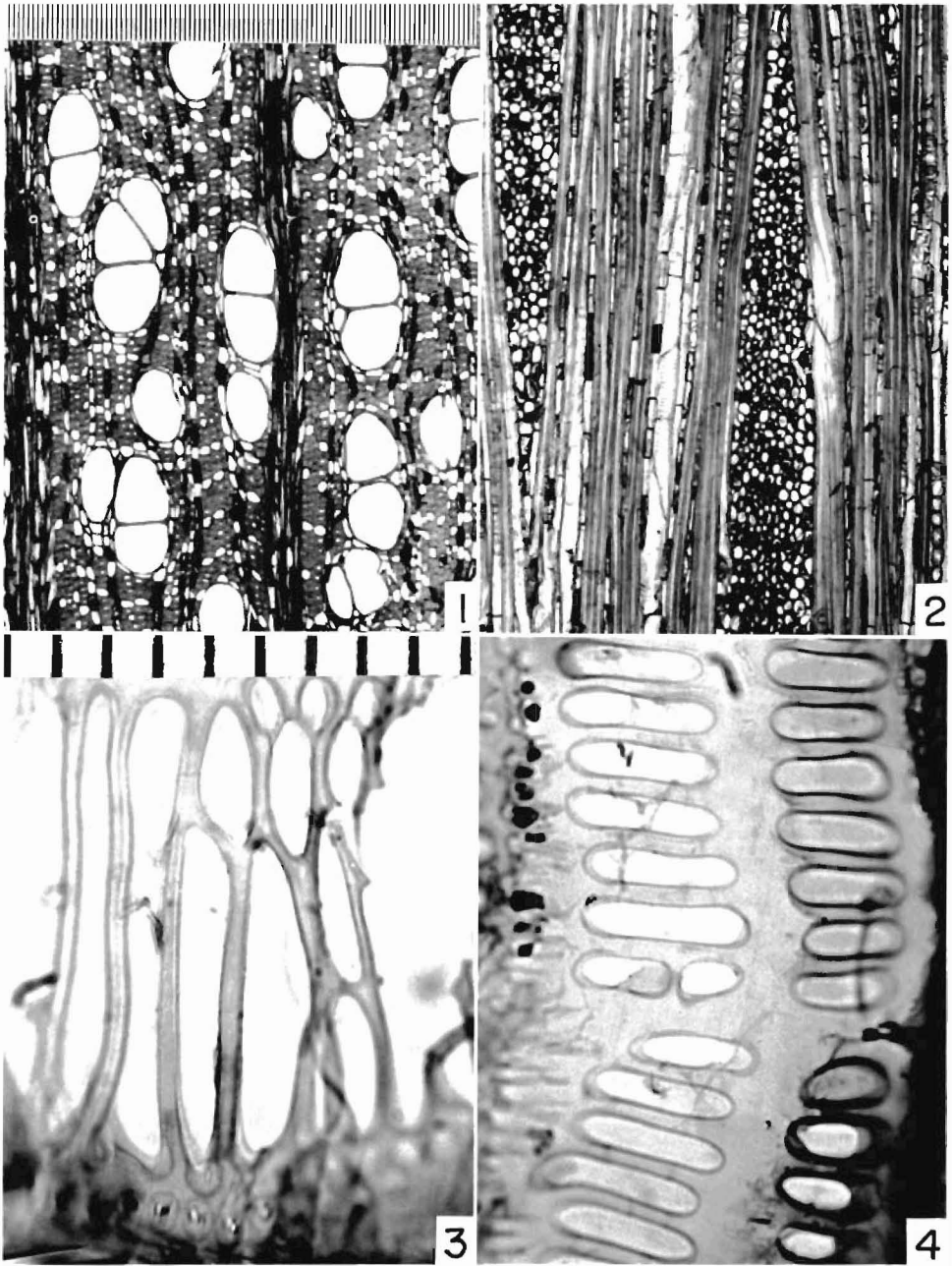


Fig. 1–4. Wood sections of *Rhaptopetalum breteleri* (Breteler 2754).—1. Transection; most vessels are not solitary.—2. Tangential section; multiseriate rays have wide portion composed mostly of procumbent cells.—3. Portion of perforation plate from radial section; bars are bordered.—4. Vessel to axial parenchyma pitting from radial section; borders on pits are very narrow. (Fig. 1, 2, magnification scale above Fig. 1 [divisions = 10  $\mu$ m]; Fig. 3, 4, scale above Fig. 4 [divisions = 10  $\mu$ m].)

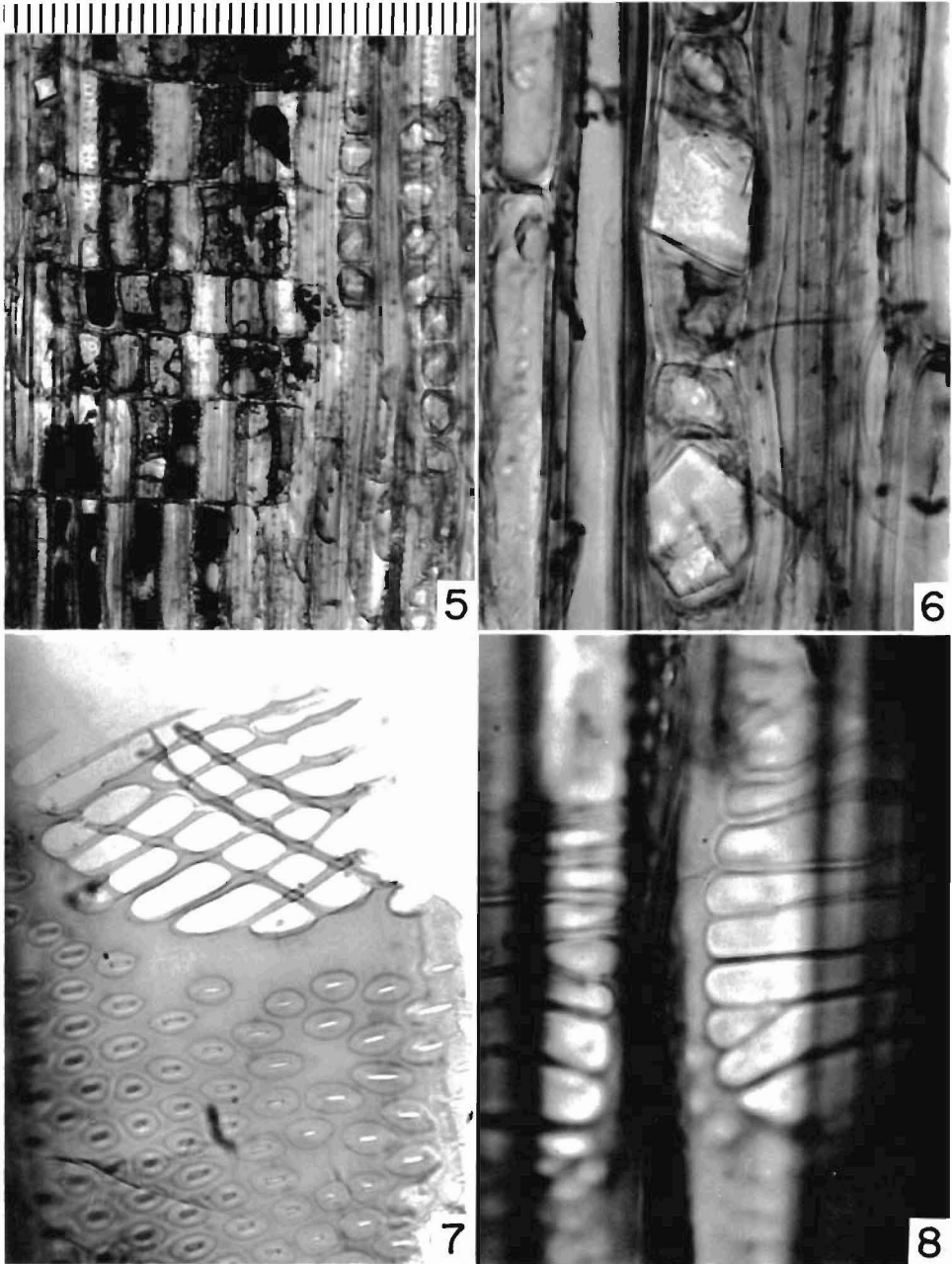


Fig. 5–8. Wood sections of *Rhaptopetalum*.—5–6. *R. breterleri* (*Breteler* 2754).—5. Radial section, showing dark-staining amorphous deposits in erect ray cells (left) and chains of chambered crystals (right).—6. Two encapsulated crystals from axial parenchyma of radial section.—7. *R. roseum* (*CTFw-19792*). Meshworklike perforation plate and lateral wall pitting of vessel from radial section.—8. *R. sessiliflorum* (*Zenker* 2051). Two perforation plates from radial section; bars are relatively thin. (Fig. 5, magnification scale above Fig. 5 [divisions = 10  $\mu\text{m}$ ]; Fig. 6–8, scale above Fig. 3).



confined to multiseriate portions of multiseriate rays. Erect cells present as uniseriate rays and uniseriate wings of multiseriate rays; only a very few erect cells present as sheath cells on multiseriate rays. Ray cell walls about  $1.2\ \mu\text{m}$  thick, pits among ray cells commonly bordered on tangentially oriented walls. Brown amorphous deposits present in axial parenchyma, ray parenchyma, and a few fiber-tracheids. Wood nonstoried.

*RHAPTOPETALUM SESSILIFOLIUM* (CTFw-20906, *Letouzey 12715*) (Fig. 8).—Growth rings absent. Solitary and paired vessels about equally frequent; mean number of vessels per group, 2.08. Mean vessel diameter,  $98.7\ \mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 19.3. Mean vessel element length,  $1356\ \mu\text{m}$ . Mean vessel wall thickness,  $2.8\ \mu\text{m}$ . Perforation plates mostly scalariform (12% simple plates observed); mean number of bars per plate if simple plates included, 9.5; mean number of bars per plate if simple plates excluded, 10.1. Some thick and bordered bars present, but slender nonbordered bars more common (Fig. 8). Lateral wall pitting of alternate circular to oval pits about  $9\ \mu\text{m}$  in diameter (apertures  $1\text{--}2\ \mu\text{m}$ ) on vessel-vessel contacts. Vessel-axial pits scalariform, vessel-ray pits scalariform or opposite, pits about  $9\ \mu\text{m}$  in vertical dimension, border  $1\text{--}2\ \mu\text{m}$  wide, apertures correspondingly wider than on vessel-vessel pits. Imperforate tracheary elements all fiber-tracheids; pits with borders about  $4\ \mu\text{m}$  in diameter traversed by narrowly elliptical aperture. Mean fiber-tracheid length,  $2628\ \mu\text{m}$ . Mean fiber-tracheid diameter at widest point,  $28\ \mu\text{m}$ . Mean fiber-tracheid wall thickness,  $6.9\ \mu\text{m}$ . Axial parenchyma primarily diffuse-in-aggregates, with a minimal tendency to form scanty vasicentric aggregations in the vicinity of vessels. Axial parenchyma in strands of about 15 cells; chains of chambered crystal-bearing cells substitute for some of these; crystals rhomboidal, one per cell, mostly encapsulated; chains of chambered crystals 4–8 cells long. Rays both multiseriate and uniseriate, the two types about equally abundant. Mean multiseriate ray height,  $2442\ \mu\text{m}$ . Mean uniseriate ray height,  $749\ \mu\text{m}$ . Mean width of multiseriate rays at widest point, 4.75 cells. Erect cells, plus a few square and moderately long procumbent cells, comprising uniseriate rays, uniseriate portions of multiseriate rays, and the few sheath cells present on multiseriate rays. Procumbent cells comprise the bulk of multiseriate portions of multiseriate rays. Ray cell walls about  $2.5\ \mu\text{m}$  thick. Pits among ray cells circular; some (especially those on tangentially oriented walls) bordered. Tanninlike deposits as well as dark-staining amorphous deposits common in axial and ray parenchyma cells. Wood nonstoried.

*SCYTOPETALUM KLAINIANUM* (CTFw-16745, *Hacq 26*) (Fig. 9–13).—Growth rings absent (Fig. 9). Vessels mostly solitary (Fig. 9); mean number of vessels per group, 1.13. Mean vessel diameter,  $191\ \mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 2.81. Mean vessel element length,  $859\ \mu\text{m}$ . Mean vessel wall thickness ranging from  $2.4\ \mu\text{m}$  (vessel to libriform fiber contacts) to  $5\ \mu\text{m}$  (vessel to vessel contacts). Perforation plates mostly simple, a few scalariform with several bordered bars (Fig. 11). Lateral wall pitting of vessels consisting of alternate pits, circular to polygonal in outline,  $5\text{--}7\ \mu\text{m}$  in diameter (apertures  $1\text{--}2\ \mu\text{m}$  in diameter) on vessel-vessel contacts. Vessel-axial parenchyma and vessel-ray pits scalariform (rarely opposite), the pits about  $9\ \mu\text{m}$  in vertical dimension, borders about  $1\text{--}2\ \mu\text{m}$  wide, the apertures correspondingly wide as compared to those of vessel-vessel pits. Imperforate tracheary elements perhaps best defined as libriform fibers because



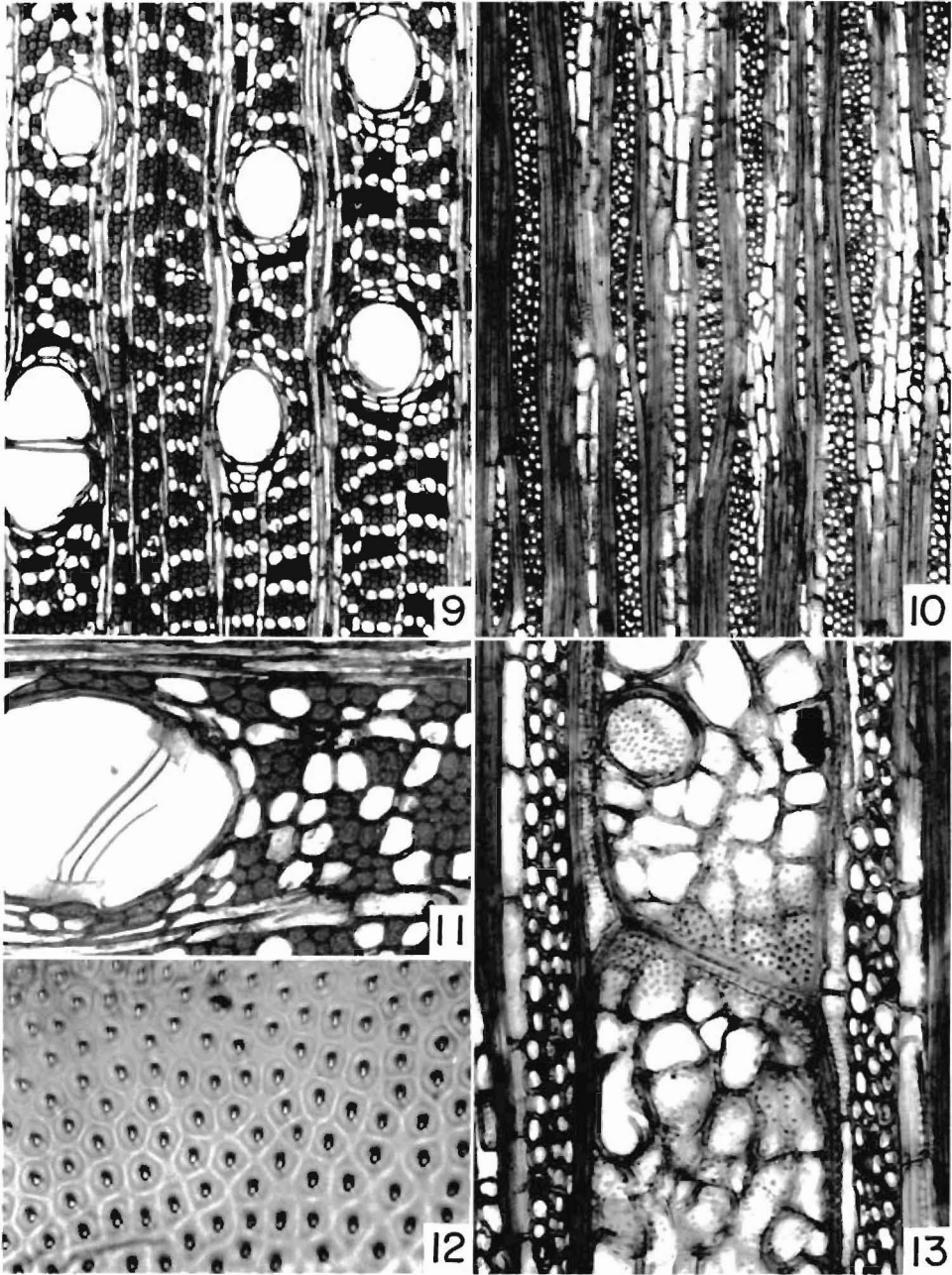


Fig. 9–13. Wood sections of *Scytopetalum klaineianum* (Hacq 26).—9. Transection, showing solitary vessels, diffuse-in-aggregates axial parenchyma.—10. Tangential section; most rays are multiseriate.—11. Portion of scalariform perforation plate from transection.—12. Vessel-vessel pitting from tangential section.—13. Variously sclerosed tyloses from tangential section. (Fig. 9, 10, magnification scale above Fig. 1; Fig. 11, 13, scale above Fig. 5; Fig. 12, scale above Fig. 3.)

pits between them apparently lack borders, but minute borders observed on pits in fiber-ray contacts. Mean libriform fiber length, 2392  $\mu\text{m}$ . Mean libriform fiber diameter at widest point, 24.7  $\mu\text{m}$ . Mean libriform fiber wall thickness, 8  $\mu\text{m}$ , the wall thickness so great that the lumen is virtually occluded in many libriform fibers (Fig. 11). Axial parenchyma present as diffuse-in-aggregates (Fig. 9, 11), but also as vasicentric scanty sheaths 1–2 cells thick around vessels (Fig. 9). Axial parenchyma in strands of about 15 cells; substituting for one of these in a typical strand is a chain of 2–4 chambered crystal-bearing cells. Rays both multiseriate and uniseriate, the former more common (Fig. 10). Mean multiseriate ray height, 983  $\mu\text{m}$ . Mean uniseriate ray height, 306  $\mu\text{m}$ . Mean width of multiseriate rays at widest point, 3.72 cells. Uniseriate rays and uniseriate wings of multiseriate rays composed exclusively of markedly long procumbent cells (Fig. 10, 13); wings on multiseriate rays moderately common but short. Borders observed on some pits among ray cells, especially on tangentially oriented walls. Amorphous deposits observed in axial and ray parenchyma (Fig. 10). Wood nonstoried (Fig. 10). Various sclerosed tyloses present in some vessels (Fig. 13).

*SCYTOPETALUM KLAINEANUM* (CTFw-5186, Normand 194). — One indistinct growth ring observed (narrower vessels in a presumptive band of latewood). Vessels mostly solitary; mean number of vessels per group, 1.23. Mean vessel diameter, 218  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 4.82. Mean vessel element length, 840  $\mu\text{m}$ . Mean vessel wall thickness about 4  $\mu\text{m}$  (thickness varies considerably). Only simple perforation plates observed. Lateral wall pitting of vessels composed of alternate pits, crowded and polygonal in outline, 7–9  $\mu\text{m}$  in diameter (apertures 1–2  $\mu\text{m}$  in diameter) on vessel-vessel contacts. Vessel-axial parenchyma pits scalariform, with reduced (1–2  $\mu\text{m}$  wide) borders and correspondingly wide apertures (compared to vessel-vessel pits). Imperforate tracheary elements with apparently simple pits, therefore libriform fibers. Mean libriform fiber length, 2839  $\mu\text{m}$ . Mean diameter of libriform fibers at widest point, 28  $\mu\text{m}$ . Mean libriform fiber wall thickness, 8  $\mu\text{m}$ , the walls of many cells so thick that lumina are virtually occluded. Axial parenchyma diffuse-in-aggregates plus vasicentric scanty, the latter forming a sheath 1–2 cells thick around vessels. Axial parenchyma in strands of about 14 cells, a chain of chambered crystals typically substituting for one of those per strand; chains of chambered crystals 2–4 (–5) cells in length. Rays nearly all multiseriate, uniseriate rays scarce. Mean height multiseriate rays, 788  $\mu\text{m}$ . Mean width multiseriate rays at widest point, 3.44 cells. Wings of multiseriate rays (plus the few uniseriate rays) composed of cells that are erect, square, or short procumbent. Multiseriate portions of multiseriate rays composed of long procumbent cells, no sheath cells present. Wings on multiseriate rays few or absent. Mean thickness of ray cell walls about 2.5  $\mu\text{m}$ . Pits among ray cells mostly simple, a few bordered ray cells present on tangentially oriented walls. Amorphous deposits present in axial and ray parenchyma as well as in some libriform fibers. Wood nonstoried. Various sclerosed tyloses seen in a few vessels.

*SCYTOPETALUM PIERREANUM* (CTFw-1822, Bertault 203). — Growth rings absent. Vessels commonly solitary or in pairs; mean number of vessels per group, 1.40. Mean vessel diameter, 159  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 5.62. Mean vessel element length, 855  $\mu\text{m}$ . Mean vessel wall thickness 3–5  $\mu\text{m}$ . Perforation plates simple. Lateral wall pitting composed of alternate pits, circular to polygonal

in outline, about 7  $\mu\text{m}$  in diameter (apertures 1–2  $\mu\text{m}$  in diameter) on vessel-vessel interfaces. Vessel-axial parenchyma and vessel-ray pitting scalariform, vertical dimension about 7  $\mu\text{m}$ , borders reduced, 1–2  $\mu\text{m}$  wide, apertures correspondingly wide compared to vessel-vessel pitting. Imperforate tracheary elements all libriform fibers, the pits apparently simple. Mean libriform fiber length 2281  $\mu\text{m}$ . Mean libriform fiber diameter at widest point, 25  $\mu\text{m}$ . Mean libriform fiber wall thickness, 7  $\mu\text{m}$ , the wall thickness nearly occluding lumina of most libriform fibers. Axial parenchyma diffuse-in-aggregates plus vasicentric scanty, the latter forming sheaths 1–2 cells thick around vessels. Axial parenchyma in strands about 13 cells long; typically substituting for one or more of these are chains of chambered crystals; chains of chambered crystals are 4–12 (mostly 4) cells in length; the single rhomboidal crystal in each of these cells is usually encapsulated; chambered crystals are somewhat more abundant in this species than in other species studied. Borders present on some pits of axial parenchyma cells. Rays mostly multiseriate, few uniseriate rays present. Mean height multiseriate rays, 703  $\mu\text{m}$ . Mean width multiseriate rays at widest point, 3.32 cells. Wings of multiseriate rays (and the few uniseriate rays present) composed of erect, square, and short procumbent cells. Uniseriate wings few or absent on multiseriate rays. Multiseriate portions of multiseriate rays composed of long procumbent cells. Ray cell wall thickness, 1.5–2  $\mu\text{m}$ . Pits among ray cells often bordered on tangentially oriented walls, otherwise mostly simple. Amorphous deposits present in axial and ray parenchyma and in some fibers. Wood nonstoried. Tyloses abundant in many vessels, relatively thin walled, lightly sclerosed.

*SCYTOPETALUM TIEGHEMII* (CTFw-100, Bertin 22).—Growth rings absent. Solitary and paired vessels about equally abundant; mean number of vessels per group, 1.37. Mean vessel diameter, 170  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 3.62. Mean vessel element length, 781  $\mu\text{m}$ . Mean vessel wall thickness about 4  $\mu\text{m}$ , but highly variable. Perforation plates simple. Lateral wall pitting of vessels consisting of alternate pits polygonal in outline, about 7  $\mu\text{m}$  in diameter (apertures 1–2  $\mu\text{m}$  in diameter) on vessel-vessel interfaces. Vessel-axial parenchyma and vessel-ray pits scalariform, about 7  $\mu\text{m}$  in vertical dimension, borders reduced (1–2  $\mu\text{m}$  wide), apertures correspondingly wider than on vessel-vessel pits. Imperforate tracheary elements all libriform fibers, pits apparently simple. Mean libriform fiber length, 2490  $\mu\text{m}$ . Mean libriform fiber diameter at widest point, 26.7  $\mu\text{m}$ . Mean libriform fiber wall thickness, 7  $\mu\text{m}$ , the walls so thick the lumina are nearly occluded. Axial parenchyma diffuse-in-aggregates plus vasicentric scanty, the latter forming a sheath 1–2 cells thick around vessels. Axial parenchyma in strands of 15–18 cells; chains of chambered crystals usually 2 cells in length, typically substituting for some of those parenchyma cells. Rays both multiseriate and uniseriate, the former much more abundant. Mean height of multiseriate rays, 1180  $\mu\text{m}$ . Mean height of uniseriate rays, 123  $\mu\text{m}$ . Mean width of multiseriate rays at widest point, 3.29 cells. Uniseriate rays and wings of multiseriate rays composed of erect, square, and short procumbent cells. Multiseriate portions of multiseriate rays composed of long procumbent cells. Pits among ray cells bordered mostly on tangentially oriented walls. Amorphous deposits in many axial and ray parenchyma and in fibers. Wood nonstoried.

*SCYTOPETALUM TIEGHEMII* (CTFw-20537, Detienne 163).—Growth rings absent. Vessels mostly solitary; mean number of vessels per group, 1.20. Mean vessel

diameter, 110  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 4.82. Mean vessel element length, 903  $\mu\text{m}$ . Mean vessel wall thickness, 3.5  $\mu\text{m}$ , but highly variable. Perforation plates mostly simple; a few perforation plates have several bars, these bars thick and bordered. Lateral wall pitting consisting of alternate pits, mostly polygonal in outline, about 6  $\mu\text{m}$  in diameter (apertures 1–2  $\mu\text{m}$  in diameter) on vessel-vessel interfaces. Vessel-axial parenchyma and vessel-ray pits scalariform, vertical dimension about 7  $\mu\text{m}$ , borders reduced (about 1–2  $\mu\text{m}$  wide), apertures correspondingly wider. Imperforate tracheary elements all libriform fibers, pits apparently simple. Mean libriform fiber length, 2105  $\mu\text{m}$ . Mean libriform fiber diameter at widest point, 24.8  $\mu\text{m}$ . Mean libriform fiber wall thickness, 6  $\mu\text{m}$ , the thickness great enough so as nearly to occlude the lumina. Axial parenchyma diffuse-in-aggregates plus vasicentric scanty, the latter forming sheaths 1–3 cells wide. Axial parenchyma forming strands about 16 cells in length; typically substituting for one or more of these cells per strand are chains of chambered crystals 2–6 (mostly 2) cells long; crystals are mostly encapsulated. Rays are both multiseriate and uniseriate, the former more common. Mean height of multiseriate rays, 678  $\mu\text{m}$ . Mean height of uniseriate rays, 262  $\mu\text{m}$ . Mean width of multiseriate rays at widest point, 3.40 cells. Uniseriate rays and uniseriate wings of multiseriate rays composed of erect, square, and short procumbent cells; uniseriate wings moderately common. Multiseriate portion of multiseriate rays composed of long procumbent cells. Ray cell walls about 1.5–2  $\mu\text{m}$  thick. Pits among ray cells mostly simple, but commonly bordered on the tangentially oriented walls. Amorphous deposits and tannins in some axial and ray parenchyma cells. Wood nonstoried.

#### SYSTEMATIC AND ECOLOGICAL COMPARISONS WITHIN THE FAMILY

The differences between *Rhaptopetalum* and *Scytometalum* can in part be ascribed to adaptation to divergent regimes to which the two genera, respectively, are adapted. As noted in the introduction, *Rhaptopetalum* consists of understory shrubs or trees whereas the species of *Scytometalum* are taller, emergent trees. This has several correlates: greater probable transpiration and greater trunk size in *Scytometalum*. Table 1 lists the differences between the two genera; familial characters may be found in Table 2 and in the Abstract.

Some of the character expressions listed for *Rhaptopetalum* traditionally have been considered more primitive: for example, presence of borders on pits of imperforate tracheary elements (thereby fiber-tracheids), presence of scalariform perforation plates, and greater length of vessel elements. However, loss of bars in perforation plates of *Scytometalum* also could be interpreted in physiological terms, related to the probable greater conductive rates or water volumes conducted in *Scytometalum*. Although those interested in physiological plant anatomy have for many years hypothesized that conductive efficiency leads to loss of bars on the perforation plate, Zimmermann (1983) has questioned this; Zimmermann curiously believes that alteration of other features leads to conductive efficiency, but perforation plates are exempt. Evidently Zimmermann wishes to promote this interpretation in order to claim that scalariform perforation plates function in sieving out bubbles formed after frozen water in vessels thaws. However, most species of dicotyledons with scalariform perforation plates occur in areas such as tropical uplands where frost never occurs (e.g., New Caledonia, Malayan highlands). Thus, not only is Zimmermann's hypothesis probably not operative, his

concept that the scalariform perforation plate is exempted from evolutionary pressure should be rejected.

If longer vessel elements were correlated with taller rays, as has been shown (Carlquist and Hoekman 1985), rays should be taller in *Rhaptopetalum* than in *Scytopetalum*, which is true. However, one mechanism advanced for that correlation, namely origin of rays (in an ontogenetic, not phylogenetic sense) by subdivision of fusiform cambial initials into a strand of ray initials (which therefore tends to be as long as a fusiform cambial initial), does not appear to be relevant to the case at hand. While this mechanism undoubtedly does operate in dicotyledons at large (Barghoorn 1941), it probably is not of importance in *Scytopetalum* because uniseriate rays are so scarce, despite the large size of trunks. This would indicate abundant time for that ontogenetic process to have operated. More abundant uniseriate rays ought to be present if this process occurred frequently, unless uniseriate rays are rapidly converted to multiseriate rays ontogenetically. Instead, other ontogenetic changes in ray structure described by Barghoorn (1941) are probably present in Scytopetalaceae. The shorter, narrower rays of *Scytopetalum* (as compared to rays of *Rhaptopetalum*) probably reflect subdivision of initials that produce multiseriate rays by intrusion of fusiform cambial initials. The more markedly elongate procumbent ray cells in multiseriate rays of *Scytopetalum* (when compared to *Rhaptopetalum*) may represent another ontogenetic trend, that of transverse or radial longitudinal subdivision of ray initials. The presence of these two trends in *Scytopetalum* would be correlated with larger trunk size in that genus as compared to *Rhaptopetalum*.

Wider vessel diameter in *Scytopetalum* as compared to *Rhaptopetalum* (with correlative lower vessel density) is interpreted here as an indication of greater conductive efficiency related to the canopy status and consequent high transpiration rates in *Scytopetalum*. The higher Mesomorphy ratio values of *Scytopetalum* (Table 1) are doubtless related to those conductive characteristics. The lower Mesomorphy ratio values of *Rhaptopetalum*, however, should not be interpreted as indicative of an enhanced degree of safety. In order to achieve that, the Mesomorphy ratio would have to be much lower, below 100 (e.g., Carlquist 1981).

Because only a third of the species of Scytopetalaceae are represented here, discussion of wood anatomical features that might represent species criteria would be premature. However, the absence of crystals in some collections of *Rhaptopetalum* might prove to be an example of a species character.

#### RELATIONSHIPS OF SCYTOPETALACEAE

Wood features of selected families are compared in Table 2. This table is constructed on the basis that presence in any genus of a family is indicated by "+" whereas "0" denotes absence of a feature from all genera of a family. Although tables such as Table 2 are often presented in studies with phylogenetic implications, such tables (including the one presented here) can be misleading. The most important fault of such a tabular summary is that comparisons are valid only to the extent that the most pertinent (closely related) families are compared. If the families closest to the one under consideration are not included—a possibility perhaps often realized to various extents—the similarities demonstrated are not reliable indicators of relationship. Because a large number of families are involved



in Theales, only a selection of families can be presented in a table—and one might wish for inclusion of families outside of these orders, if only for the sake of contrast. Ochnaceae and Quinaceae were selected because they and Scytopetalaceae share presence of cristarque cells adjacent to leaf veins (Metcalf and Chalk 1950). The remaining families in Table 2 were selected because they are listed close to Scytopetalaceae in one or more recent systems (Hutchinson 1973; Thorne 1976; Dahlgren 1980; Takhtajan 1980; Cronquist 1981). In addition, I have added Cunoniaceae, because the wood features of at least some species of that family (e.g., *Weinmannia luzonensis* Vid.) are remarkably like those of *Scytopetalum*, and all features of wood of Scytopetalaceae, including the distinctive mode of chambered crystal strand occurrence, have been reported in Cunoniaceae (Metcalf and Chalk 1950).

However, a potential source of error in tabular comparisons of features in families is the bias introduced by large, polymorphic families. In such families, the wider range of character expressions means that there is a tendency for polymorphic families to appear more closely related to the one under consideration than do families that are smaller, more uniform, or both. For example, one could demonstrate numerous similarities in wood anatomy between Euphorbiaceae and Scytopetalaceae because Euphorbiaceae is so polymorphic with respect to wood features.

A further source of potential bias in tabular (as well as nontabular) comparisons is the implication of relationship in features that represent independent adaptations to similar ecological conditions. Lack of relationship can also be inferred inadvisably, as when Takahashi (1985) claims that woods of Illiciaceae and Schisandraceae are basically different and therefore not closely related because the vessels of *Schisandra* have fewer bars per perforation plate, an adaptation to the vining habit. Presence of scalariform versus simple perforation plates is an indicator of conductive characteristics, rather than relationship; presence of scalariform perforation plates can be indicative of a degree of primitiveness in wood, however, and is included in Table 2 for that reason—similarly primitive woods can be an expression of relationship provided one can demonstrate that these primitive features are likely shared because of common descent, as in a single family or a closely related pair of families. The families in Table 1 mostly have solitary vessels, but that feature has not been included because degree of vessel grouping has an ecological explanation in those families in which imperforate tracheary elements are fiber-tracheids or libriform fibers (Carlquist 1984).

In conclusion, Scytopetalaceae appear to be related most closely to thealean families such as Lecythidaceae, Ochnaceae, and Theaceae (other thealean families not cited may be equally close to Scytopetalaceae). Families of other orders appear mostly less closely related to Scytopetalaceae, but the similarity in wood features between Cunoniaceae and Scytopetalaceae is intriguing, and suggests that we would be well advised not to be restrictive when citing features possibly related to such a family as Scytopetalaceae.

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#### LITERATURE CITED

- Aubréville, A. 1959. La flore forestière de la Côte d'Ivoire. ed. 2, vol. 2. Centre Technique Forestier Tropical. Nogent-sur-Marne, France. 341 p.
- Baas, P. 1972. Anatomical contributions to plant taxonomy. II. The affinities of *Hua* Pierre and *Afrostryax* Perkins et Gilg. *Blumea* 20:161-192.
- Barghoorn, E. S. 1941. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. II. Modification of the multiseriate and uniseriate rays. *Amer. J. Bot.* 28:273-282.
- Carlquist, S. 1980. Anatomy and systematics of Balanopaceae. *Allertonia* 2:191-246.
- . 1981. Wood anatomy of Pittosporaceae. *Allertonia* 2:355-392.
- . 1984. Vessel grouping in dicotyledon wood: significance and relationship to imperforate tracheary elements. *Aliso* 10:505-525.
- , and D. A. Hoekman. 1985. Wood anatomy of Staphyleaceae: ecology, statistical correlations, and systematics. *Flora* 177:195-216.
- Cronquist, A. 1981. An integrated system of classification flowering plants. Columbia Univ. Press, New York. 1262 p.
- Dahlgren, R. M. T. 1980. A revised system of classification of the angiosperms. *J. Linn. Soc. Bot.*, 80:91-124.
- Hutchinson, J. 1973. The families of flowering plants arranged according to a new system based on their probable phylogeny. Ed. 3. Clarendon Press, Oxford. 968 p.
- IAWA Committee on Nomenclature. 1964. Multilingual glossary of terms used in wood anatomy. Verlagsanstalt Buchdruckerei Konkordia, Winterthur, Switzerland. 186 p.
- Irvine, F. R. 1961. Woody plants of Ghana. Oxford Univ. Press, London. 868 p.
- Jansen, W. T., and P. Baas. 1973. Comparative leaf anatomy *Kokoona* and *Lophopetalum* (Celastraceae). *Blumea* 21:153-178.
- Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford. 1500 p.
- Oliver, D. 1868. Flora of tropical Africa. Vol. 1. L. Reeve & Co., Ashford, Kent, England. 479 p.
- Stern, W. L. 1978. Index xylariorum. Institutional wood collections of the world. 2. *Taxon* 27:233-269.
- Takahashi, A. 1985. Wood anatomical studies of Polycarpiceae. I. Magnoliales. *Sci. Rep. Osaka Univ.* 34:29-83.
- Takhtajan, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev.* 46: 225-359.
- . 1987. *Systema magnoliophytorum*. Officina Editoria "NAUKA," Leningrad. 439 p.
- Thorne, R. F. 1976. A phylogenetic system of the dicotyledons. *Evol. Biol.* 9:35-106.
- Zimmermann, M. H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin. 143 p.