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WOOD ANATOMY OF SABIACEAE (S. L.); ECOLOGICAL AND
SYSTEMATIC IMPLICATIONS

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ABSTRACT

Quantitative and qualitative data were offered for 30 taxa of *Meliosma* and one species each of *Ophiocaryon* and *Sabia*; qualitative data were available for additional species of *Meliosma* and *Sabia*. For a small family restricted to mesic sites, Sabiaceae had a wide range of wood anatomical expressions (e.g., long scalariform to simple perforation plates; heterocellular to homocellular multiseriate rays; tracheids, fiber-tracheids, or libriform fibers as imperforate tracheary elements; presence or absence of silica bodies and calcium oxalate crystals in rays). Growth ring type, vessel diameter, vessel density, and vessel element length were sensitively related to ecology, but to degree of winter cold rather than to aridity. *Ophiocaryon* differed somewhat from all or most species of *Meliosma* in quantitative features, but the genera agreed in qualitative features. Some authors segregate these arborescent or arboreal genera in Meliosmaceae because of distinctive features of *Sabia*, a liana genus; wood of lianas differs in anatomy from that of trees, and these features account for the wood differences between *Sabia* and *Meliosma*. All wood features of Sabiaceae are widespread in the genera of Rutales (Sapindales), even scalariform perforation plates. Sabiaceae are therefore best placed in Rutales, although wood of Sabiaceae is modally more primitive than that of other Rutales. Characters restricted to particular species were cited, but designation of them as diagnostic criteria was not advocated because the sampling of the family was rather incomplete.

Key words: ecological wood anatomy, Meliosmaceae, Rutales, Sabiaceae, Sapindales.

INTRODUCTION

Sabiaceae consist of three genera: *Sabia* Colebr. (53 species, east and southern Asia: Chen 1943); *Meliosma* Blume (25 species, east and southern Asia, Central and South America: Beusekom 1971); and *Ophiocaryon* R. Schomb. (7 species including *Phoxanthus* Benth., northern South America: Barneby 1972). All species are woody, but *Meliosma* and *Ophiocaryon* are trees, whereas *Sabia* is lianoid. Wood samples have not been frequently collected: *Sabia* is especially poorly

known with respect to wood. This has delayed production of a monograph on the wood anatomy of the family. Another reason is microtechnical: woods of *Meliosma* and *Ophiocaryon* are very soft, so that sections made by means of a sliding microtome are often not satisfactory.

Wood anatomy of Sabiaceae is of interest because of the data it can provide with respect to several systematic questions. The majority of authors have claimed rutalean (= sapindalean) relationship for the family, but relationships to Berberidales (e.g., Lardizabalaceae, Menispermaceae), Theales (Icacinaceae), or Magnoliales (Schisandraceae) have also been claimed to include Sabiaceae (see Chen 1943). The similarity in lianoid habitat between Sabiaceae and the families Lardizabalaceae, Menispermaceae, and Schisandraceae may have been persuasive to some workers. Data from wood anatomy are pertinent, but in this case the interpretative problem is that wood of Sabiaceae contains features modally more primitive than those of probably related plants. Although features relating to evolutionary level are not relevant, other characters prove to be informative.

Another question to which wood data can be applied relates to the question of whether one family or two should be recognized. Airy Shaw (1966) segregated *Meliosma* and *Ophiocaryon* as Meliosmaceae. Where wood data are concerned, the question is complicated by the fact that *Sabia* is lianoid, whereas *Meliosma* and *Ophiocaryon* are trees: these growth forms have modally different wood features in dicotyledons at large. One can, however, subtract these features and see whether residual wood features point toward two phylads or one.

Wood anatomy of *Meliosma* proves to be unusually diverse for a medium sized genus restricted to mesic habitats. We will compare this wood diversity to differences with these mesic habitats. Winter cold proves to be the likely cause of many differences in wood anatomy with respect to growth rings, vessel diameter, vessel density, and vessel element length.

One would like to apply wood data to infrageneric taxonomy of *Meliosma*, and to a certain extent, this can be done despite the incomplete sampling of the genus. The monograph of Beusekom (1971) is conservative, with many hitherto recognized species reduced to subspecies or to synonymy. Our wood data shows that some of the species that Beusekom reduces do, however, have distinctive wood features.

MATERIALS AND METHODS

Publication of preliminary results (Carlquist and Morrell 1992) came to the attention of Steven Manchester. He had prepared an account of wood anatomy of *Meliosma* and *Ophiocaryon* as an undergraduate, and kindly placed his results and wood-section slides at the disposal of Carlquist and Morrell. Manchester's slides proved particularly valuable: his sliding microtome sections are thicker than typical for that method, a successful way of countering the crushing of cells in these soft woods during sliding microtome sectioning. The value of thick sections is that larger portions of scalariform and multiperforate perforation plates (as well as other structures) are intact. Macerations were not available for most Manchester slides, so quantitative data in Table 1 are based mostly on sections and macerations prepared by Morrell.

Morrell prepared sections using a method in which woods are softened in ethylenediamine, embedded in paraffin, and sectioned on a rotary microtome

(Carlquist 1982). This method provided excellent results. Sections were stained with a safranin-fast green combination to help resolve presence of pit borders in imperforate tracheary elements. Macerations were prepared with Jeffrey's Solution and stained with safranin. Vessel diameter in Table 1 is lumen diameter. Vessel wall and imperforate tracheary element wall thickness are estimated from a typical condition in each taxon, because more numerous measurements cannot increase the reliability of those particular figures. Other means are based on 25 measurements or as many as could reliably be obtained, and are the work of Morrell. Terminology for wood features follows the recommendations of the IAWA Committee on Nomenclature (1964). SEM photographs were prepared from sections that had already been made into permanent slides. Cover slips were soaked off with xylene, all resin was then removed with xylene changes, and the dried sections were observed with an ISI scanning electron microscope.

Wood sections were mostly obtained from blocks from the SJRW and MADW collections provided by the Forest Products Laboratory, courtesy of Regis B. Miller and Donna Christensen. The Building Advisory Service, Princes Risborough, England (PRFW) and the Kyoto Forestry Institute, University of Kyoto (KYOW) contributed other samples (see Table 1). *Meliosma dilleniifolia* (both subspecies) and *M. veitchiorum* have been cultivated at the Royal Botanic Gardens, Kew. From these trees, figured photographically in the monograph by Beusekom (1971), the first author was furnished with fresh samples sent by air; these were preserved in dilute ethyl alcohol upon arrival in Claremont, and thereby presence of nuclei and starch in septate fibers could be demonstrated. Collections of *M. myriantha* and *S. japonica* were made during travel by Carlquist in 1982, thanks to a grant from Japan Society for Promotion of Science. Two collections per species were available in only a few instances; in these cases, there was little difference between the collections, and the one that provided better slides was selected.

Locations where the specimens studied were collected are given in the Ecological Conclusions section below. In addition, locality data from xylarium records, unfortunately minimal in some instances, is given below (collection numbers given in Table 1):

Meliosma alba (Potrero Redondo, Villa Santiago, Nuevo Leon, Mexico); *M. allenii* (Darien, Panama); *M. arnottiana* (India); *M. cuneifolia* (China); *M. dentata* (Mexico); *M. dilleniifolia* subsp. *dilleniifolia* (cult. Kew); *M. dilleniifolia* subsp. *flexuosa* (cult. Kew); *M. ellipticifolia* (El Cairo, between Darien and Mediacanoa, Depto. del Valle, Colombia); *M. fisheriana* (China); *M. glabrata* (Prov. Alajuela, Costa Rica); *M. glossophylla* (Cordillera Occidental, 2160 m, Depto. del Valle, Colombia); *M. hachijoensis* (Japan); *M. herbertii* (Puerto Rico); *M. kirkii* (China); *M. lanceolata* (Sumatra); *M. macrophylla* (Philippines); *M. myriantha* (cult. Nikko Botanic Garden); *M. nitida* (W. Java); *M. occidentalis* (El Retiro, Cordillera Occidental 260 m, Depto. del Valle, Colombia); *M. oldhamii* (Iriomote I., Ryukyu Is., Japan); *M. parviflora* (China); *M. pittieriana* (Venezuela); *M. rhoifolia* (Taiwan); *M. rigida* (Kyushu, Japan); *M. simplicifolia* (Burma); *M. squamulata* (Ryukyu Is., Japan); *M. sumatrana* (Sumatra); *M. tenuis* (Ashiu Forest, Japan); *M. veitchiorum* (cult. Kew); *M. wallichii* (India); *Ophiocaryon paradoxum* (Guayana); *Sabia japonica* (cult. Tokyo University Botanic Garden).

The monograph of Beusekom (1971) for *Meliosma* exclusive of sect. *Lorenzanea* is very valuable for bringing together all literature, including that on fossil species;

Table 1. Wood features of Sabiaceae.

Species	Collection	1 VG	2 VD	3 VM	4 VL	5 VW	6 BP	7 TD	8 TL	9 TW	10 MH	11 MW	12 UH	13 RH	14 ME
<i>Meliosma alba</i> (Schlecht.) Walp.	SJRw-37935	2.67	92	29.0	868	2.3	0	30	1762	3.0	491	47	121	usP	2754
<i>M. allenii</i> Standl. & L. Williams	SJRw-51639	2.26	120	25.2	1106	4.6	4.6	37	1407	6.9	1486	204	—	usP	5267
<i>M. arnotiana</i> (Wight) Walp.	PRFw-6165	1.96	181	5.4	875	4.6	3.3	41	1524	2.3	3276	151	524	USP	29,329
<i>M. cuneifolia</i> Franch.	PRFw-14717	2.59	63	32.6	684	4.6	12.0	18	964	2.3	1811	74	447	USP	1322
<i>M. dentata</i> Urban	SJRw-55354	2.25	78	32.6	673	4.0	9.5	27	985	2.7	1380	104	731	usP	1610
<i>M. dillenifolia</i> (Wall.) Walp. ssp. <i>dillenifolia</i>	K 73.16360	3.18	106	57.6	622	2.3	9.9	24	902	2.3	2392	185	458	usP	1145
<i>M. d. ssp. flexuosa</i> (Pamp.) Beus.	K 308.67.30803	3.52	77	66.1	605	2.3	10.4	29	621	2.3	1709	114	269	USP	705
<i>M. ellipticifolia</i> Cuatrecasas	SJRw-42685	1.87	86	53.3	899	3.5	11.1	34	1246	5.1	1445	70	302	uSp	1451
<i>M. fischeriana</i> Rehd. & Wils.	SJRw-21735	2.07	75	11.3	854	2.3	13.0	27	1226	3.4	1015	78	499	usP	5668
<i>M. glabrata</i> (Liebm.) Urb.	SJRw-35418	2.08	106	15.5	905	2.3	14.5	28	1307	3.0	1612	74	—	Usp	6189
<i>M. glossophylla</i> Cuatrecasas	SJRw-43275	2.23	52	35.5	994	3.1	17.0	44	1652	5.1	1375	70	615	uSp	1456
<i>M. hachijoensis</i> Nakai	KYOW-8507	7.00	154	12.8	770	2.2	3.6	33	1240	5.2	1521	137	355	usP	9264
<i>M. herbortii</i> Rolfe	PRFw-22557	1.88	131	12.1	1267	2.3	12.6	30	1783	2.3	1267	109	—	usP	13,717
<i>M. kirkii</i> Hemsl.	KYOW-6432	1.21	115	13.8	1023	6.6	13.3	20	1512	3.5	4430	114	—	usP	8525
<i>M. lanceolata</i> Blume	PRFw-4392	1.92	162	7.2	1018	3.4	6.8	30	1561	2.3	1558	68	547	usP	22,905
<i>M. macrophylla</i> Merr.	SJRw-5740	1.38	76	39.4	989	4.8	12.7	23	1110	2.3	1054	70	316	USP	1908
<i>M. myriantha</i> Sieb. & Zucc.	Carluist 15722	1.69	83	52.3	655	3.8	4.4	21	1279	3.8	1687	73	459	uSp	1039
<i>M. nitida</i> Blume	MADw-30615	2.15	148	11.2	1102	3.4	12.2	32	1412	2.3	1404	77	802	USP	14,562
<i>M. occidentalis</i> Cuatrecasas	MADw-42851	1.60	99	14.9	923	3.5	M	44	953	3.5	1298	54	886	uSp	6133
<i>M. oldhamii</i> Maxim.	USw-14176	4.10	90	6.2	1113	4.6	5.2	49	1545	5.2	955	59	640	sP	16,156

Table 1. Continued.

Species	Collection	1 VG	2 VD	3 VM	4 VL	5 VW	6 BP	7 TD	8 TL	9 TW	10 MH	11 MW	12 UH	13 RH	14 ME
<i>M. parviflora</i> Lecomte	PRFw-14716	1.37	100	13.4	663	2.8	3.2	37	1290	4.5	1314	89	253	uSP	4948
<i>M. pittieriana</i> Steyermark	PRFw-22687	2.03	111	13.3	1135	4.8	7.9	42	1670	4.9	1328	68	620	sP	9472
<i>M. rhoifolia</i> Maxim.	SJRw-6424	4.50	113	11.2	1034	2.3	2.5	44	1415	2.5	1115	61	369	sP	10,432
<i>M. rigida</i> Sieb. & Zucc.	PRFw-14119	1.34	128	31.0	1111	3.7	12.8	30	1333	2.3	2130	101	556	uSP	4587
<i>M. simplicifolia</i> (Roxb.) Walp.	SJRw-12564	1.67	171	15.3	835	2.3	6.3	30	1256	2.3	1826	78	495	sP	9332
<i>M. squamulata</i> Hance	KYOw-919	2.00	86	6.6	785	2.3	13.9	23	1711	2.3	2512	135	887	uSP	10,229
<i>M. sumatrana</i> (Jack) Walp.	PRFw-14117	1.40	131	8.0	1167	4.6	13.8	41	958	2.3	1444	125	683	uSP	19,110
<i>M. tenuis</i> Maxim.	KYOw-9519	2.10	74	30.8	768	2.3	7.7	30	1256	2.3	1826	78	495	sP	1839
<i>M. veitchiorum</i> Hemsl.	K 000.13.52813	3.51	66	59.2	430	2.3	<1	37	1711	2.3	2512	135	887	Usp	479
<i>M. wallichii</i> Planch.	SJRw-46612	2.86	113	15.1	933	2.3	7.3	62	958	2.3	1444	125	683	uSP	6982
<i>Meliosma</i> , generic means		2.43	106	23.5	855	3.3	8.8	32	1318	3.2	1661	100			6236
<i>Ophiocaryon paradoxum</i> R. Schomb.	SJRw-43891	2.00	153	4.8	1267	2.3	M	36	1751	3.5	1508	102	645	uSp	40,386
<i>Sabia japonica</i> Maxim.	Carlquist 15975	1.00	99	57.4	642	2.3	0	23	1013	2.8	>5000	185	255	sP	1107

Legend for columns: 1 (VG), mean number of vessels per group; 2 (VD), mean diameter of vessel lumen, μm ; 3 (VM), mean number of vessels per mm^2 ; 4 (VL), mean length of vessel elements, μm ; 5 (VW), mean thickness of vessel walls, μm ; 6 (BP), mean number of bars per perforation plate (M = multiperforate plates only); 7 (TD), mean diameter of imperforate tracheary elements at widest point, μm ; 8 (TL), mean length of imperforate tracheary elements, μm ; 9 (TW), mean wall thickness of imperforate tracheary elements, μm ; 10 (MH), mean height of multiseriate rays, μm ; 11 (MW), mean width of multiseriate rays, μm ; 12 (UH), mean height of uniseriate rays, μm ; 13 (RH), ray histology (u = upright, s = square, p = procumbent; upper case indicates predominant cell type or types); 14 (ME), Mesomorphy index (vessel diameter times vessel element length divided by vessels per mm^2). Localities for specimens given in Materials and Methods.

for demonstrating the value of endocarp morphology to the classification of species; and for offering hypotheses that subsequent studies can test. Nevertheless, the species nomenclature of Beusekom (1971) has not been followed here. The reasons are: (1) evidence from wood anatomy indicates that a number of the species reduced to synonymy by Beusekom may be worthy of recognition (e.g., *M. hachijoensis*); (2) several important recent floras have not used Beusekom's nomenclature, so that earlier names are, in fact, more current; (3) Beusekom did not monograph most of the New World species (sect. *Lorenzanea*), so that his conservative concepts for Old World species, if used here, would coexist with more liberal concepts with New World species; and (4) Beusekom's phyletic concepts are notably paraphyletic (e.g., he believes that *M. sarawakensis* Ridley is derived from *M. pinnata* subsp. *ridleyi* (King) Beusekom).

For the taxa employed in the present study, the names at left, supplied with specimens, would correspond to the Beusekom (1971) nomenclature at right:

M. arnottiana (Wight) Walp. = *M. pinnata* (Roxb.) Walp. subsp. *arnottiana* (Walp.) Beus.

M. cuneifolia Franch. = *M. dilleniifolia* subsp. *cuneifolia* (Franch.) Beus.

M. fischeriana Rehd. & Wils. = *M. simplicifolia* subsp. *yunnanensis* (Franch.) Beus.

M. hachijoensis Nakai = *M. pinnata* subsp. *arnottiana*

M. kirkii Hemsl. & Wils. = *M. pinnata* subsp. *arnottiana*

M. macrophylla Merr. = *M. pinnata* subsp. *macrophylla* (Merr.) Beus.

M. nitida Blume = *M. sumatrana* (Jack) Walp.

M. oldhamii Maxim. = *M. pinnata* subsp. *arnottiana* var. *oldhamii* (Maxim.) Beus.

M. rhoifolia Maxim. = *M. pinnata* subsp. *arnottiana*

M. rigida Sieb. & Zucc. = *M. simplicifolia* (Roxb.) Walp. subsp. *rigida* (Sieb. & Zucc.) Beus.

M. squamulata Hance = *M. lepidota* Blume subsp. *squamulata* (Hance) Beus.

M. tenuis Maxim. = *M. dilleniifolia* subsp. *tenuis* (Maxim.) Beus.

M. wallichii Planch. = *M. pinnata* subsp. *arnottiana*.

The taxa of *Meliosma* in the present study would fall under the infrageneric groupings recognized by Beusekom (1971) as follows:

Subgenus *Meliosma*

Section *Lorenzanea*: *M. allenii*, *M. dentata*, *M. ellipticifolia*, *M. glabrata*, *M. glossophylla*, *M. panamaensis*, *M. pittieriana*.

Section *Meliosma*

Subsection *Simplices*: *M. cuneifolia*, *M. dilleniifolia*, *M. fischeriana*, *M. myriantha*, *M. nitida*, *M. parviflora*, *M. rigida*, *M. simplicifolia*, *M. squamulata*, *M. tenuis*.

Subsection *Pinnatae*: *M. arnottiana*, *M. hachijoensis*, *M. kirkii*, *M. macrophylla*, *M. pinnata*, *M. rhoifolia*, *M. sumatrana*, *M. wallichii*.

Subgenus *Kingsboroughia*

Section *Kingsboroughia*: *M. alba*, *M. veitchiorum*.

ANATOMICAL RESULTS

Growth Rings

Growth ring types in Sabiaceae can be cited according to the scheme offered earlier (Carlquist 1988). The distribution of these is as follows:

Growth rings absent (at least in the material examined): *M. dentata*, *M. ellipticifolia*, *M. nitida*.

Growth rings Type 1B (vessels narrower in latewood, but not markedly): *M. arnottiana*, *M. sumatrana* (Fig. 1).

Growth rings Type 1C (vessels a little wider and a little more numerous in earlywood than in latewood): *M. herbertii*.

Growth rings Type 1D (vessels slightly wider in earlywood, imperforate tracheary elements slightly wider in earlywood): *M. simplicifolia* (Fig. 2).

Growth rings Type 1E (vessels somewhat wider in earlywood, imperforate tracheary elements slightly thicker walled in earlywood): *M. fischeriana*, *M. glossophylla*, *M. lanceolata*, *M. macrophylla*, *M. oldhamii*, *M. pittieriana*, *M. rigida* (Fig. 3), *M. squamulata*, and *M. wallichii*.

Growth rings Type 3 (vessels at least twice as wide in earlywood as in latewood; in *Meliosma*, tracheary elements thinner walled in earlywood): *M. cuneifolia* (Fig. 5), *M. dilleniifolia* subsp. *flexuosa* (Fig. 6), *M. hachijoensis* (Fig. 4), *M. rhoifolia*, *M. tenuis*, *Sabia japonica* (Fig. 49).

Growth rings type 9 (vessels moderately wider in earlywood, earlywood vessels all with simple perforation plates, latewood vessels with scalariform perforation plates): *M. veitchiorum* (Fig. 7, 8).

Growth rings Type 11 (vessels wider in earlywood, but parenchyma bands also present in earlywood, latewood, or both): *M. alba*, *M. myriantha*, *M. kirkii*, *M. parviflora* (Fig. 35), *Ophiocaryon paradoxum* (Fig. 45).

Growth rings Type 12 (parenchyma bands indicate juncture between earlywood and latewood, but vessels not clearly wider in earlywood): *M. allenii*, *M. glabrata*. Heimsch (1942) indicates that *Meliosma* has diffuse porous woods. Although this proves not to be true when a wider sampling is undertaken, his statement is valid to the extent that growth rings in *Meliosma* are not as sharply defined as they are in, say, temperate species of *Quercus*.

The stereotyped image one may have of ring porous or semi-ring porous growth rings assumes a gradual decrease in diameter of vessels from earlywood to latewood. In the Sabiaceae with appreciable vessel diameter difference between earlywood and latewood (e.g., Type 3, Type 11), only a few latewood vessels are narrower and only a few earlywood vessels are wider than the prevailing median size during most of the growth ring. This characteristic suggests that seasonality is moderate in the habitats of most Sabiaceae. Species of *Meliosma* do not occur in temperate climates with markedly cold winters of a continental sort or with markedly dry summers. An indication that *Meliosma* is unable to penetrate into areas with such extremes is the absence of the genus in the New World north of southernmost Mexico.

Vessel Grouping

In *Meliosma*, vessel grouping ranges from 1.21 to 7.00 vessels per group (Table 1, column 1). Low degrees of vessel grouping are illustrated here for *M. sumatrana*

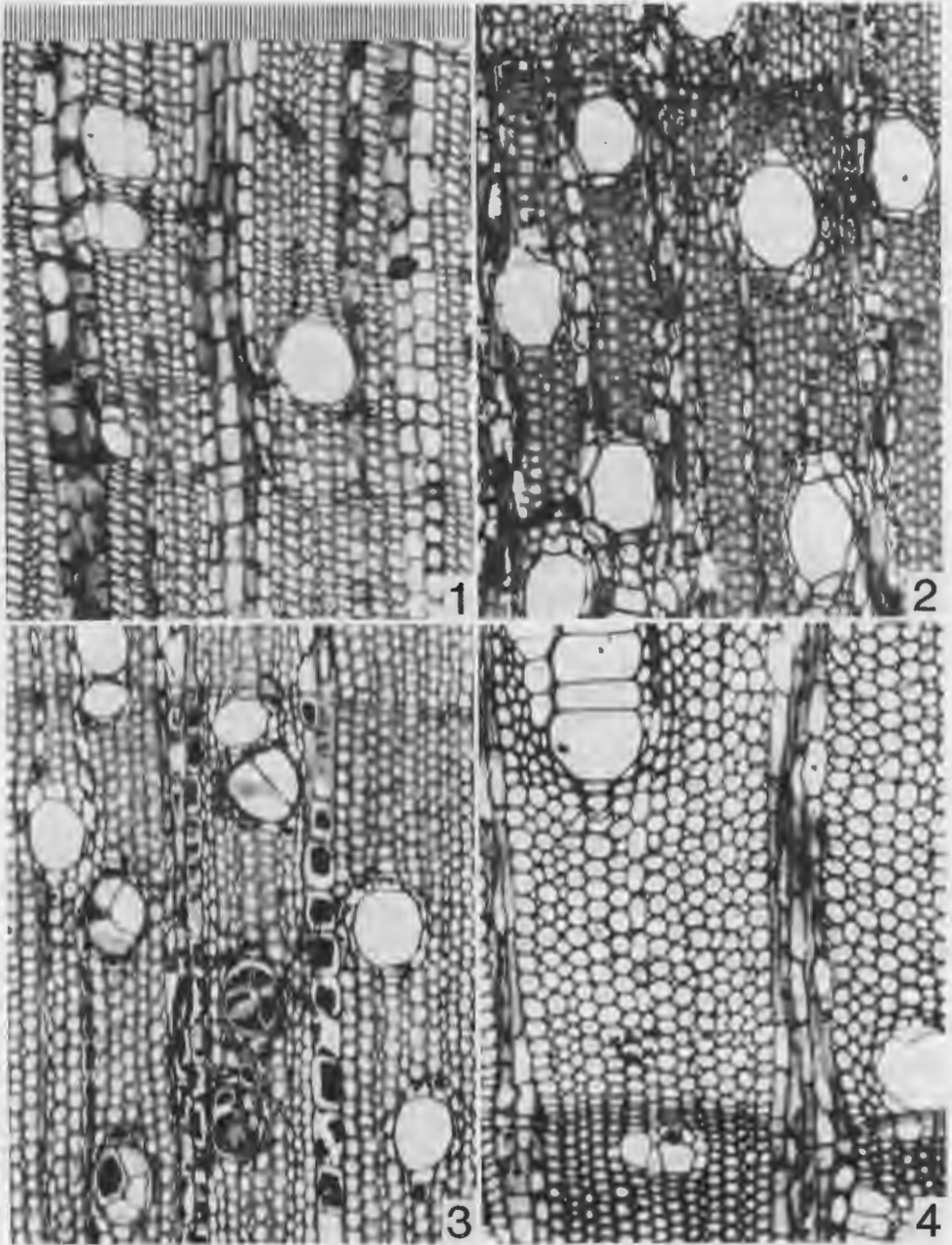


Fig. 1-4. Wood transections of species of *Meliosma*.—1. *M. sumatrana*; slight radial narrowing in fiber diameter one-quarter way from bottom of photograph denotes the minimal growth ring activity.—2. *M. simplicifolia*; vasicentric parenchyma can be seen around vessels.—3. *M. rigida*; tyloses can be seen within some vessels.—4. *M. hachijoensis*; narrow vessels and thicker-walled fibers of latewood near bottom of photograph contrast clearly with earlywood in the remainder of the photograph. Collections indicated in Table 1. (Fig. 1-4, scale above Fig. 1 [divisions = 10 μ m].)

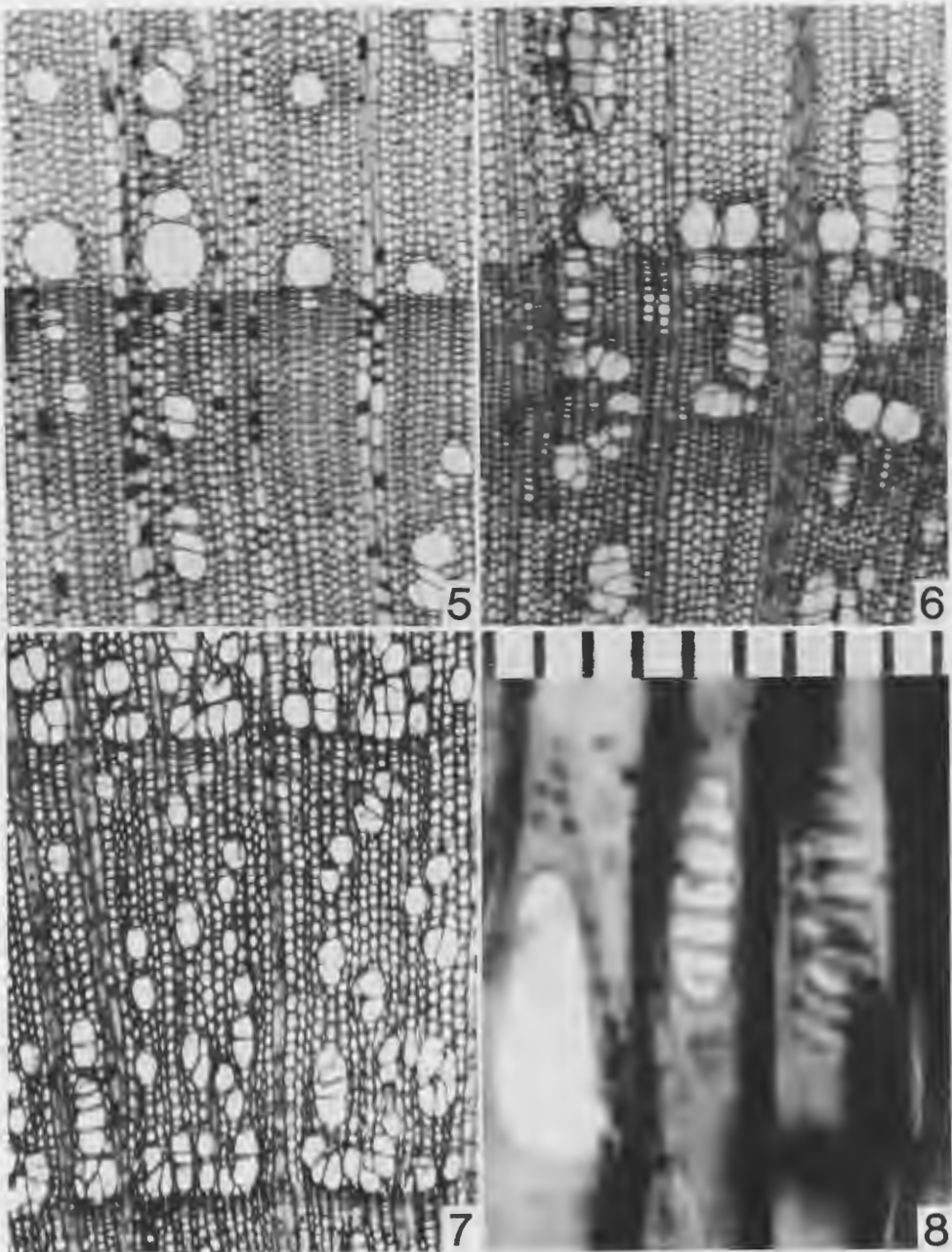


Fig. 5-8. Wood sections of temperate species of *Meliosma*.—5. *M. cuneifolia*, transection; terminus of growth ring just above center of photograph.—6. *M. dillenifolia* subsp. *flexuosa*, transection; vessels commonly in radial multiples.—7, 8. *M. veitchiorum*.—7. Transection; margins of two growth rings visible; vessels notably narrow.—8. Radial section; earlywood vessel with simple perforation plate at left, two latewood vessels with scalariform plates at right. Collections in Table 1. (Fig. 5-7, scale above Fig. 1; Fig. 8, scale above Fig. 8 [divisions = 10 μ m].)

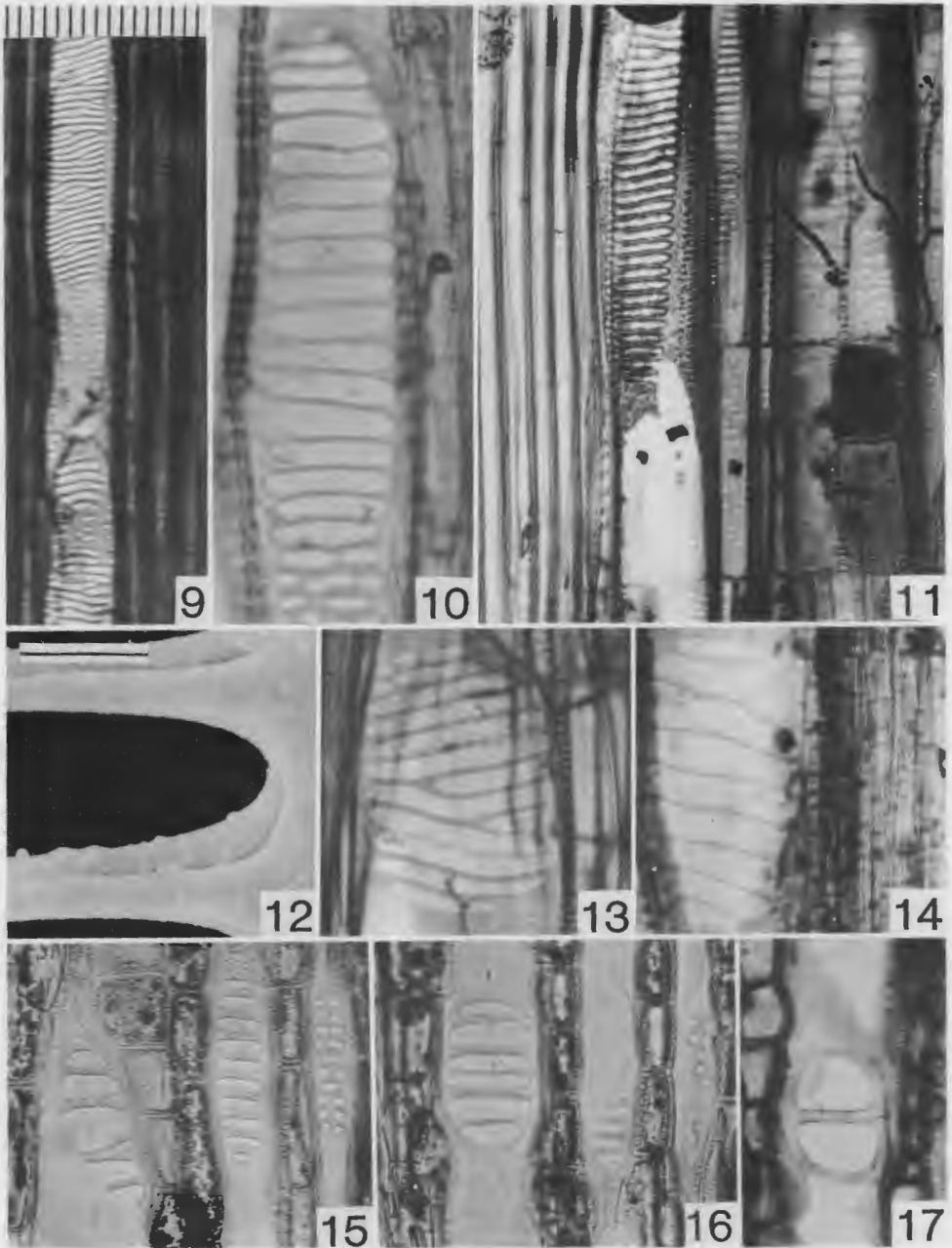


Fig. 9–17. Radial sections of wood of Sabiaceae to show details of scalariform perforation plates. — 9. *Sabia olacifolia* (Petelot 1774, UC); larger perforation plate above, a double perforation plate below. — 10. *Meliosma dilleniifolia* subsp. *flexuosa*; plate is typical for the genus. — 11–12. *M. squamulata*. — 11. Most of a long perforation plate, upper left; other scalariform plates, top center and top right, respectively. — 12. SEM of end of a perforation, showing bordered condition. — 13. *M. simplicifolia*; perforation plate with forked bars. — 14. *M. pittieriana*; perforation plate with very slender bars. — 15–17. *M. myriantha*. — 15. Three perforation plates; the narrowest, at right, is multiperforate. — 16. Three perforation plates; mixed wide and narrow bars in the plate at left. — 17. Plate with a single thick bar. Collections in Table 1 except for Fig. 9. (Fig. 9, 11, scale above Fig. 9 [divisions = 10 μm]; Fig. 10, 13, 14, 15–17, scale above Fig. 8; Fig. 12, scale at upper left [bar = 1 μm].)

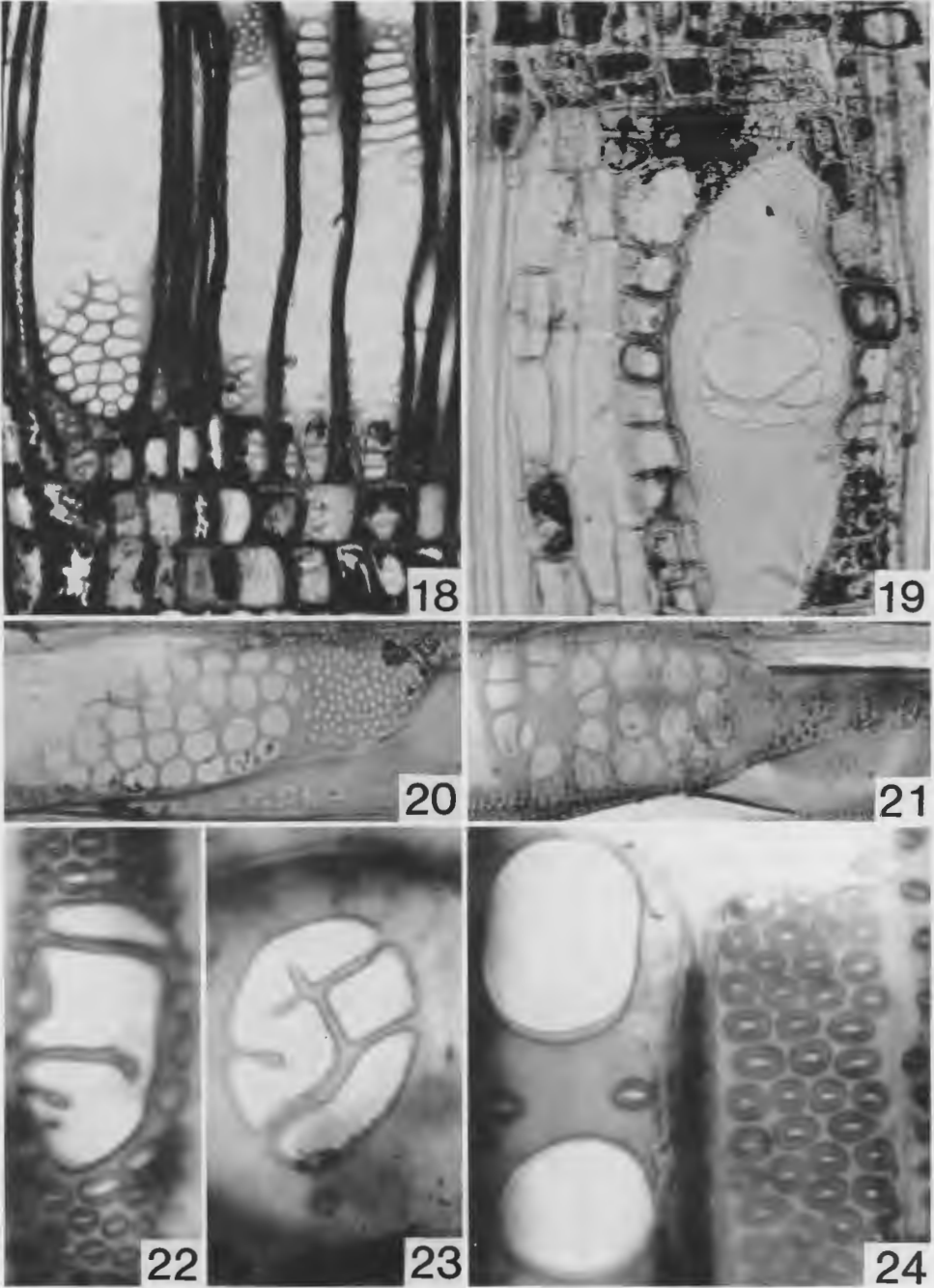


Fig. 18–24. Radial sections of woods of *Meliosma*, showing variant perforation plate types.—18. *M. ellipticifolia*; multiperforate plate at left, two scalariform plates at right.—19. *M. myriantha*; near-simple plate traversed by a few bars.—20. *M. occidentalis*; multiperforate plate.—21. *M. panamaensis* Standl. (MADw-11972); multiperforate perforation plate.—22–24. *M. veitchiorum*.—22. Plate traversed with one entire bar and other partial bars.—23. Networklike bars.—24. Double perforation plate at left; lateral wall pitting on vessels at right. Collections in Table 1, except for Fig. 21. (Fig. 18–21, scale above Fig. 9; Fig. 20–24, scale above Fig. 8.)

(Fig. 1: 1.40 vessels per group), *M. simplicifolia* (Fig. 2: 1.61 vessels per group), and *M. rigida* (Fig. 3: 1.34 vessels per group). Greater degrees of vessel grouping are shown for *M. hachijoensis* (Fig. 4: 7.00 vessels per group), *M. cuneifolia* (Fig. 5: 2.59 vessels per group), and *M. dilleniifolia* subsp. *flexuosa* (Fig. 6: 3.52 vessels per group). In *Ophiocaryon paradoxum*, vessel grouping is low (Fig. 45, 2.00 vessels per group). In *Sabia japonica*, however, vessels are entirely solitary (Fig. 49: 1.00 vessels per group). The ecological correlations of these various degrees of vessel grouping will be discussed later. According to an earlier hypothesis (Carlquist 1984), dicotyledons with tracheids as imperforate tracheary elements do not group vessels, whereas those with fiber-tracheids or libriform fibers may group vessels. *Sabia* has tracheids and thereby validates this hypothesis.

Vessel Diameter

Vessel diameter in *Meliosma* ranges from 63 μm to 181 μm (Table 1, column 2). Species with notably wide vessels (above the mean for the genus as a whole, 106 μm) are illustrated in the first plate: *M. sumatrana* (Fig. 1, mean vessel diameter = 131 μm), *M. simplicifolia* (Fig. 2, 171 μm), *M. rigida* (Fig. 3, 128 μm), and *M. hachijoensis* (Fig. 4, 154 μm). *Meliosma hachijoensis* may have the largest vessels in the genus in a sense, because the mean, 154 μm , includes measurements of notably narrow latewood vessels (Fig. 4, bottom), whereas earlywood vessels (Fig. 4, above) are wider than vessels in the other species with notably wide vessels (Fig. 1–3). The second plate (Fig. 5–8) illustrates species with notably narrow vessels: *M. cuneifolia* (Fig. 5, mean vessel diameter = 77 μm), *M. dilleniifolia* subsp. *flexuosa* (Fig. 2, 77 μm), and *M. veitchiorum* (Fig. 3, 66 μm). The ecological significance of the wide range of vessel diameter expressions in *Meliosma* will be discussed in the section on Ecological Conclusions. The vessels in *Ophiocaryon paradoxum* (Fig. 45) are wide (mean = 153 μm) compared with those of most species of *Meliosma*. Vessels of *Sabia japonica* (Fig. 45) range widely in diameter but average 99 μm .

Vessel Density

Vessel density in *Meliosma* shows a more than tenfold range, from 5.4 to 59.2 vessels per mm^2 (Table 1, column 3). The species with relatively wide vessels in general have low density, such as *M. sumatrana* (Fig. 1, 8.0 vessels per mm^2), *M. simplicifolia* (Fig. 2, 15.3 vessels per mm^2), *M. rigida* (Fig. 3, 31.0 vessels per mm^2), or *M. hachijoensis* (Fig. 4, 12.8 vessels per mm^2). The species with narrow vessels have greater density: *M. cuneifolia* (Fig. 5, 32.6 vessels per mm^2), *M. dilleniifolia* subsp. *flexuosa* (Fig. 2, 66 vessels per mm^2), and *M. veitchiorum* (Fig. 3, 59.2 vessels per mm^2). Vessel density for *Ophiocaryon paradoxum* (Fig. 45) is 4.8 vessels per mm^2 , lower than for any of the *Meliosma* species. In contrast, the mean vessel density for *Sabia japonica* (Fig. 49) is 57.4 per mm^2 , close to the highest figure in *Meliosma*.

Vessel Element Length

Vessel element length for Sabiaceae as a whole is relatively long compared with that in most families of dicotyledons. The range of means is from 430 μm (*M.*

veitchiorum) to 1267 μm (*M. herbertii*, *Ophiocaryon paradoxum*). The significance of vessel element length will be examined in Ecological Conclusions below.

Vessel Wall Thickness

Evident in the transections of wood (Fig. 1–7, 35, 45, 49) is the thinness of vessel walls in the family. This is confirmed by the figures of Table 1, column 5: a range from 2.2 μm to 6.6 μm , with a mean for *Meliosma* of 3.3. The thinness of walls in both vessel elements and imperforate tracheary elements accounts for problems in sectioning of these woods.

Perforation Plates

The range in perforation plate morphology within Sabiaceae is unusual: from simple to long scalariform or multiperforate, with variations on these types and combinations of them within some species. Exemplary of the range are the two species of *Sabia* examined in this study: *S. olacifolia* (Fig. 9) has scalariform perforation plates exclusively, whereas *S. japonica* (Fig. 49) has simple plates exclusively. The basic form in *Meliosma* is long scalariform, as exemplified by *M. dilleniifolia* subsp. *flexuosa* (Fig. 10) or *M. squamulata* (Fig. 11). The mean number of bars per perforation plate in *Meliosma* is 8.8, with a range in means from 0 (*M. alba*) to 17.0 in *M. glossophylla* (Table 1, column 6).

Bars on perforation plates are bordered (Fig. 12), less conspicuously if the bars are slender. A mixture of simple and scalariform perforation plates—the scalariform plates in latewood—can be found in *M. veitchiorum* (Fig. 8). In any given species, bars tend to be more slender in wide vessels (Fig. 13, 14) than in narrow vessels. In latewood vessels, bars may be not only more numerous, but also thicker (Fig. 15). Unusually thick bars are shown for *M. myriantha* (Fig. 15–17). The vessels at right in Fig. 15 and 16 possess small pitlike perforations (lateral wall pitting of vessels in this species are much smaller than these perforations, as these photographs show). These plates should be designated as multiperforate, despite the wide spacing of the perforations. Another type of multiperforate plate is shown for wider vessels in *M. ellipticifolia* (Fig. 18), although the narrower vessels in that section have scalariform plates. Multiperforate perforation plates characterize all or most vessels in *M. occidentalis* (Fig. 20), *M. panamaensis* (Fig. 21), and *Ophiocaryon paradoxum* (Fig. 47).

Aberrant types of scalariform perforation plates with partial bars and various orientation of bars are not uncommon in *Meliosma*. Some of these are illustrated for *M. myriantha* (Fig. 19) and *M. veitchiorum* (Fig. 23). These may be considered types of intermediacy between scalariform and simple. Double perforation plates were observed in *M. veitchiorum* (Fig. 24).

Lateral Wall Pitting of Vessels

Vessel-to-vessel pits in *Meliosma*, *Ophiocaryon*, and *Sabia* are elliptical to, less commonly, circular, as in *M. veitchiorum* (Fig. 22, 24). The range in pit diameter in *Meliosma* is wide: from about 5 μm (*M. dilleniifolia* subsp. *dilleniifolia*, *M. kirkii*, *M. macrophylla*, *M. myriantha*, and *M. parviflora*) to about 10 μm (12–15 μm long axis if pits are elliptical) in *M. alba*, *M. allenii*, *M. lanceolata*, *M. nitida*,

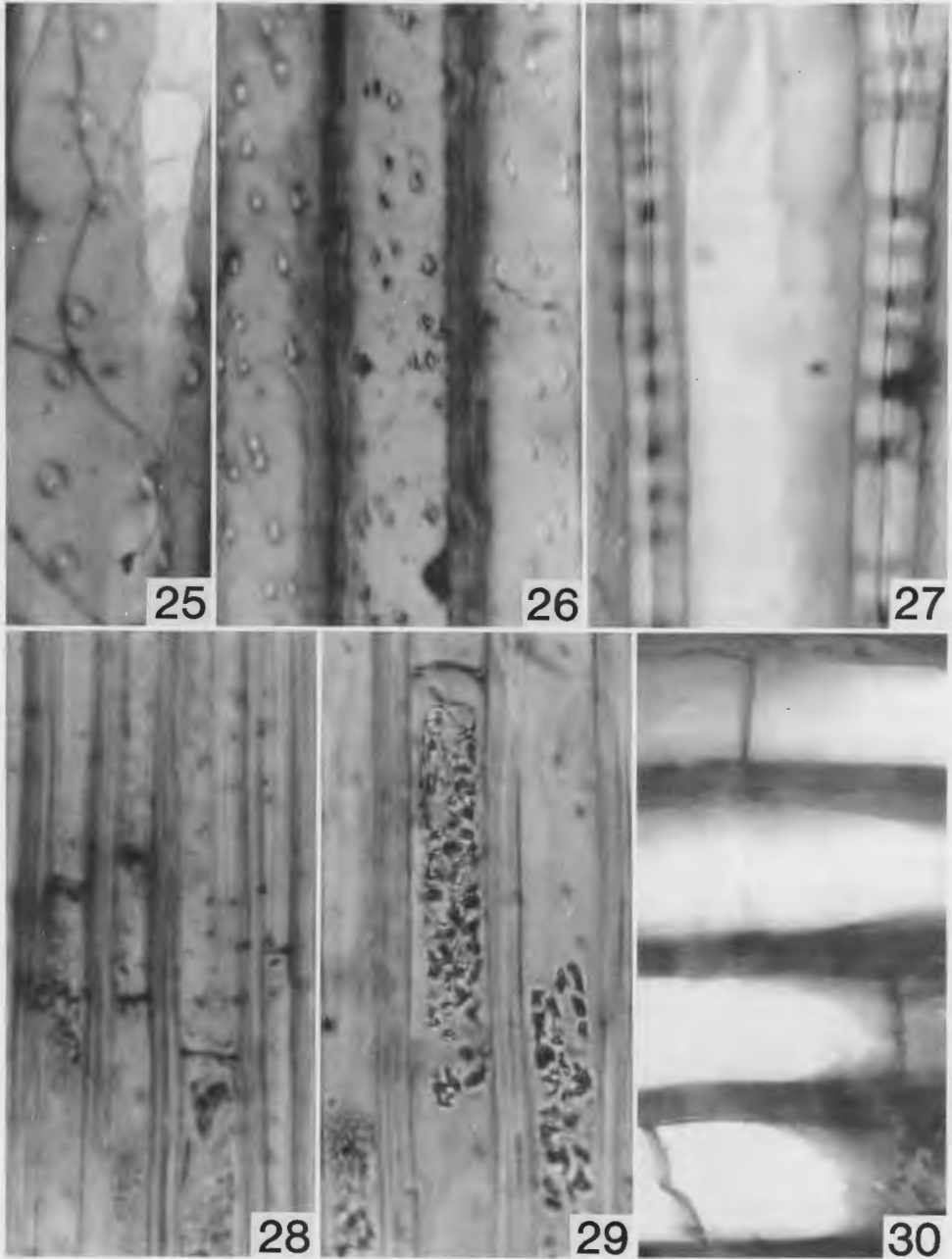


Fig. 25-30. Sections of wood of *Meliosma* to show nature of imperforate tracheary elements.—25. *M. lanceolata*; fiber-tracheid from radial section, showing bordered pits (fungal hypha also visible).—26. Three libriform fibers from radial section, showing simple pits.—27. *M. hachijoensis*; walls of libriform fibers from tangential section, showing simple pits in sectional view.—28-29. *M. dillenii-fo- lia* subsp. *flexuosa*, septate fibers from radial sections.—28. Fibers with nuclei.—29. Fibers containing starch-grain remnants.—30. *M. ellipticifolia*, radial section showing septa in three fibers. Collections in Table 1. (Fig. 25-30, scale above Fig. 8.)

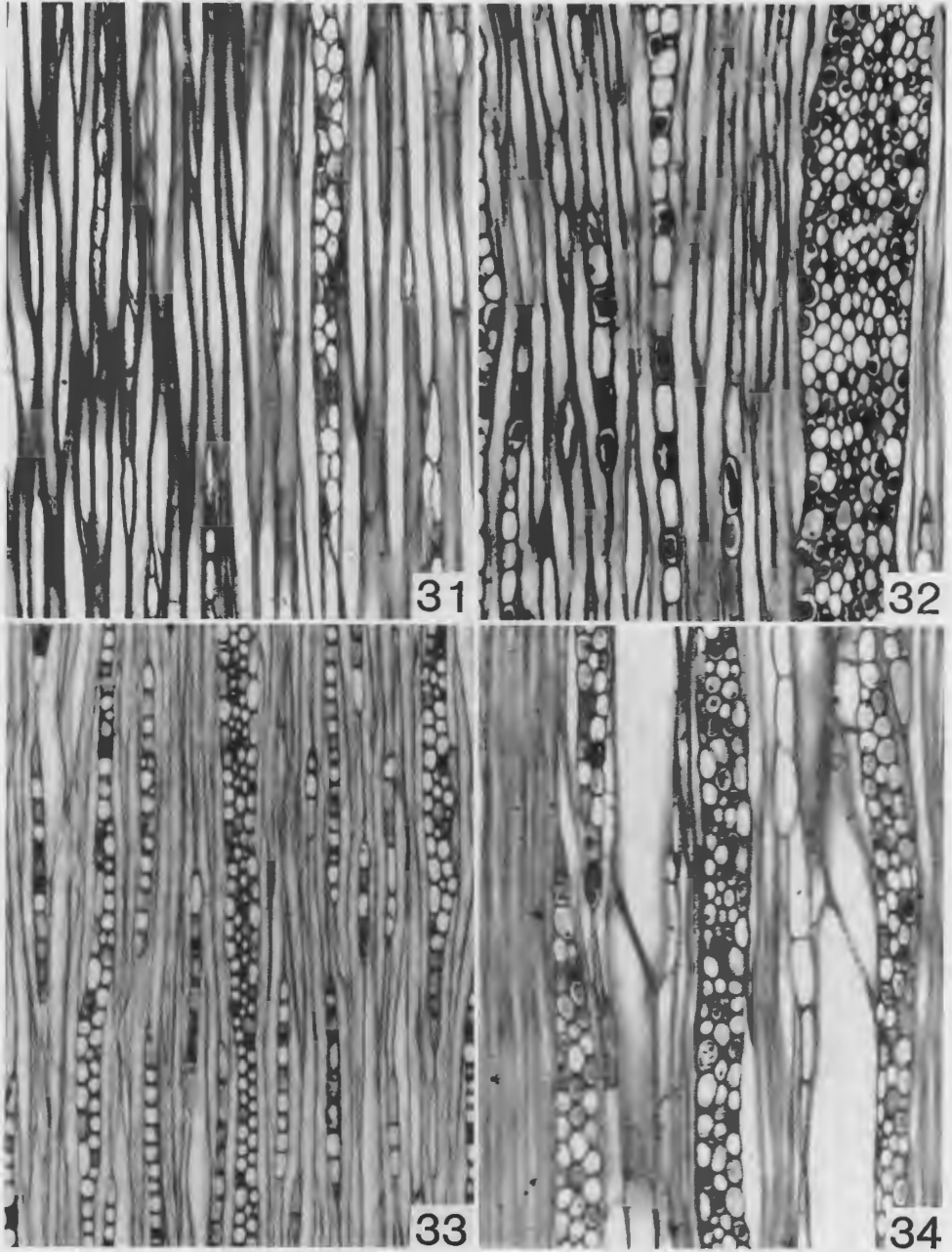


Fig. 31-34. Tangential sections of *Meliosma*.—31. *M. glossophylla*; biseriate and uniseriate rays present.—32. *M. arnottiana*; rays of two distinct widths (note wide ray at right) present.—33. *M. cuneifolia*; uniseriate rays outnumber multiseriate rays.—34. *M. kirkii*; uniseriate rays are scarce. Collections given in Table 1. (Fig. 31-34, scale above Fig. 1.)

M. oldhamii, *M. pittieriana*, *M. rhoifolia*, and *M. veitchiorum*. The remaining species of *Meliosma* are intermediate between these extremes. *Ophiocaryon paradoxum* has intervacular pits unusually large in diameter (16 μm), but they are relatively small (about 7 μm) in *Sabia japonica* (Fig. 51). Vessel-to-ray and vessel-to-axial parenchyma pitting ranges between alternate and scalariform, with transitional pitting present occasionally (Fig. 11).

Helical Thickenings

Although *Sabia japonica* has conspicuous helical thickenings on vessel walls (Fig. 51), helical thickenings are lacking in vessels of *S. olacifolia*. Interestingly, in *S. japonica*, the thickenings do not run entirely between pits, but may overlie some of them. Further studies to determine the distribution of helical thickenings in *Sabia* are desirable. The report by Metcalfe and Chalk (1950) of helical thickenings in "one specimen of *M. rhoifolia*" is dubious, and no helical thickenings were observed in any collection of *Meliosma* in the present study.

Imperforate Tracheary Elements

Sabiaceae contain a wide range of tracheary elements. *Sabia japonica* and *S. olacifolia* have tracheids that are densely covered with bordered pits, the pit cavities of which average about 7 μm in diameter.

Fiber-tracheids with sparsely distributed bordered pits with pit cavities about 4 μm in diameter were observed with certainty in a minority of the species of *Meliosma*: *M. alba*, *M. glabrata*, *M. kirkii*, *M. lanceolata* (Fig. 25), *M. parviflora*, *M. sumatrana*, and *M. veitchiorum*. Fiber-tracheids of this sort also occur in *Ophiocaryon paradoxum* (Fig. 48).

Species of *Meliosma* other than those listed in the preceding paragraph have libriform fibers with pits apparently lacking borders on fiber-to-fiber pit pairs. Such pits are illustrated for *M. arnottiana* (Fig. 26) and *M. hachijoensis* (Fig. 27). Dark circles around the pit cavities in these photographs are effects of refractiveness of the pit cavity or stain extending beyond the pit cavity, they are not vestigial borders. The 23 taxa of *Meliosma* claimed to have libriform fibers can in many cases be demonstrated to have vestigial borders on fiber-to-ray pit pairs.

Of the 23 taxa claimed to have libriform fibers, the following were observed to have septate fibers: *M. allenii*, *M. dentata*, both subspecies of *M. dilleniifolia* (Fig. 28, 29), *M. ellipticifolia*, (Fig. 30), *M. glossophylla*, *M. hachijoensis*, *M. occidentalis*, *M. pittieriana*, and *M. rigida* (only a few septate fibers in *M. rigida*). Because material of *M. dilleniifolia* was liquid preserved, nuclei could be detected in septate fibers (Fig. 28). Starch grain remnants were also observed in septate fibers of this taxon (Fig. 29); the altered nature of starch grains may be ascribed to the action of ethylenediamine (see Materials and Methods). Septate fibers in Sabiaceae tend to be restricted to zones close to vessels in *Meliosma* according to Metcalfe and Chalk (1950), and that was confirmed by the present study. Septate fibers were reported by Heimsch (1942) in *Sabia*, but this seems unlikely in view of the presence only of tracheids in the two species of *Sabia* studied.

Diameter of imperforate tracheary elements is given in Table 1, column 7: the range is from 18 to 62 μm , an exceptionally wide range. There is not a close correlation to vessel diameter in the family. Imperforate tracheary element length

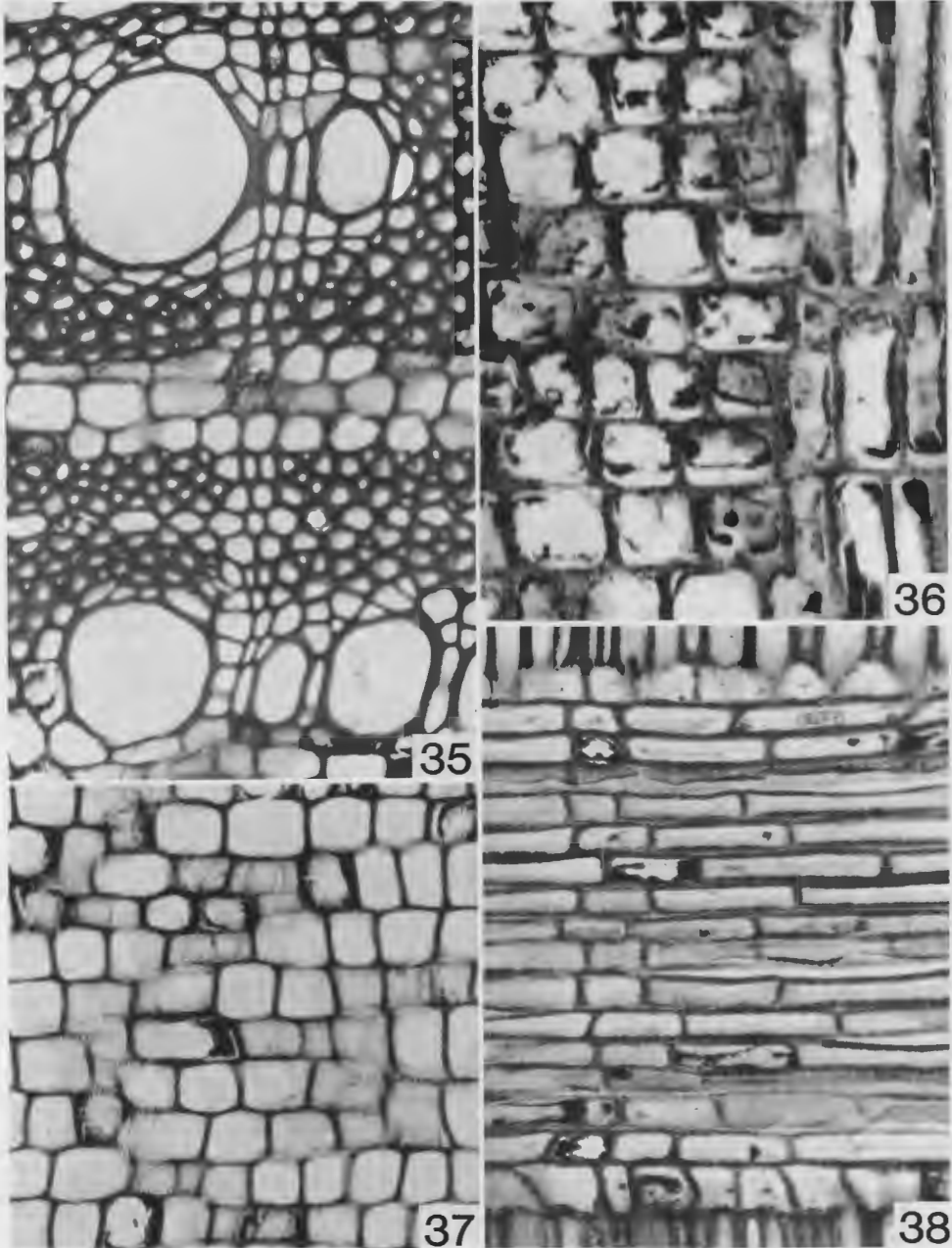


Fig. 35-38. Wood sections of *Meliosma*.—35. *M. parviflora*; transection, showing vasicentric parenchyma around vessels, plus a band or apotracheal banded parenchyma running from top to bottom, center of photograph.—36. *M. glossophylla*, radial section; cells approximately square, left, plus upright sheath cells of multiseriate ray, right.—37. *M. parviflora*, radial section; cells mostly square, a few procumbent.—38. *M. alba*, medial radial section of ray, showing mostly procumbent cells plus square cells at top and bottom of ray. Collections listed in Table 1. (Fig. 35-38, scale above Fig. 9.)

(Table 1, column 8) ranges from 621 to 1783 μm . For *Meliosma*, the mean ratio of imperforate tracheary element length to vessel element length is 1.54, but on a species by species basis, the ratio fluctuates from 1.03 (*M. dilleniifolia* subsp. *flexuosa*) to 2.07 (*M. veitchiorum*). Wall thickness of imperforate tracheary elements ranges from 2.3 to 6.9 μm , but most species have relatively thin walls (Table 1, column 9): 3.5 μm is the mean for *Meliosma*. Although figures for this feature are not available for dicotyledons as a whole, the figure in Sabiaceae is comparatively low, and accounts (at least in part) for the softness of woods in the family.

Axial Parenchyma

In all Sabiaceae, vasicentric axial parenchyma is present. In most species the axial parenchyma can be termed scanty, with two cells thick (or less) around vessels or vessel groups. In the photomicrographs presented, axial parenchyma is most easily seen in *M. simplicifolia* (Fig. 2) and *M. rigida* (Fig. 3), in which the axial parenchyma is relatively abundant, as it is also in *M. fischeriana*, *M. lanceolata*, *M. macrophylla*, and *M. parviflora* as well as in *Ophiocaryon paradoxum* (Fig. 45). Axial parenchyma is very scanty—only a few cells adjacent to vessels or vessel groups—in *M. cuneifolia*, *M. dentata*, *M. ellipticifolia*, *M. glabrata*, *M. hachijoensis*, *M. herbertii*, *M. tenuis*, and *M. veitchiorum*. The number of axial parenchyma cells per strand ranges from 3 to 18 in *Meliosma*.

In addition of vasicentric axial parenchyma, tangential bands occur in some Sabiaceae. These bands are widest (three to four cells) in *Ophiocaryon paradoxum* (Fig. 45, between pairs of arrows), but are also present in species of *Meliosma*: *M. glabrata*, *M. macrophylla*, *M. myriantha*, *M. parviflora* (Fig. 35), and *M. veitchiorum*.

Ray Types and Sizes

All three genera of Sabiaceae have both multiseriate and uniseriate rays (Figs. 31, 32, 33, 46, 50). The ray types in Sabiaceae are of the Heterogeneous Types IIA and IIB of Kribs (1935), as reported by Metcalfe and Chalk (1950). In some species of *Meliosma*, uniseriate rays are absent or infrequent: *M. ellipticifolia*, *M. fischeriana*, *M. glabrata*, *M. glossophylla*, *M. hachijoensis*, and *M. kirkii* (Fig. 34). Multiseriate rays are more frequent than uniseriate rays in most Sabiaceae; exceptions occur in *M. arnottiana* (Fig. 32), *M. cuneifolia* (Fig. 33), *M. dilleniifolia* subsp. *flexuosa*, *M. glossophylla* (Fig. 31), *M. rhoifolia*, and *M. wallichii*. In a few species, notably wide multiseriate rays are present, resulting in the condition known as "rays of two distinct widths": *M. arnottiana* (Fig. 32), *M. oldhamii*, *M. wallichii*, and *Sabia japonica* (Fig. 50).

Multiseriate ray height (Table 1, column 10) does not correlate well with vessel element length in Sabiaceae, although it does in some dicotyledon families. Notably tall rays occur in *M. arnottiana* (Fig. 32), *M. kirkii* (Fig. 32), *M. wallichii*, and, especially, *Sabia japonica* (Fig. 50). Ray width means (Table 1, column 11) reveal differences among species of *Meliosma*. The range in ray widths is unusually great, from 47 μm (*M. alba*) to 225 μm (*M. wallichii*). Doubtless ray width increases with age of stem in Sabiaceae as it does in other families, but difference in stem age does not account for the wide range of ray widths observed. Uniseriate ray

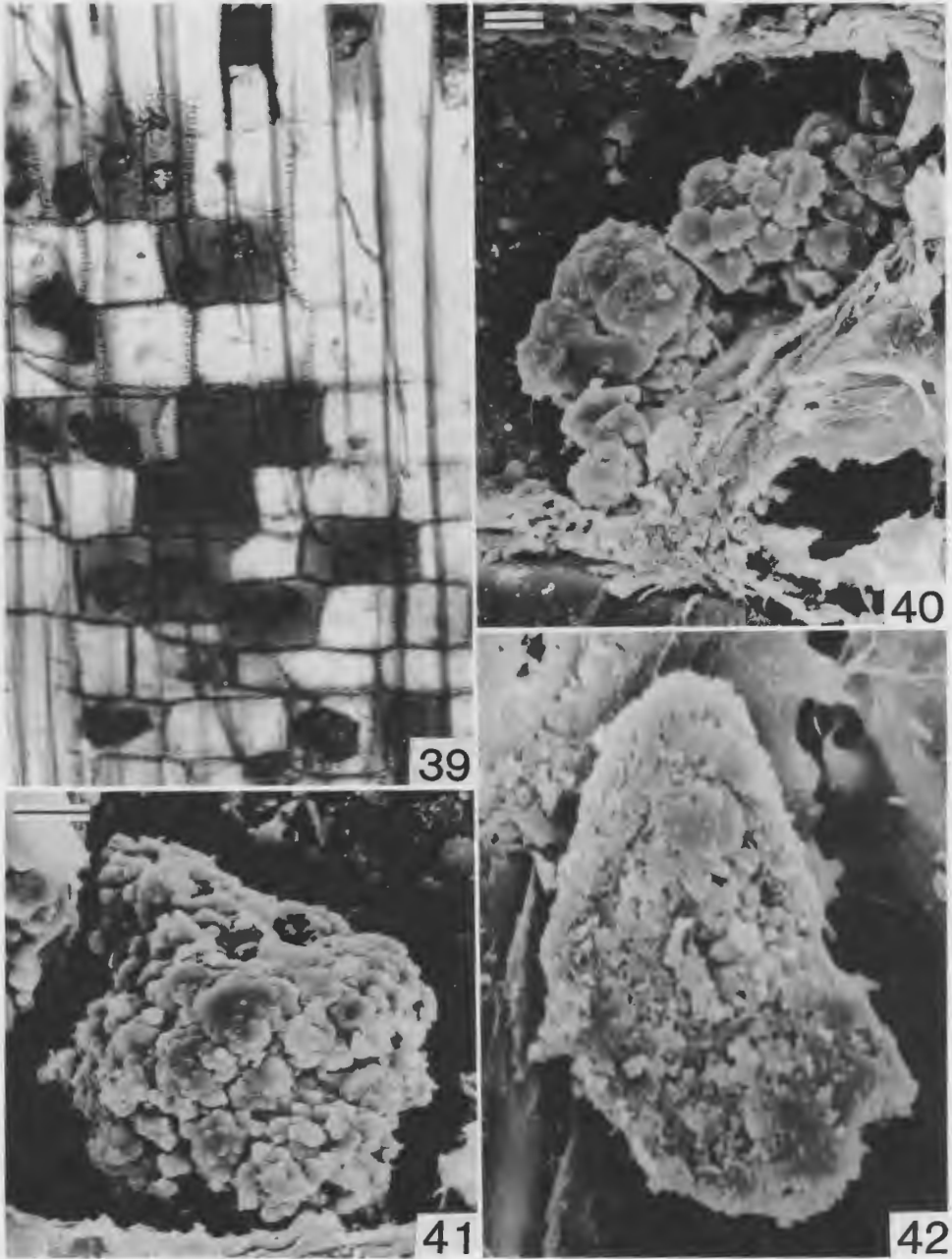


Fig. 39-42. Silica bodies from radial sections of *Meliosma* woods.—39. *M. panamaensis* (MADw-11972), radial section to show silica bodies, variously visible in cells with dark-staining contents.—40-42. *M. herbertii* (PRFw-22557), SEM photos.—40. A series of smaller silica bodies in a ray cell.—41. A single large silica body in a ray cell.—42. Sectional view of silica body, showing porous nature. (Fig. 39, scale above Fig. 9; Fig. 40, bar at upper left = 1 μm ; Fig. 41, 42, bar at upper left in Fig. 41 = 1 μm .)

heights are given in Table 1, column 12; these heights do not correlate with multiseriate ray heights in the family. Figures are not given for uniseriate ray heights for species in which uniseriate rays are infrequent.

Ray Histology

Histology of multiseriate rays is summarized in Table 1, column 13. Metcalfe and Chalk (1950) claim that multiseriate rays in the family consist predominantly of upright cells, corresponding to the condition shown for *M. glossophylla* (Fig. 36). Such rays were found in *M. arnottiana*, *M. cuneifolia*, and *M. glabrata*. In a few species, such as *M. myriantha*, *M. occidentalis*, *M. parviflora* (Fig. 37), and *Ophiocaryon paradoxum* (Fig. 46), cells approximately square as seen in radial section outnumber both upright and procumbent cells. However, contrary to Metcalfe and Chalk, procumbent cells predominate in *M. alba* (Fig. 38), *M. allenii*, *M. dentata*, *M. dilleniifolia* (both subspecies), *M. fisheriana*, *M. hachijoensis*, *M. herbertii*, *M. kirkii*, *M. lanceolata*, *M. macrophylla*, *M. nitida*, *M. oldhamii*, *M. pittieriana*, *M. rhoifolia*, *M. simplicifolia*, *M. squamulata*, *M. tenuis*, *M. veitchiorum*, *M. wallichii*, and *Sabia japonica*. Where ray cells are characterized as being procumbent, marginal cells (at top and bottom of a ray) tend to be square, as in Fig. 38. If upright cells are present in multiseriate rays, they are found in ray margins and as sheathing cells. Uniseriate rays in Sabiaceae consist of square and upright cells, even if ray cells are predominantly procumbent in multiseriate rays of a given species. One must remember that abundance of procumbent cells in multiseriate rays may be an ontogenetic matter: procumbent cells become more common as a stem increases in diameter (Barghoorn 1941), so that scarcity or abundance of procumbent cells in multiseriate rays may be more an indication of size of stem sampled than of a systematic distinction.

Ray cell walls in Sabiaceae are generally 2–5 μm in thickness and are lignified (Fig. 36–38). Bordered pits among ray cells are common, and are present in all species examined. One must stress that attempts to view borders of ray cell pits in face view are unlikely to be successful, and one must look at sections of pits, as in *M. dilleniifolia* subsp. *flexuosa* (Fig. 43).

Silica bodies occur in a scattering of *Meliosma* species. Silica bodies are shown here by light microscopy for *M. panamaensis* (Fig. 39) and *M. dilleniifolia* subsp. *dilleniifolia* (Fig. 43), and by means of SEM for *M. herbertii* (Fig. 40–42). The bodies are usually single per ray cell (Fig. 41, 42), but several smaller bodies occur occasionally, as shown in Fig. 40; *M. oldhamii* characteristically shows this condition. Where the interior of a silica body is revealed by sectioning, the bodies tend to be porous (Fig. 42). In addition to the species just cited, *M. dilleniifolia* subsp. *flexuosa* (Fig. 43) has silica bodies in rays.

Hexagonal calcium oxalate crystals were observed to be abundant in *Meliosma simplicifolia* (Fig. 44). Similar crystals, although less abundant, were observed in ray cells of *M. fisheriana*, *M. kirkii*, *M. macrophylla*, *M. parviflora*, and *M. rigida*. Crystals are generally borne singly per ray cell in *Meliosma*, but several smaller crystals per cell characterize *Sabia japonica* (Fig. 52).

Starch grains in ray cells were demonstrated by means of SEM for ray cells of *Sabia japonica* (Fig. 52). Starch grains were observed by means of light microscopy in *M. dilleniifolia* subsp. *flexuosa*, *M. glabrata*, *M. tenuis*, and *M. veitchiorum*.

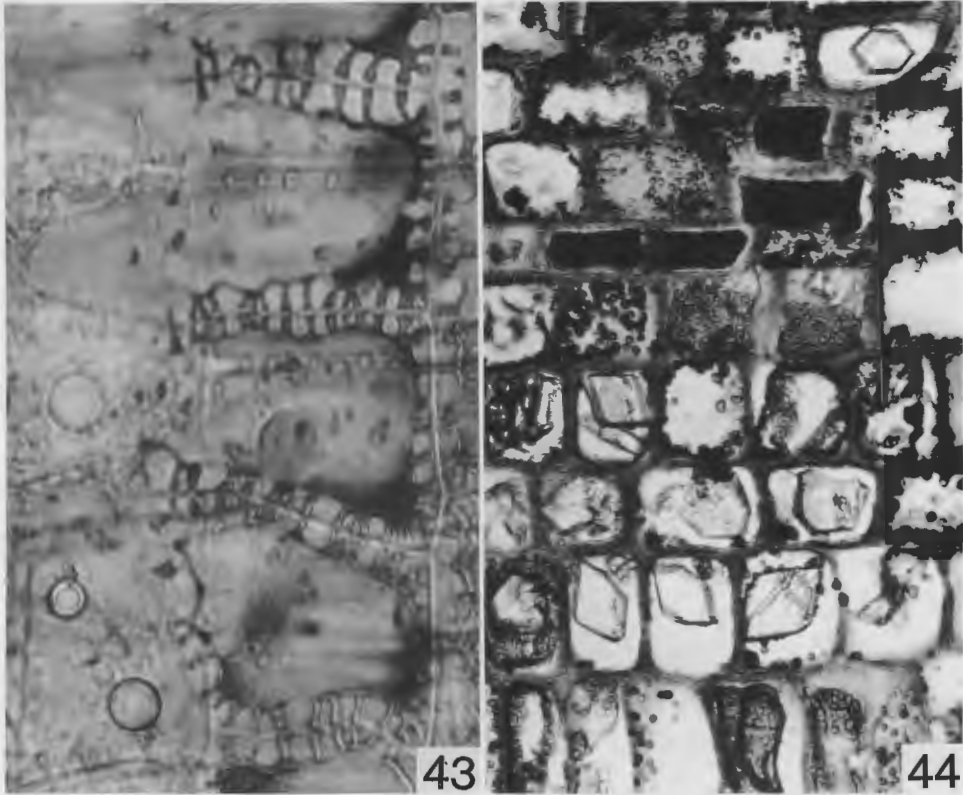


Fig. 43, 44. Radial sections of ray cells of *Meliosma*.—43. *M. dilleniifolia* subsp. *flexuosa*; silicified bodies (lower left) and borders on ray cell walls (at right).—44. *M. simplicifolia*; hexagonal crystals and dark-staining contents in ray cells. Collections given in Table 1. (Fig. 43, scale above Fig. 8; Fig. 44, scale above Fig. 9.)

Starch is to be expected in other species as well, and may be absent in particular preparations because of how the specimen was processed or because of the season at which the sample was collected.

Conspicuously present in ray and axial parenchyma cells of Sabiaceae are darkly colored and darkly staining deposits. The deposits may be homogeneous, as in Fig. 39, but are more commonly droplets or large aggregations, as in Fig. 18, 36, 38, and 44. Deposits most commonly are massive, (Fig. 1, 2, 3, 19, 32, 34, 39). In addition to these deposits, one may see grayish granular contents (which often stain purple with the safranin-fast green combination) in many of the species studied; these are probably tannins.

Tyloses

Thin-walled tyloses were observed in a scattering of Sabiaceae. They are illustrated here for *Meliosma rigida* (Fig. 3) and *Ophiocaryon paradoxum* (Fig. 45). Similar tyloses were observed in *M. glossophylla*, *M. myriantha*, *M. tenuis*, and *M. wallichii*. Sclerosed tyloses with lignified walls 5–7 μm thick were observed in *M. dilleniifolia* subsp. *dilleniifolia*.

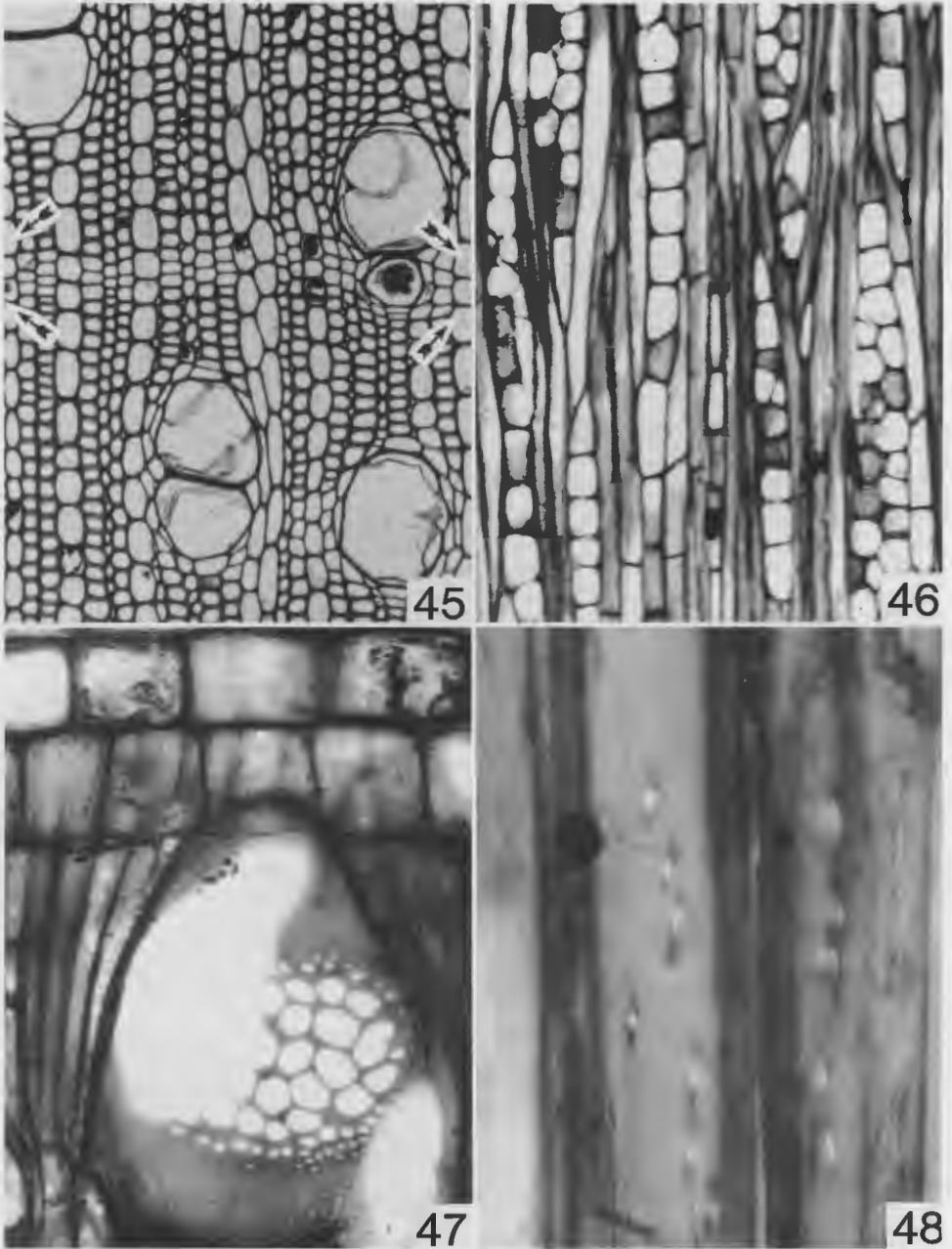


Fig. 45–48. Wood sections of *Ophiocaryon paradoxum* (SJRw-43891).—45. Transection; thin-walled tyloses present in vessels; tangential band of apotracheal axial parenchyma runs horizontally between pairs of arrows.—46. Tangential section; ray cells larger than in other Sabiaceae.—47. Radial section, showing multiperforate perforation plate in a vessel element.—48. Radial section, showing borders on pits of fiber-tracheids. (Fig. 45, 46, scale above Fig. 1; Fig. 47, scale above Fig. 9; Fig. 48, scale above Fig. 8.)

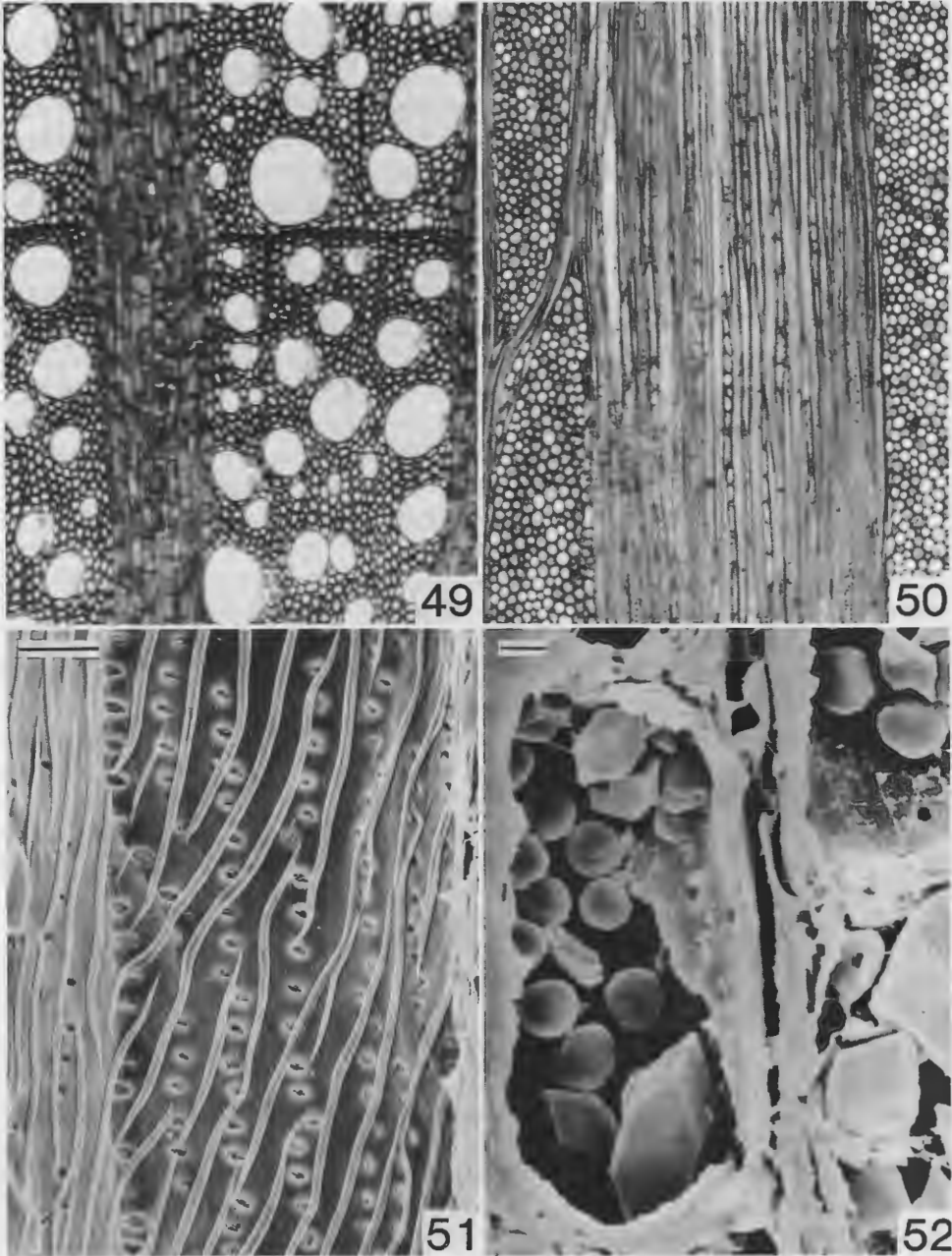


Fig. 49–52. Wood sections of *Sabia japonica* (Carlquist 15975; RSA).—49. Transection, showing a growth ring margin; vessels are solitary.—50. Tangential section; large multiseriate rays at left and right, with numerous uniseriate rays in remainder of section.—51. SEM photograph of vessel wall from radial section, showing helical thickenings.—52. SEM photograph of crystals and starch grains in ray cells. (Fig. 49, 50, scale above Fig. 1; Fig. 51, bar at upper left = 5 μm .; Fig. 52, bar at upper left = 5 μm .)

ECOLOGICAL CONCLUSIONS

Conductivity, according to the Hagen-Poiseuille equation, is proportional to the fourth power of the vessel diameter; this figure is often used as an indicator of conductive capability and therefore the ecological status of the wood (Zimmermann 1983). In practical terms, we can rarely use that indicator as a way of understanding wood structure because most woods are a compromise between the contradictory demands of conductive efficiency on the one hand and conductive safety on the other. The Hagen-Poiseuille equation cannot be used to indicate safety or delineate the kinds of structure that would lead to prevention of embolisms (or achieve rapid recovery after embolism formation). The Mesomorphy index, now used in numerous papers, has the merit of being an indicator, admittedly arbitrary, of both conductive efficiency and safety (Carlquist 1988). Tropical rain forest is the ecological site that has conductive efficiency minimally compromised by adaptations to conductive safety. In this habitat, the canopy transpires enormous quantities of water, and water supply to roots is unlimited, so conductive safety is not a major consideration. Other habitats illustrate much higher degrees of adaptation by woods to conductive safety, and thus the Mesomorphy value is widely usable. The Mesomorphy values for species of Sabiaceae (Table 1, column 14) reinforce this concept. *Ophiocaryon paradoxum*, from the lower Essequibo, Guayana (Barneby 1972) exemplifies the rain forest habitat, and not surprisingly, this species has the highest Mesomorphy value of any species studied here. The next highest Mesomorphy figures are represented by *M. arnottiana*, *M. lanceolata*, and *M. sumatrana*. The specimen of *M. arnottiana* studied came from "India" (no further locality data) according to xylarium records, but according to Beusekom (1971), *M. arnottiana* occurs in such wet tropical areas of India as Assam, Darjeeling, and the Western Ghats. *Meliosma lanceolata* and *M. sumatrana* were collected in lowland Sumatra, a definitive equatorial rain forest habitat.

By contrast, if one looks at the lowest Mesomorphy values in the family, one finds the following taxa, ranked beginning with the lowest Mesomorphy values: *Meliosma veitchiorum* (479); *M. dilleniifolia* subsp. *flexuosa* (705); *M. myriantha* (1039); *M. dilleniifolia* subsp. *dilleniifolia* (1145); *M. cuneifolia* (1322); *M. ellipticifolia* (1451); *M. glossophylla* (1456); *M. tenuis* (1839); and *M. macrophylla* (1908).

Given that all Sabiaceae grow in mesic habitats, dryness of climate or soil is not a factor involved in these low values. Rather, the effect of cold is evident. The two New World species in the above list are *M. glossophylla* (the wood from the type collection, 2160 m in the Cordillera Occidental of Colombia) and *M. ellipticifolia* (wood from the type collection, 1700 m, Depto. Del Valle, Colombia). Montane central to northern Japan and Korea qualify as having cold winters, with at least 10 degrees of frost. From this geographical region come the specimens of *M. myriantha* (cult. Nikko Botanic Garden) and *M. tenuis* (Ashiu Forest). *Meliosma cuneifolia* comes from a region of central China probably similar in climate to northern Japan. The *M. macrophylla* material was collected in montane Quezon Province, Luzon, Philippines. The two collections of *M. dilleniifolia* and the material of *M. veitchiorum* were from trees cultivated at the Royal Botanic Gardens, Kew—itsself an area subject to freezing, and this is indicative that these

species are from habitats climatically similar to that of Kew. *Meliosma dilleniifolia* subsp. *dilleniifolia* is from evergreen oak forest, 2000–3000 m, southern Himalayas (Beusekom 1971), and *M. dilleniifolia* subsp. *flexuosa* occurs in eastern central China, 600–1300 m (Beusekom 1971). *Meliosma veitchiorum* is native to 600–1300 m, eastern central China, 2700–2900 m in Yunnan (Beusekom 1971). Clearly the habitats of these temperate species contrast in terms of winter cold with those of the species with high Mesomorphy values. Do narrow, short vessel elements, more numerous per mm², resist freezing better than those with wide, long vessel elements, few per mm²? Wider vessels produce the largest bubbles when frozen water in them thaws, thereby resulting in more embolisms (Ewers 1985; Yang and Tyree 1992).

The species of *Meliosma* with low Mesomorphy values all have relatively prominent (for Sabiaceae) growth rings, although one could add that quite pronounced growth rings occur in *M. hachijoensis*, which has relatively large vessel elements and therefore a relatively high Mesomorphy figure. Interestingly, *M. hachijoensis* has the highest degree of vessel grouping in the family. Large vessel groupings form a device for achieving conductive safety, because if one or several vessels in a group are embolized, intact vessels in a particular group can maintain the same pathway within the wood (Carlquist 1984). Vessel grouping is an effective tactic only when the background cells of the wood are nonconductive or nearly so (fiber-tracheids or libriform fibers). If the background of the wood is composed of tracheids (which are conductive cells), vessels are embedded in a tissue that can serve as a subsidiary conductive system, in which case grouping of vessels becomes irrelevant for maintaining conductive pathways (Carlquist 1984). These principles are well illustrated by the contrast between *Meliosma* and *Sabia*, since the latter has tracheids (and solitary vessels) and the former has libriform fibers or fiber-tracheids (and at least some grouping of vessels in all species, more markedly in the case of species from areas of cold winters).

Sabia japonica differs from *S. olacifolia* by having simple perforation plates and helical thickenings in vessels; *S. olacifolia* has scalariform perforation plates exclusively, and lacks helical thickenings. *Sabia japonica* is from montane Japan, at the northern fringe of the range of the genus, whereas *S. olacifolia* is from Vietnam. Simple perforation plates and helical thickenings tend to be much more common in temperate than in tropical climates (see discussion in Carlquist 1988).

The presence of septate fibers near vessels, at least in some species of *Meliosma*, is of interest because likely these fibers contain starch, as shown for *M. dilleniifolia* (Fig. 29). Starch-containing septate fibers offer a substitute for vasicentric parenchyma, and, indeed, the species for which vasicentric parenchyma is quite scanty are the same as the species that form septate fibers near vessels.

In *Meliosma*, there is an interesting correlation for which possibly there is a functional correlation. The species with fiber-tracheids (rather than libriform fibers) have tangential bands of apotracheal axial parenchyma (which is absent in the species with libriform fibers): *M. allenii*, *M. glabrata*, *M. kirkii*, *M. myriantha*, *M. parviflora*, and *M. sumatrana*. These species do not form a single subgenus or section in Beusekom's (1971) treatment, but are scattered among the sections he recognizes. *Ophiocaryon* also has fiber-tracheids plus bands of apotracheal axial parenchyma. Certainly nucleate and septate fibers (in *Meliosma*, septate fibers are evidently nucleate for prolonged periods [Fig. 28]), and these fibers accumulate

starch (Fig. 29). Having protoplasts that can accumulate starch is a function of parenchyma. The species with fiber-tracheids do not have these capabilities in imperforate tracheary elements, because fiber-tracheids are not, generally, nucleate and do not accumulate starch; therefore, presence of apotracheal parenchyma bands in species with fiber-tracheids might possess a function like that of the nucleate or septate fibers.

The growth rings of *M. veitchiorum* are noteworthy in that the earlywood vessels have simple perforation plates, whereas latewood perforation plates are scalariform. The simple earlywood plates likely represent an adaptation to peak flow rates, as suggested earlier (Carlquist 1988).

SYSTEMATIC AND EVOLUTIONARY CONCLUSIONS

One Family or Two?

Airy Shaw (1966) has contrasted *Sabia* with the other genera, which he segregated as Meliosmaceae. The majority of authors who have dealt with the family, whether in floras or in phylogenies of angiosperms, have followed an inclusive definition (e.g., Beusekom 1971; Gentry 1980), but a few recognize Meliosmaceae (e.g., Barneby, 1972). What does evidence from wood anatomy show?

First, one must remember that *Meliosma* and *Ophiocaryon* are trees or arborescent, whereas *Sabia* is a genus of lianas. The modalities of wood structure in these two growth forms are notably different: in lianas, rays tend to be wide and tall, vessel density is greater, and more commonly than in dicotyledons as a whole, tracheids are the imperforate tracheary element type (Carlquist 1985). In fact, these are precisely the differences in wood anatomy between *Sabia* and the other genera. No other difference separates *Sabia* from *Meliosma* and *Ophiocaryon*. Of these differences, the clearest is the occurrence of tracheids in *Sabia*. Are any other dicot families similarly split, with lianoid genera provided with tracheids but arboreal genera with fiber-tracheids or libriform fibers? The list of families in which this combination occurs is rather impressive: Actinidiaceae, Caprifoliaceae, Celastraceae, Goodeniaceae, Hydrangeaceae, Icacinaceae, Loganiaceae, Menispermaceae, and Rubiaceae (Carlquist 1985). Likely more instances could be cited. If wood anatomy were to be considered a valid criterion for segregation of Meliosmaceae, one should segregate the lianoid genera from the families just cited as independent families. Interestingly, those who segregate Meliosmaceae from Sabiaceae nevertheless place Meliosmaceae close to Sabiaceae (e.g., Dahlgren 1980). Other recent phylogenies, such as Cronquist (1988), Takhtajan (1987), and Thorne (1992), recognize Sabiaceae as including *Meliosma* and *Ophiocaryon*.

Ordinal Position of Sabiaceae

All modern phylogenists place Sabiaceae in Rutales (Sapindales) or a similarly constituted order: Cronquist (1988), Dahlgren (1980), Takhtajan (1987), and Thorne (1992). The only exception in recent times is in the tree to dicotyledons as a whole based on the plastid gene *rbcl* (Chase et al. 1993). In this tree, the sister genus of *Sabia* is held to be *Lambertia* (Proteaceae), with Tetracentraceae, Trochodendraceae, Nelumbonaceae and Platanaceae as other taxa in the clade that contains *Sabia*. Such a series of relationships is radically different from the phylogenetic localities assigned on the basis of other kinds of evidence.

Disregarding this latter concept of relationships for Sabiaceae and comparing Sabiaceae to other families of Rutales, what does wood anatomy show? For wood evidence to be suggestive of relationships other than rutalean, one would have to find one or more wood characters of moderately limited distribution within angiosperms whereby Sabiaceae differs from other Rutales. Heimsch (1942) excluded Sabiaceae from Rutales ("Terebinthales") on the basis that the family has scalariform perforation plates, whereas rutalean families have simple perforation plates. One could argue against Heimsch's suggestion merely on the basis that in numerous phylads of dicotyledons, scalariform perforation plates have given rise to simple ones, and evolutionary level in perforation plate morphology is not a reliable indicator of relationships. However, the data are not as Heimsch (1942) suggests. Heimsch (1942) reports scalariform perforation plates (bars 20 or fewer) in *Comocladia*, *Euroschinus*, and *Lithraea* (Anacardiaceae). The family with the most significant exceptions is Rutaceae, in which Metcalfe and Chalk (1950) report scalariform plates in at least some species of *Acronychia*, *Adenandra*, *Adiscanthus*, *Agathosma*, *Barosma*, *Boeninghausenia*, *Calodendrum*, *Clausena*, *Leptothrysa*, and *Paramignya*. Modified scalariform plates are reported by Metcalfe and Chalk (1950) in *Adiscanthus* and *Platydesma* (Rutaceae) and in *Ailanthus altissima* (Simaroubaceae) and some Aceraceae. *Billia* and *Aesculus* (Hippocastanaceae) are listed by them as having some scalariform perforation plates. All of the families just cited are included in the Rutales of Thorne (1992).

The axial parenchyma type (vasicentric scanty) and ray types (Heterogeneous Type IIA and IIB) in Sabiaceae are commonly found in families of Rutales, although one can certainly find these commonly outside of Rutales. Crystals in ray cells, found in some Sabiaceae, can also be found in at least some genera of Aceraceae, Anacardiaceae, Burseraceae, Cneoraceae, Fabaceae, Julianaceae, Moringaceae, Rutaceae, Sapindaceae, and Simarubaceae (Carlquist 1988). Silica bodies, seen in ray cells of four species of *Meliosma*, can be found in the rutalean families Anacardiaceae, Burseraceae, Fabaceae, Meliaceae, Rutaceae, and Simaroubaceae. The distinctive darkly staining deposits in ray cells or axial parenchyma seen in Sabiaceae are quite characteristic of woods of Anacardiaceae, Burseraceae, Rutaceae, and Sapindaceae, and may be found in other rutalean families. Thus, there seem to be multiple lines of evidence for inclusion of Sabiaceae in Rutales, but no line of evidence that would exclude Sabiaceae from Rutales.

Generic and Infrageneric Distinctions

The distinctness of *Sabia* is clear from the comments in Ecological Conclusions. Wood of *Ophiocaryon* has no features not also seen in *Meliosma*, but it is distinguishable in quantitative features. *Ophiocaryon* has notably large cell size; mean vessel diameter equals that of the species of *Meliosma* with widest vessels, and mean vessel density is lower than that reported for any *Meliosma* collection. The multiperforate perforation plates of *Ophiocaryon* are like those in a few species of *Meliosma*, such as *M. nitida* and *M. occidentalis*.

The perforation plates (simple or nearly so) and imperforate tracheary elements (fiber-tracheids rather than libriform fibers) in *Meliosma* subgenus *Kingsboroughia* sect. *Kingsboroughia* support Beusekom's (1971) recognition of that section. Beusekom regards that section as rich in primitive features for the family. Although the two species of that section studied here have fiber-tracheids, which are more

primitive than libriform fibers, they also have simple perforation plates, with scalariform plates in latewood of *M. veitchiorum*. More primitive wood structure is seen in species of *Meliosma* with both long scalariform perforation plates and fiber-tracheids, such as *M. glabrata* and *M. sumatrana*.

There is some confirmation from wood data for certain of Beusekom's groupings but not others. *Meliosma simplicifolia* has calcium oxalate crystals in rays; so do *M. fischeriana* and *M. rigida*, which Beusekom regards as subspecies of *M. simplicifolia*. However, *M. kirkii*, *M. macrophylla*, and *M. parviflora* also have such crystals in rays. Beusekom regards *M. macrophylla* and *M. kirkii* as subspecies of *M. pinnata*, but crystals were not observed in other taxa Beusekom regarded as subspecies of *M. pinnata*: *M. arnottiana*, *M. hachijoensis*, *M. oldhamii*, and *M. rhoifolia*. All of the taxa with crystals in rays belong to subgenus *Meliosma* sect. *Meliosma* in the Beusekom monograph, but they fall into different subsections and series.

Two of the species of *Meliosma* with silica bodies, *M. herbertii* (Puerto Rico) and *M. occidentalis* (southeastern Costa Rica and adjacent Panama) are New World species and belong in subgenus *Meliosma* sect. *Kingsboroughia*. However, the only other species in which silica bodies were observed is *M. dilleniifolia*, an Old World species in subgenus *Meliosma* sect. *Meliosma*.

Attention is drawn in the above discussion to "presence or absence" types of characters rather than characters that represent points along a continuum. The "presence or absence" characters offer the best chance for finding characters that would support or not support Beusekom's system. Features relating to ray histology have not been selected because ray histology does change during ontogeny (Barghoorn 1941). The presence of wide multiseriate rays in the taxa merged by Beusekom (1971) as *M. pinnata* subsp. *arnottiana* is suggestive of relationship, but one should know the relative size of stems before concluding that. The New World species other than *M. alba* fall into section *Lorenzanea*; this section is not distinct from the remainder of the genus in wood anatomy.

Beusekom (1971) justifies the recognition of few but polymorphic species by saying that *Meliosma* can self-pollinate, so that distinctive variants tend to develop readily. However, *M. alba* is a remarkably disjunct species, occurring in both Mexico and in Asia, apparently native in both, with no hint that long-distance dispersal has achieved this distribution: therefore, at least one pair of populations has been separated for a long period of time without developing distinctive features. Our material of *M. alba* comes only from Mexico, so we have no evidence from wood on this point.

Some of the characters observed in wood anatomy might, if an exhaustive survey of wood in the family were performed, prove to be correlated with species lines. However, the number of collections of this family is so small that development of any wood characters as species criteria would not be justified at present.

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FOOTNOTE

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