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WOOD AND STEM ANATOMY OF MENISPERMACEAE

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ABSTRACT

Qualitative and quantitative data are presented for 17 collections of 15 species representing 14 genera. One species is a shrub (*Cocculus laurifolius*), one a subshrub (*C. trilobus*), and the remainder are lianas. Successive cambia are analyzed with respect to ontogeny and histology of products. Whether any Menispermaceae may or may not plesiomorphically lack successive cambia would require a more extensive survey of the family. Apomorphic absence of successive cambia is likely for species with subshrub growth forms (*Cocculus trilobus*, *Menispermum canadense* L.). Lianoid Menispermaceae share the following features: successive cambia, wide vessels, wide rays, high conductive area per transectional unit area, and tracheids as imperforate tracheary elements. All of these features are more common in lianoid dicotyledons than in their nonlianoïd relatives. Vessels are solitary in the lianoid species on account of tracheid presence, but grouped in *Cocculus trilobus*, which has septate libriform fibers. Large multiseriate rays (combined with scarcity or absence of uniseriate rays) and storied structure of cambia (and cambial products that elongate little during maturation) characterize Menispermaceae and link the family to other families of Ranunculiflorae, as well as, in all likelihood, to the “paleoherb” families Aristolochiaceae, Lactoridaceae, Piperaceae, and Saururaceae.

Key words: Berberidales, cambial variants, lianas, Ranunculales, Ranunculiflorae, successive cambia.

INTRODUCTION

The significance of Menispermaceae in the phylogeny of Ranunculiflorae (variously known under the ordinal names Berberidales, Papaverales, and Ranunculales) is considerable because of particular character expressions in the family. Tracheids, regarded as the primitive type of imperforate tracheary element, are present in the vast majority of Menispermaceae. However, successive cambia, rather than the single cambium thought primitive in dicotyledons, also occur in the vast majority of Menispermaceae. Most Menispermaceae are woody lianas, but the family also contains shrubs, subshrubs, and even trees, and the relationships of wood anatomy to these growth forms is of interest. Wood anatomy may illuminate what the basic growth form of the family was. Habit and attendant features of wood anatomy are of significance in Ranunculiflorae, because phyletic constructions hypothesize several changes in degree of woodiness during phyletic evolution of Ranunculiflorae (e.g., Oganezowa 1975, Loconte and Estes 1989, Qiu et al. 1993), and these phylogenies do not agree with each other. In turn, Ranunculiflorae are often placed close to those families, such as Chloranthaceae, Piperaceae, etc., regarded as “paleoherbs” thought by some authors (e.g., Taylor and Hickey 1992) to be primitive in dicotyledons.

The wood anatomy or, considering that wood is only one product of the successive cambia, stem anatomy of Menispermaceae has never been surveyed in a monographic way. Only the very condensed summaries of Solereder (1908) or Metcalfe and Chalk (1950) serve as sources of information. Even data in pharmacological literature are so few as to be of little use (see Miller 1974). Lack of materials can be cited as a prime reason for the paucity of information: Menispermaceae are mostly lianas of tropical forests. Lianas are neglected (compared to trees) where wood sample collection is concerned: the soft tissues of lianas require greater effort for drying or for other methods of preservation, and tropical forests are more difficult of access and provide collecting difficulties (great height of canopy) in comparison to other plant associations. In addition, the family is not geographically localized; it occurs on all continents where rain forest occurs, as well as on major islands such as Madagascar and New Guinea (Diels 1910). The family is relatively large: most authors follow the estimate of about 65 genera and 350 species (e.g., Thorne 1992). Aside from a few minor pharmacological uses, the family has virtually no economic importance (Diels 1910). Thus, numerous circumstances have mitigated against collection of stem and root material, and samples in xylaria are remarkably few in number. A synoptical survey of woods of Menispermaceae is an interesting possibility for a future time when more collecting has been done.

Another reason for lack of studies on wood anatomy

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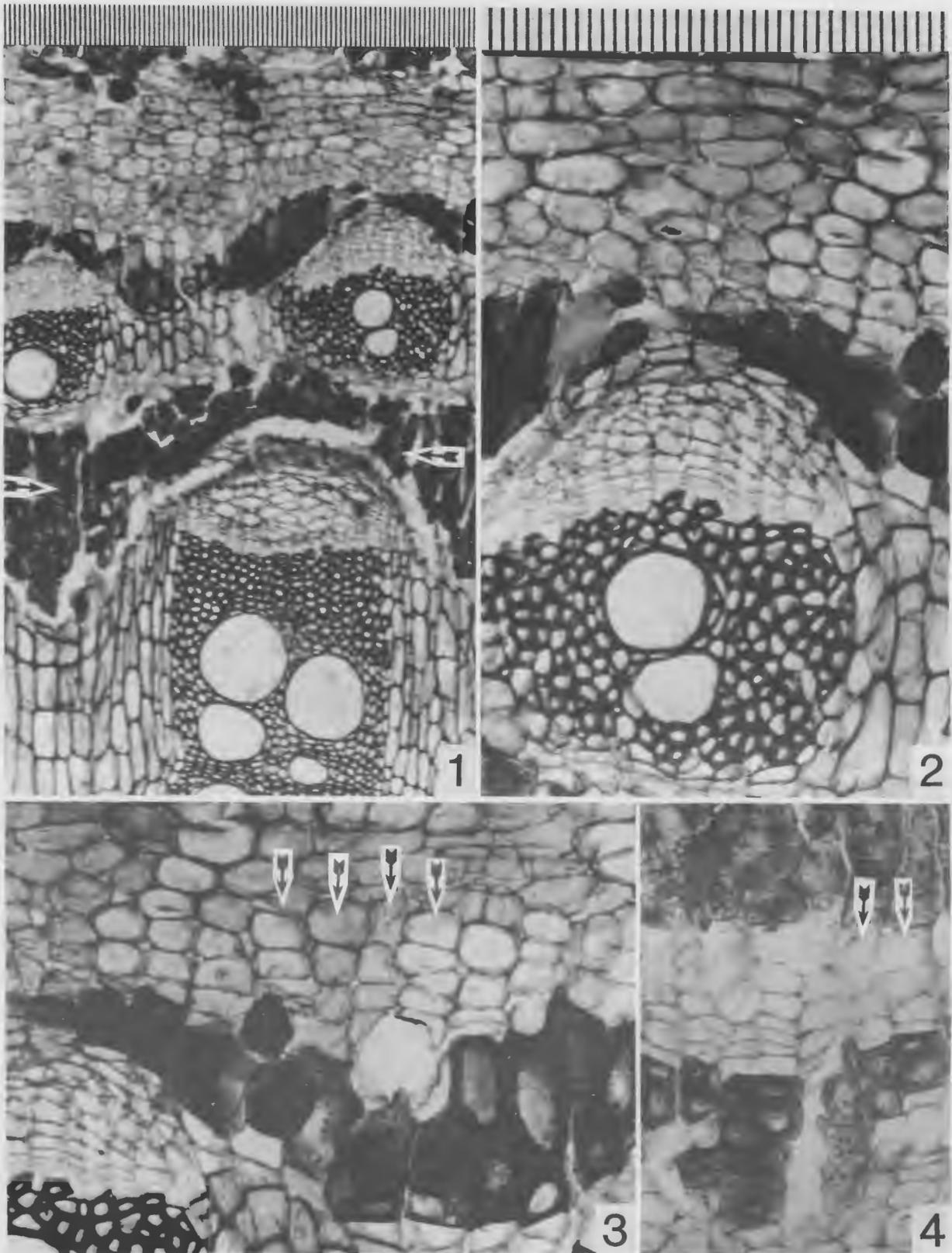


Fig. 1-4. Transection of outer portion of stem of *Hypserpa decumbens* to show histology and origin of meristematic activity.—1. Low magnification orientation photograph to show bark (top), vascular tissue formed from deactivated cambium (bottom), and vascular and ray tissue being formed from active cambium (center); arrows are embedded in sclerenchyma band of the conjunctive tissue.—2. Enlarged upper right portion of Fig. 1 photograph, to show exterior to (above) the dark sclerenchyma band (center), radial files that show activity of a meristem that produces conjunctive tissue.—3. Area to right of the zone shown in Fig. 2; the tangential continuity of the meristem (indicated by radial files of cells, four of which are indicated by arrows) producing conjunctive tissue is evident.—4. A portion of a

of Menispermaceae may be the microtechnical difficulty. Metcalfe and Chalk (1950) state that vessels in Menispermaceae fall in the small (50–100 μm) or medium (100–200 μm) category, but in fact, over half of the species studied here have vessels that are wider than 200 μm . Large vessels fracture easily when sectioned with a sliding microtome. Moreover, a sliding microtome tends not to produce good sections of materials in which very hard tissues, such as sclerenchyma bands in the conjunctive tissue of Menispermaceae, and soft tissues, such as the rays and phloem of the family, are intermixed. A recently devised technique (Carlquist 1982) has permitted good results with materials of this nature.

Some anatomical features in wood (e.g., ray histology, crystal distribution) offer promise for systematic anatomical studies of the family. The extremely small degree to which the family has been sampled in the present study merely exposes character state diversity without being able to cite how these character states may be distributed among genera and species. This, and the related matter of comparing anatomy to the full range of habits in the family, offer interesting challenges for future study.

Among Ranunculiflorae, Menispermaceae are unique in having successive cambia. This feature, although accurately presented by Pfeiffer (1926), requires further study. In the present study, an attempt is made to present ontogeny of this activity based on the few species in which suitable stages were visible.

The present paper is one of a series concerned with Ranunculiflorae. Other papers in the series include contributions on Lardizabalaceae (Carlquist 1984a), Papaveraceae (Carlquist and Zona 1988; Carlquist et al. 1994), Ranunculaceae and allied families (Carlquist 1995a), and Berberidaceae (Carlquist 1995b).

MATERIALS AND METHODS

All wood samples were available in dried form except for *Cocculus laurifolius*, stems of which were preserved in 50% aqueous ethanol. None of the wood samples studied was sectioned on a sliding microtome, because of problems in admixture of textures; these can be appreciated by viewing the sections in Fig. 1–4: cooccurrence of sclereids, thin-walled phloem, and wide vessels embedded in a background of tracheids provide exceptional difficulties. By softening the sclerenchyma and dense xylem with ethylenediamine, then embedding the stem portions in paraffin, cells are sup-

ported during the process of sectioning on a rotary microtome. This method has been described in detail earlier (Carlquist 1982), and includes some essential steps not mentioned in the present paper. Paraffin sections were stained in a safranin–fast green combination. A few sections were mounted on scanning electron microscope (SEM) aluminum stubs and examined with an ISI WB-6 SEM after paraffin had been dissolved. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Terminology follows that of the IAWA Committee on Nomenclature (1964), except for ray types and terms describing cambial variants, in which the usages of Carlquist (1988) have been followed. The concepts of successive cambia and conjunctive tissue are discussed in that reference. Means (Table 1) are based on 25 measurements except for pit diameter and wall thicknesses, where conditions deemed typical for a species have been recorded. Some vessels are markedly oval in transection, and either the narrow or the wide diameter is misleading. Therefore, a compromise diameter has been estimated for vessels that do not approach a circular outline closely.

Two xylaria contributed substantially to this study, and are acknowledged accordingly: the Forestry Commission of New South Wales (SFCw) and the Koninklijk Museum voor Midden Afrika, Tervuren, Belgium (Tw). The courtesy of Roger Dechamps at the latter institution in providing samples of lianas from Shaba, Central Africa, is gratefully acknowledged.

Localities for the specimens studied are as follows: *Abuta racemosa*, T. B. Croat 15109 (RSA), Barbour Trail, 2250', Barro Colorado Island, Panama; *Anamirta cocculus*, H. Cramer 3959 (RSA), On top of Elwagala Rock, Madegama, Kurunegala Dist, N. Central Sri Lanka; *Anamirta cocculus*, F. R. Fosberg 53157 (POM), 4 miles E of Bibile, Monaragala Dist., Sri Lanka; *Chasmathera welwitschii*, Tw-39939, Shaba, Central Africa; *Cocculus laurifolius*, cultivated at Pomona College, Claremont, California; *Cocculus trilobus*, Carlquist 8164 (RSA), among lava blocks above the beach, Makapuu Beach, E. Oahu, Hawaii; *Hypserpa decumbens*, SFCw-R1191-8, Queensland; *Legnephora moorei*, SFCw-R1211-30, Queensland; *Pachygone ovata*, SFCw-R1211-16, Queensland; *Pycnarrhena* sp., SFCw-R1191-27, Queensland; *Strychnopsis thouarsii*, C. E. Schatz & P. P. Lowry 2283, E. of Ambanizawa in hills above village, Masala Peninsula, Madagascar; *Tiliacora funifera*, Tw-29744, Shaba, Central Africa;

←

cambium that has formed in conjunctive tissue; outer conjunctive tissue is sclerenchyma (above), the sclerenchyma below is from the previous increment of conjunctive tissue; radially narrow cells in the radial files of cells (two radial files indicated by arrows) are the first indication of formation of xylem and phloem from cambium. (Fig. 1, magnification scale above Fig. 1 [divisions = 10 μm]; Fig. 2–4, magnification scale above Fig. 2 [divisions = 10 μm].)

Table 1. Wood characteristics of Menispermaceae.

Species	Collection	1 VG	2 VD	3 VR	4 VM	5 VL	6 VW	7 VP	8 TL	9 TW	10 TP	11 AP	12 MH	13 MW	14 CR	15 ME
<i>Abuta racemosa</i> (Thunb.) Triana	Croat 15109	1.20	164	120-212	16	325	3-6	5	1105	3	5	DA, V	>1000	7.2	rS	3373
<i>Anamirta cocculus</i> (L.) W. & A.	Cramer 3595	1.10	59	18-184	36	343	2-10	6	1217	5	5	A, DA	>1000	18.0	ArS	657
	Fosberg 53137	1.08	179	52-312	6	315	3-7	6	1107	3	5	A, DA, V	>5000	16.0	M	8810
	Tw-39939	1.24	324	47-437	5	269	5-10	8	941	3	8	A, D, V	>5000	>20	M	18,157
<i>Chasmanthera welwitschii</i> Treuf.	PRFw-11380	1.12	154	94-198	11	430	5-11	4	992	3	5	D, DA, V	>5000	16.8	AlrS	5860
<i>Cissampelos</i> sp.	cult. Claremont	1.04	62	35-92	253	248	2-3	6	999	4	5	DA, V	3786	10.4	AlrS	31
<i>Cocculus laurifolius</i> DC.	Tw-45068	2.93	28	7-64	128	236	2-5	3	432	2	1	V	1144	4.1	—	52
<i>C. trilobus</i> (Thunb.) DC.	Clarquist 8164	1.18	62	35-92	92	229	3-6	3	499	3	4	D, V	3081	11.2	RT	152
<i>Epinetrum excelsum</i> Treuf.	Tw-45068	1.18	62	35-92	92	229	3-6	3	499	3	4	D, V	3081	11.2	RT	152
<i>Hypserpa decumbens</i> Diels	SFCw R1191-8	1.03	153	32-270	9	373	3-7	4	1208	2	5	DA, V	>1000	10.2	S	6485
<i>Legnephora moorei</i> Miers	SFCw-R1211-30	1.00	263	187-364	7	483	5-10	7	1699	5	6	D, DA	>5000	28.5	Ar	17,642
<i>Pachygone ovata</i> (Poir.) Miers	SFCw-R1211-16	1.07	87	25-219	18	290	2-6	6	1040	3	5	DA, V	>1000	12.8	AR	1425
<i>Pycnarrhena</i> sp.	SFCw-1191-27	1.20	97	51-127	21	244	3-10	3	848	3	5	DA, V	3671	14.3	r	1155
<i>Strychnopsis thoursii</i> Baill.	Schatz 22832	1.05	104	52-208	70	270	2-3	3	758	5	3	DA, V	1040	17.8	R	402
<i>Telitoxicum krakovii</i>	PRFw-B6912	1.00	197	41-299	5	388	5-11	5	1426	4	6	D, DA, V	>5000	18.3	—	15,924
<i>Tiliacora funifera</i> (Miers) Oliv.	Tw-29774	1.03	98	41-173	14	308	3-7	5	893	4	6	D, DA, V	>1000	18.2	—	2203
	Tw-31260	1.13	76	41-184	18	276	3-6	5	792	5	6	D, DA	>1000	19.0	Ar	1185
<i>Tinospora ciffra</i> Miers	Tw-38214	1.55	210	83-416	5	234	5-10	10	743	3	10	D, V	>5000	>20	ARS	10,238
Lianoid Menispermaceae averaged		1.13	149		22	318		5	1018	4	6			17.1	MR	6245

Key to columns: 1 (VG), mean number of vessels per group; 2 (VD), mean diameter of vessel elements, μm ; 3 (VR), range in vessel diameters, μm ; 4 (VM), mean number of vessels per mm^2 ; 5 (VL), mean length of vessel elements, μm ; 6 (VW), range in vessel wall thickness, μm ; 7 (VP), vertical diameter of pit cavities, μm ; 8 (TL), mean length of imperforate tracheary elements, μm ; 9 (TW), thickness of wall of imperforate tracheary elements, μm ; 10 (TP), diameter of pit cavities of imperforate tracheary elements, μm ; 11 (AP), types of axial parenchyma present (A = apotracheal banded, D = diffuse, DA = diffuse-in-aggregates, V = scanty vascentric); 12 (MH), mean height of multiseriate rays, μm ; 13 (MW), mean width of multiseriate rays, cells; 14 (CR), crystal distribution (A = axial parenchyma, I = inner conjunctive tissue, M = marginal ray cells, r = some ray cells, R = virtually all ray cells, S = sclerenchyma of conjunctive tissue); 15 (ME), Mesomorphy ratio (mean vessel diameter times mean vessel element length divided by mean number of vessels per mm^2).

Tiliacora funifera, Tw-31260, Shaba, Central Africa;
Tinospora caffra, Tw-29714, Shaba, Central Africa.

ANATOMICAL RESULTS

Successive Cambia

Metcalf and Chalk (1950) have characterized the phloem produced by variant cambial activity in Menispermaceae as "included (interxylary) phloem." As several authors have noted, "interxylary" phloem is a misnomer for what we see in Menispermaceae, because the phloem is located not *within secondary xylem*, but *within conjunctive tissue*. Conjunctive tissue is tissue produced internally from a meristem located near the periphery of a stem. Cambia, and vascular tissue produced by those cambia, develop within conjunctive tissue (Fig. 1–4). The term successive cambia is therefore the appropriate one; this term is equivalent to the term "sukzessive Zuwachsringe" used by Pfeiffer (1926). The term "successive cambia" is now becoming more common in the literature. It is the only accurate term for the variant cambial activity type observed in Menispermaceae. The term "interxylary phloem distributed in a concentric fashion" has also been used, but is erroneous, because the phloem is not embedded within xylem in this case. "Interxylary phloem" does exist, but is produced by an entirely different type of cambial activity: production of phloem strands internally from a single cambium that also produces secondary xylem internally (e.g., *Strychnos*, Onagraceae, etc.). Accurate terminology is based on ontogenetic studies, which leads some wood anatomists to believe the newer terms cannot be used if they study only mature structure. Mature structure of stems with cambial variants is quite adequate for applying accurate terms, however, because the ontogeny can almost always be detected from the mature structure.

In most Menispermaceae, as in *Hypserpa decumbens* (Fig. 1–4) or *Pachygone ovata* (Fig. 16), the innermost portion of each increment of conjunctive tissue consists of thin walled parenchyma, whereas the outer portion consists of sclerenchyma, often brachysclereids with extremely thick walls. The sclerenchyma associated with the first cambium may contain proto-phloem fibers, but the sclerenchyma associated with subsequent cambia lacks any phloem fibers. The sclerenchyma begins to differentiate before xylem and phloem are produced by a cambium (Fig. 1–4, 8). The outer face of the sclerenchyma band demarcates the products of a given cambium, and should be designated as one kind of conjunctive tissue, at least in tissue produced by all cambia after the first cambium.

Radial files of thin-walled cells often can be found outside of the sclerenchyma of the most recently formed conjunctive tissue (Fig. 1, right; Fig. 3, indicated by arrows). These radial files indicate action of

a meristem that produces meristematic conjunctive tissue. The radial files in this position are not in evidence at all times: the meristematic action is quiescent much of the time, and radial files are evident at times when the meristem is producing conjunctive tissue.

Within the meristematic conjunctive tissue, the first steps in production of a vascular cambium are evident when radially narrow cells are produced (Fig. 4; Fig. 8, lower right). These divisions appear to occur in localized pockets, because divisions leading to ray cells are few compared to those that are forming fascicular tissue.

The duration of each cambium varies within the family. In *Cocculus laurifolius*, a cambium may produce more than one cm of secondary xylem, but in other Menispermaceae, only 1–2 mm may be produced by a given cambium (Fig. 5). In some Menispermaceae, only a single cambium has been reported (Solereder 1908). In several species with only a single cambium, such as *Cocculus trilobus* and *Menispermum canadense*, stems (and roots) are relatively small and finite in duration, so that reduced size may be associated with formation of only a single cambium. Other species in the list for which no more than one cambium has been formed (given in Metcalf and Chalk 1950), may have been studied on the basis of small stems, even stems from herbarium material. These stems may be too small for a second cambium to have developed. Some fairly large stems (e.g., *Legnephora moorei* in the present study, a sample 3 cm in diameter) may show products of only a single cambium. There is a possibility that some species of Menispermaceae that form large lianas or even shrubs or trees may never develop a second cambium. Because there are over 300 species of lianoid Menispermaceae, this possibility cannot be eliminated easily. Basal stems are best for demonstrating whether more than one cambium forms, but cutting the basal portions of a liana, shrub, or tree is likely to be regarded as excessively destructive. However, any worker able to locate a large stem (or root) of Menispermaceae in which only a single cambium has operated should report it.

One might be tempted to think that a growth ring ought to terminate with the cessation in function of one cambium, and that earlywood of the next season begins with the secondary xylem production of the next cambium. Although this is a possibility, one can find evidence in Menispermaceae (as well as in some other families with successive cambia) that a growth ring can terminate and a new one begin within the secondary xylem produced by a particular cambium. In many Menispermaceae, growth rings likely never form because temperature and moisture availability are relatively uniform throughout the year. Formation of growth rings was noted in *Pycnarrhena* sp. (Fig. 9),

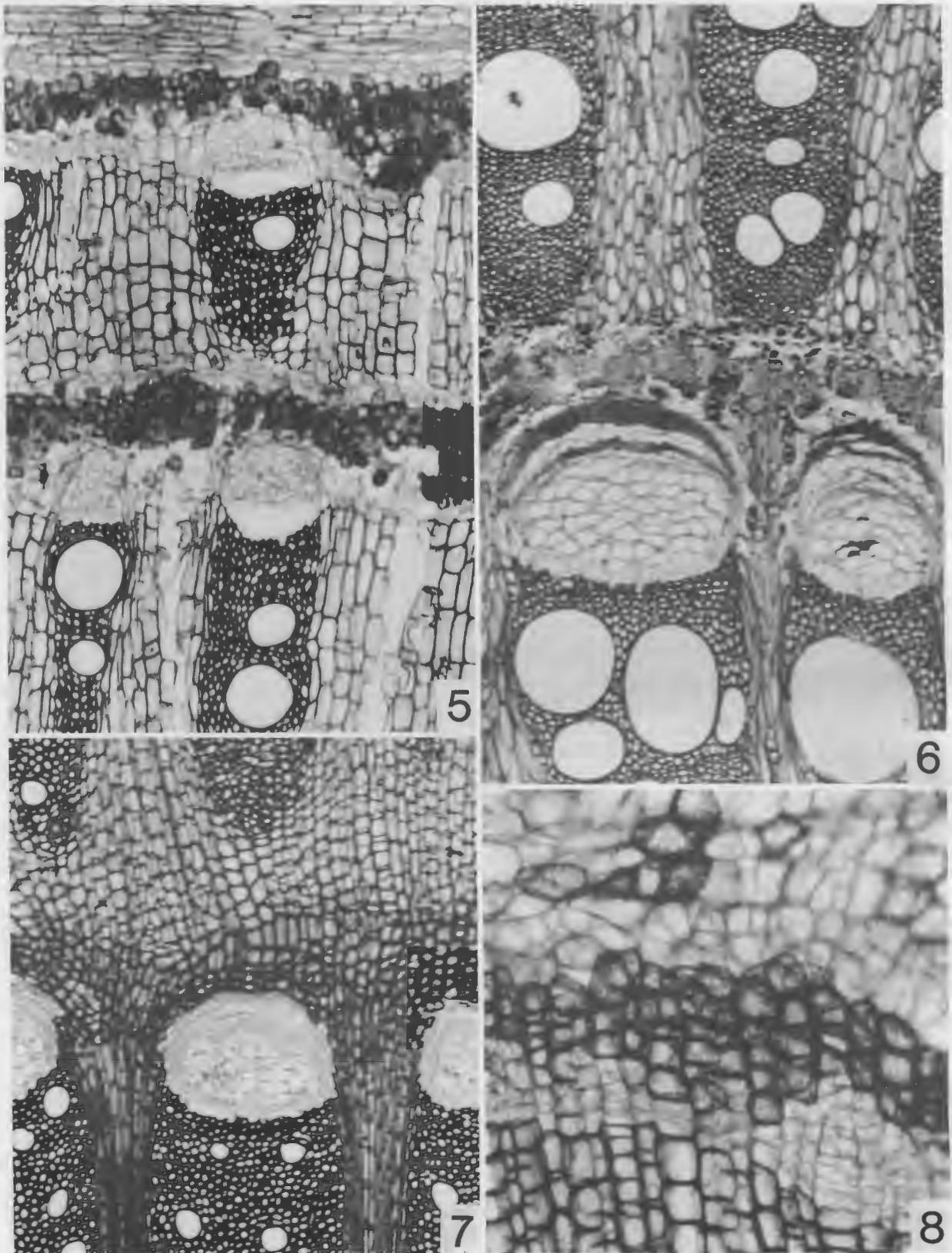


Fig. 5-8. Transections of stems of Menispermaceae to show products of successive cambia.—5. *Tiliacora funifera*, products of two successive cambia; sclerenchyma is the outermost in each increment of conjunctive tissue.—6. *Abuta racemosa*, portions of tissue produced from two successive cambia; crystal-containing sclerenchyma, center; more recently formed secondary phloem has compressed earlier formed secondary phloem.—7-8. *Cocculus laurifolius*.—7. Vascular tissue from successive cambia; note narrowness of vessels.—8. Active cambium (thin-walled cells near bottom) near periphery of stem; the portion of the cambium at lower right corner of photograph is forming cells that will become xylem and phloem. (Fig. 5-7, scale above Fig. 1; Fig. 8, scale above Fig. 2).

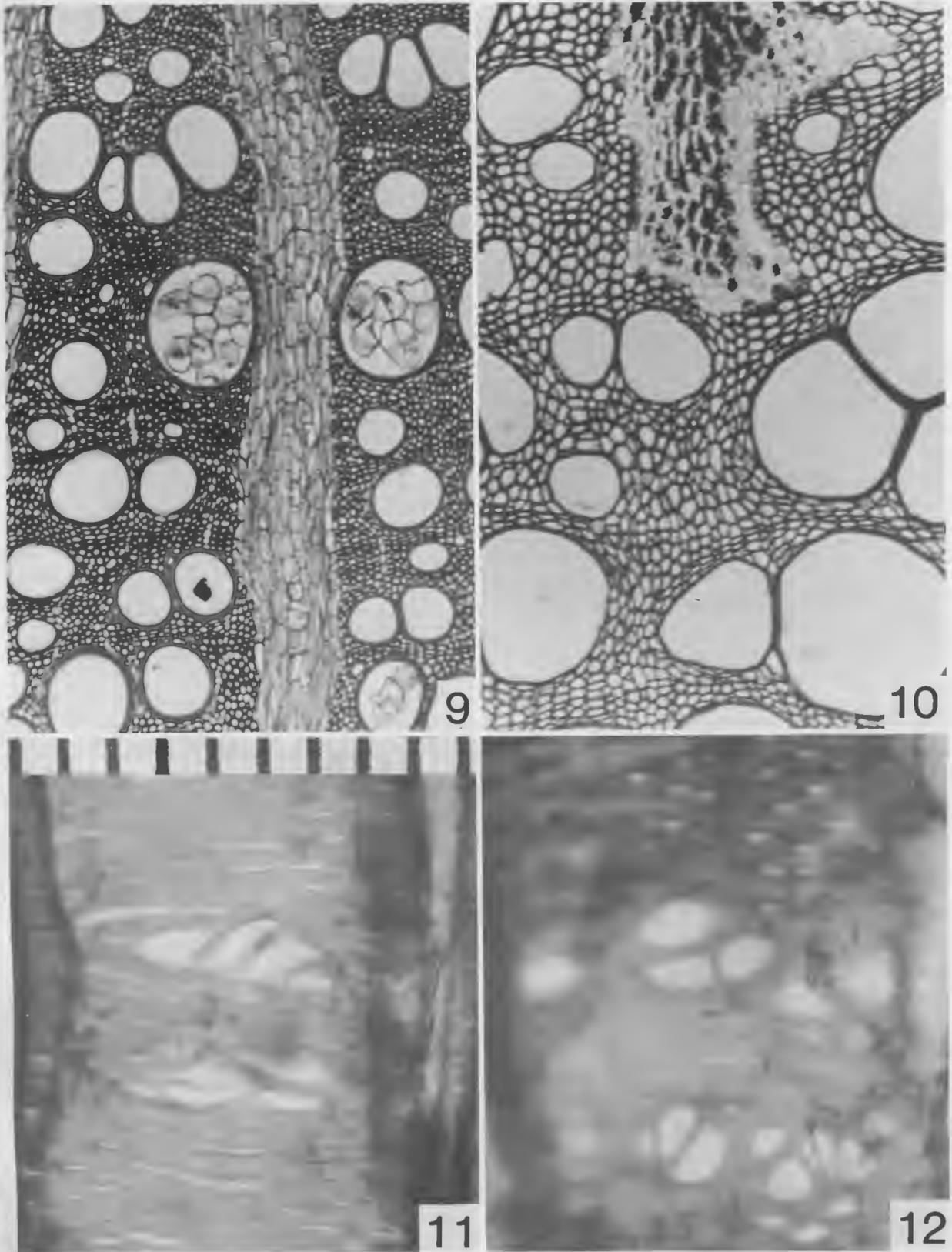


Fig. 9–12. Details of secondary xylem of Menispermaceae.—9. *Pycnarrhena* sp., transection; tyloses present in earlywood (just above center); ray cells thin walled.—10. *Tinospora caffra*, transection, wide multiserial ray (top center) originates suddenly rather than gradually from a narrower ray.—11–12. Portions of vessels from tangential sections; in each, the juncture between two vessel elements lies between the groups of enlarged pits.—11. *Pycnarrhena* sp., enlarged pits have tapering ends; elongate grooves interconnecting pit apertures occur above and below the enlarged pits.—12. *Anamirta cocculus*, enlarged pits with rounded forms. (Fig. 9, 10, scale above Fig. 1; Fig. 11, 12, scale above Fig. 11 [divisions = 10 μ m].)

in which narrow vessels (latewood) are followed by large vessels that contain tyloses (earlywood).

Vessel Elements

In most Menispermaceae, vessels are mostly solitary (Fig. 1, 5, 6, 7, 9, 10, 15, 16), although in many of the species, small groups of vessels are visible occasionally in transections (Fig. 9, 10). If one calculates the mean number of vessels per group, one finds that species other than *Cocculus trilobus* have figures that range from 1.00 to 1.55 vessels per group. In two species, *Legnophora moorei* and *Telitoxicum krukovii*, no grouped vessels were observed. In some Menispermaceae where grouped vessels were observed, a few intervening cells, crushed or pushed aside during vessel enlargement, may have separated vessels earlier in ontogeny. Consequently, one must be careful in designating vessels as grouped. Even discounting this possibility, the large diameter of vessels in Menispermaceae would lead to occasional contacts if vessels are distributed randomly. Nevertheless, the figure for vessel grouping in Menispermaceae other than *Cocculus trilobus* is very low. The Menispermaceae other than *C. trilobus* have tracheids as imperforate tracheary elements, whereas *C. trilobus* has septate libriform fibers. Thus, Menispermaceae conform to the principle enunciated earlier (Carlquist 1984b) that vessels are not grouped in species that have tracheids as the imperforate tracheary element type. In such woods, tracheids serve as an excellent subsidiary conductive system, more effective in maintaining conductive pathways when vessels embolize than the strategy of grouped vessels would be. Where libriform fibers or fiber-tracheids are present instead of tracheids, as in *Cocculus trilobus*, no conductively effective imperforate tracheary element is present and grouping of vessels does enhance conductive safety. In species with fiber-tracheids or libriform fibers, degree of grouping of vessels is proportional to dryness of locality (Carlquist 1984b). *Cocculus trilobus* grows in relatively dry lowland areas, notably on lava flows.

Mean vessel diameter (Table 1, column 2) is rather great in Menispermaceae. Range in vessel diameter (Table 1, column 3) is also presented as a way of showing that relatively narrow vessels and very wide vessels accompany the vessels close to median diameter in any given species. Very wide vessel elements are usually wider than they are long, as seen in macerations. Although Metcalfe and Chalk (1950) report that vessels in Menispermaceae range from small (50–100 μm) to medium (100–200 μm) in diameter, three species exceed the medium range in mean diameter (*Chasmanthera welwitschii*, *Legnophora moorei*, and *Tinospora caffra*), whereas one species falls short of the small diameter category (*Cocculus trilobus*). If one

takes into account the range in diameter, nine of the species studied have vessels less than 50 μm in diameter, and nine species have vessels wider than 200 μm in diameter (Table 1, column 3).

Vessel density (Table 1, column 4) is generally considered to vary inversely with vessel diameter, and one can say that this operates in Menispermaceae, but the vessel density is a little higher than one would expect in tree species that have similar vessel diameters (see Carlquist 1975). The mean vessel density for lianoid Menispermaceae (22 vessels per mm^2) is much lower than what one would find for shrubs. The shrub *Cocculus laurifolius* and the subshrub *C. trilobus* have vessels much more numerous per mm^2 than in any of the lianas.

Mean vessel element length (Table 1, column 5) varies relatively little in Menispermaceae, regardless of habit: the range is from 229 μm to 430 μm (these extremes both in lianoid species). Possible interpretations of vessel element lengths in comparison to those of other families of Ranunculiflorae are given below.

Vessel wall thickness varies considerably, depending on vessel diameter: a range, rather than a mean, is given in Table 1, column 6. Thicker walls are invariably found in wider vessels. This phenomenon may be seen in Fig. 15–16. The tendency of notably wide vessels to be thicker walled has received comment earlier (Carlquist 1975).

No scalariform perforation plates have been observed in secondary xylem of Menispermaceae by earlier workers (Solereider 1908; Metcalfe and Chalk 1950), and only simple perforation plates were observed in the present study. However, Bierhorst and Zamora (1965) report both scalariform and simple perforation plates in the primary xylem of *Anamirta cocculus*, *Cocculus laurifolius*, *Stephania japonica* (Thunb.) O. Kuntze, and *Tinospora rumphii* Boerl.

Exceptionally wide pits that may remind one of perforations occur near the ends of vessel elements in many Menispermaceae (Metcalfe and Chalk 1950). Such large pits are shown here for *Pycnarrhena* sp. (Fig. 11) and *Anamirta cocculus* (Fig. 12). No such pits were observed in *Cocculus trilobus*; the large pits vary in size, shape, and abundance in the remaining species. I know of no similar pitting dimorphism in vessels of other dicotyledonous families. Careful examination of wood longisections showed that the large pits represent vessel-to-axial parenchyma contacts. The parenchyma cells related to these large pits appear often to be short and distorted in shape compared with strands of axial parenchyma elsewhere in the woods (such parenchyma cells are not shown in Figs. 11 and 12).

Vessel-to-tracheid pits are oval to broadly elliptical in outline and alternate in arrangements (Fig. 13). The vertical dimensions of these pits are given in Table 1,

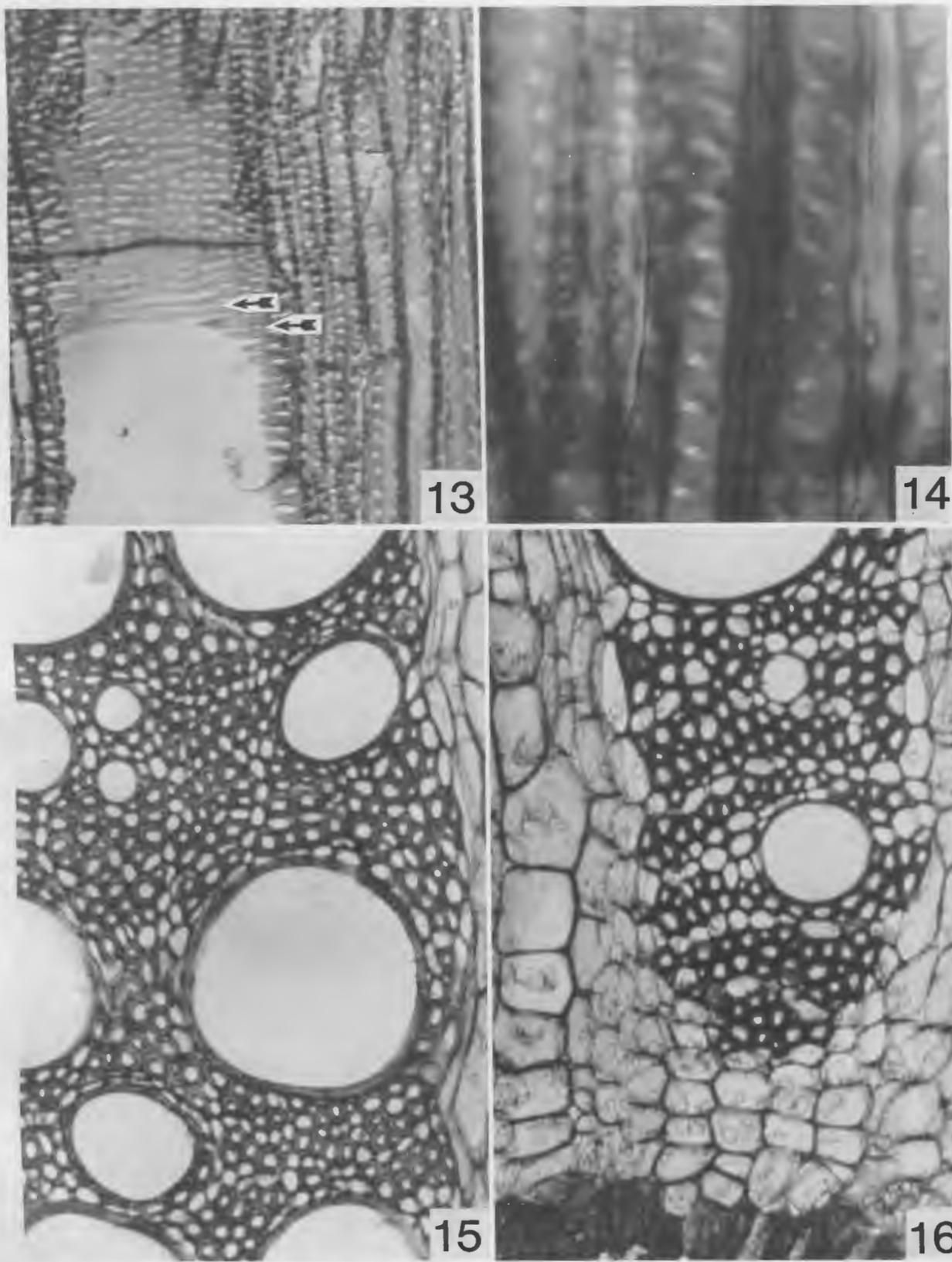


Fig. 13-16. Sections of Menispermaceae stems to show details of secondary xylem.—13. *Tinospora caffra*; tangential section to show portion of a vessel (pitting is alternate) and, axial parenchyma walls; two small portions of grooves interconnecting pit apertures indicated by arrows, although evidence for this phenomenon is much more extensive than shown in this photograph.—14. *Anamirta cocculus*; portion of tangential section to show tracheids with large, densely placed, bordered pits.—15. *Tiliasporea funifera*, transection with solitary vessels of various sizes; axial parenchyma is diffuse, diffuse-in-aggregates, and vasicentric.—16. *Pachygone ovata*, transection; ray (left) and inner conjunctive tissue (near bottom) contain crystals; axial parenchyma is diffuse-in-aggregates. (Fig. 13, 15, 16. magnification scale above Fig. 2; Fig. 14, scale above Fig. 11.)

column 7. Vessel-to-tracheid pits appreciably larger than the mean for the family are present in *Legnophora moorei* and especially *Tinospora caffra* (Fig. 13). Grooves interconnecting pit apertures ("coalescent pit apertures" of some authors) were observed in all Menispermaceae studied except for *Cocculus laurifolius*, *Epinetrum excelsum*, *Hypserpa decumbens*, and *Telotoxicum krukovii*. Long grooves can be seen in a few species, and are shown here for *Pycnarrhena* sp. (Fig. 11) and *Tinospora caffra* (Fig. 13, center of lower vessel element). Only short grooves interconnecting two or three pit apertures were observed in *Anamirta cocculus*, *Cissampelos* sp., *Pachygone ovata*, and *Strychnopsis thouarsii*. Striae on sparsely pitted portions of vessel walls in addition to grooves interconnecting pit apertures were observed in *Tiliacora funifera* (Tw-29744).

Imperforate Tracheary Elements

The Menispermaceae studied divide into two groups with respect to imperforate tracheary elements: *Cocculus trilobus* has libriform fibers, whereas the remainder of the species have tracheids. The libriform fibers of *C. trilobus* are septate and have slitlike pits with apertures 1–2 μm long. The tracheids in the other species are rarely septate (a few septate tracheids were noted in *Chasmanthera welwitschii* and *Tiliacora funifera*) and have the large, densely placed, circular bordered pits (shown for *Anamirta cocculus* in Fig. 14) characteristic of tracheids in the usage of the IAWA Committee on Nomenclature (1964).

Mean length of imperforate tracheary elements (Table 1, column 8) ranges in the species studied from 432 μm (*Cocculus trilobus*) to 1217 μm (*Anamirta cocculus*). Note should be taken that the shortest libriform fibers occur in a small subshrub.

Imperforate tracheary element wall thickness tends to be less than vessel wall thickness for any given species (Table 1, column 9). The range, from 1.5 to 5 μm , does not reveal that most imperforate tracheary elements tend to deviate little from the mean wall thickness for the species studied, 3.6 μm . The tracheids of *Chasmanthera welwitschii* (Fig. 20) are obviously wider and thinner walled than those of *Pycnarrhena* sp. (Fig. 15) or *Pachygone ovata* (Fig. 16).

Pit diameter of imperforate tracheary elements (Table 1, column 10) is relatively uniform in the family, deviating little from the mean diameter (5.6 μm) except for *Cocculus trilobus*, the only species with libriform fibers, and *Tinospora caffra*, in which the pit cavities on tracheids are 10 μm in diameter. The tracheids of Menispermaceae have pits of roughly the same diameter as those of vessels in any given species. This is not surprising in view of the fact that many of the pits on vessel walls interconnect with tracheid pits.

Axial Parenchyma

Of the distributions of axial parenchyma in Menispermaceae studied (Table 1, column 11), diffuse-in-aggregates is the most common type. Diffuse-in-aggregates may be seen here most clearly in the transections of *Hypserpa decumbens* (Fig. 2) and *Pachygone ovata* (Fig. 16). As shown in Table 1, column 11, a scattering of diffuse axial parenchyma cells was observed in seven of the species studied.

Scanty vascentric axial parenchyma (an incomplete sheath one to two cells thick around vessels) was observed in 12 of the species studied. In designating a species as having scanty vascentric axial parenchyma, I attempted to exclude instances in which a band of diffuse-in-aggregates intersected a vessel. Thus, the instances I cite as vascentric represent axial parenchyma somewhat more abundant adjacent to vessels than what would be expected on the basis of random contacts of diffuse-in-aggregates with vessels. *Cocculus trilobus* has only vascentric axial parenchyma.

Some instances of apotracheal banded axial parenchyma were observed (Table 1, column 11). Such banded parenchyma is shown here for *Chasmanthera welwitschii* (Fig. 20). The cells of the band adjacent to rays have thin nonlignified walls like those of the ray cells, whereas the apotracheal parenchyma cells farther away from the rays have somewhat thicker lignified walls. Although Metcalfe and Chalk (1950) reported diffuse-in-aggregates and diffuse axial parenchyma for the family, they did not record apotracheal banded or paratracheal patterns for the family.

Strands of axial parenchyma are composed of relatively few cells: as few as two, as many as five vertically superposed cells. Species in which strands are most commonly composed of two cells include *Abuta racemosa*, *Chasmanthera welwitschii*, *Cissampelos* sp., *Hypserpa decumbens*, and *Tiliacora funifera*. Strands of three cells predominate in *Anamirta cocculus*, *Cocculus laurifolius*, *C. trilobus*, *Epinetrum excelsum*, *Legnophora moorei*, *Pachygone ovata*, *Pycnarrhena* sp., and *Telotoxicum krukovii*. Strands of four cells predominate in *Tinospora caffra* (Fig. 13); strands of five cells characterize *Strychnopsis thouarsii*.

Rays

Vascular rays are multiseriate or nearly so in most Menispermaceae. Uniseriate rays were observed in appreciable numbers only in *Anamirta cocculus* (Cramer 3595), in which the mean height of uniseriate rays is 123 μm . Multiseriate rays in the family are notably tall (Table 1, column 12). In tangential sections, most rays are not included in their entirety. If virtually no rays are included in their entirety in a tangential section, the ray height is indicated as >5000 μm . If about

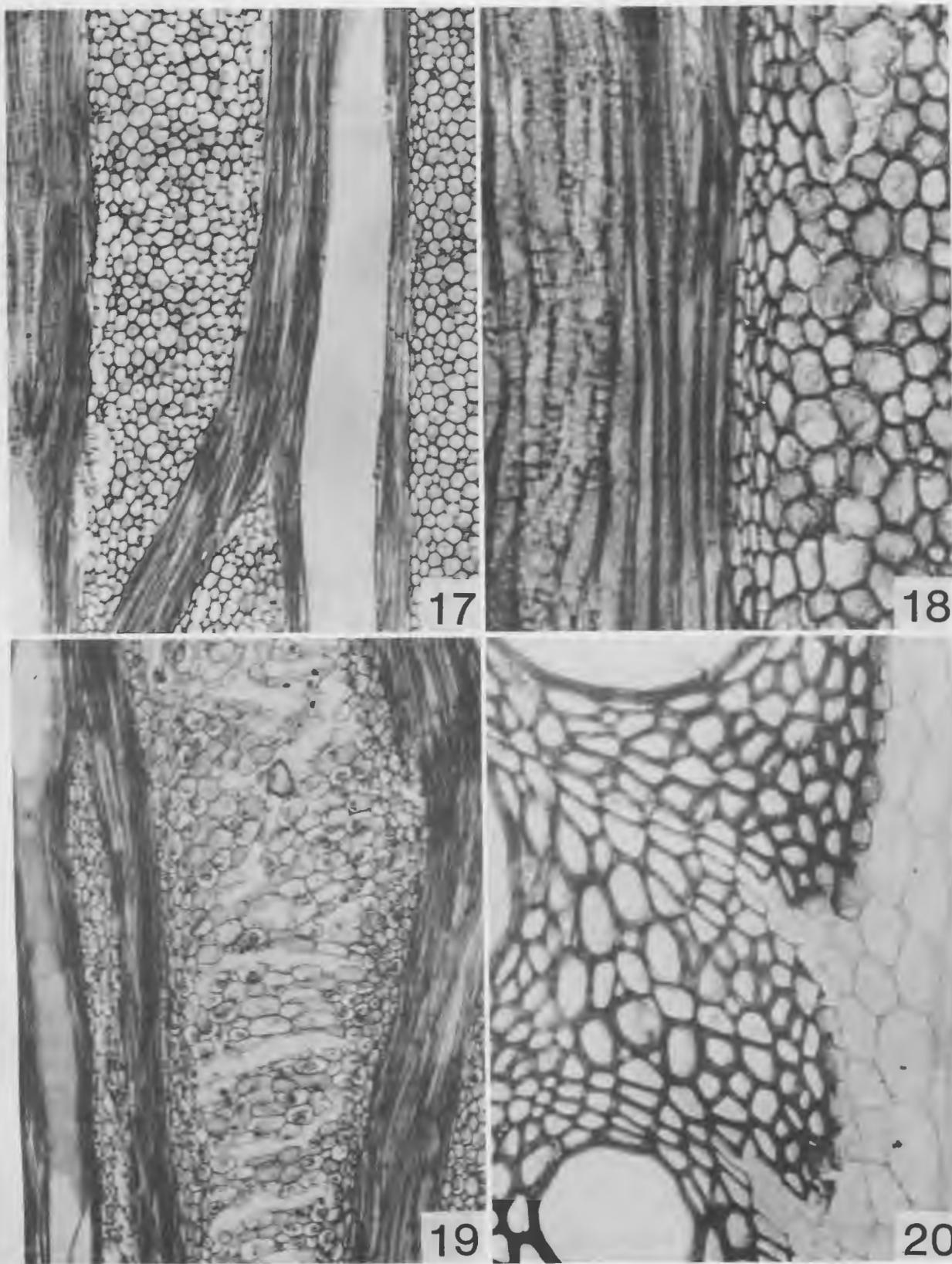


Fig. 17-20. Sections of secondary xylem of Menispermaceae to show ray features.—17. *Tiliacora funifera*, tangential section, wide, tall rays with very few upright sheathing cells.—18. *Pachygone ovata*, tangential section, ray at right; the narrow cells that sheathe the ray are upright ray cells.—19. *Pycnarrhena* sp., tangential section to show a ray that has widened by means of radial longitudinal cell divisions.—20. *Chasmathera welwitschii*, transection; two bands of apotracheal parenchyma in fascicular xylem, cells of which are thin walled where they intersect with the ray right); a single layer of crystal-containing cells sheathes the ray. (Fig. 17, 19, scale above Fig. 1; Fig. 18, 20, scale above Fig. 2.)

half of the rays were included within a section, ray height is expressed as $>1000 \mu\text{m}$. If one measures only rays included within a section that also has rays not completely within the section one obtains a mean that is skewed downward. Accurate determination of ray height in a species with such tall rays could be accomplished only by exposing a large tangential surface of a secondary xylem portion of a stem and measuring rays as seen in gross aspect.

Multiseriate rays in Menispermaceae are exceptionally wide (Fig. 17), except for *Cocculus trilobus* (Table 1, column 13). Multiseriate rays are composed mostly of procumbent cells (Fig. 17, 18) except for *Cocculus trilobus*, in which ray cells are upright. Rays in that species can be referred to Paedomorphic Type II (Carlquist 1988). In the remaining species, predominance of procumbent cells brings rays closest to Homogeneous Type II of Kribs (1935). Ray cells much larger in the central portion of rays than in the ray margins were observed in *Pachygone ovata* (Fig. 18). Relatively few upright sheath cells on rays were observed in *Anamirta cocculus* (Fosberg 53137), *Hypserpa decumbens*, and *Pycnarrhena* sp. One to two layers of sheath cells characterize rays of the remaining species other than *Cocculus trilobus*. If the upright sheath cells of rays are relatively abundant, as in the rays illustrated for *Pachygone ovata* in Fig. 18, the ray can be considered transitional between Homogeneous Type II and Paedomorphic Type II. Such rays can be found commonly in a scandent genus of Ranunculaceae, *Clematis* (Carlquist 1995a).

Radial longitudinal division of ray cells, resulting in lateral expansion of rays, were observed in large multiseriate rays of *Pycnarrhena* sp. (Fig. 19). These radial longitudinal divisions are visible in both transverse and tangential sections. Such divisions were not observed in rays of the other species examined.

Ray cells of most species studied had lignified walls about $2 \mu\text{m}$ in thickness (Fig. 1, 2, 5, 6, 7, 9, 15, 16, 18). Thinner, nonlignified cells were observed in *Anamirta cocculus*, *Chasmanthera welwitschii*, *Cissampelos* sp., *Pachygone ovata*, and *Pycnarrhena* sp. (Fig. 17). In the species with thicker, lignified walls, the sparseness of pits, compared to density typical for dicotyledonous rays, was apparent. Inconspicuous borders (as seen in sectional views of the pits) were also visible in ray cells of the species with thicker ray cells.

In two species, distinctive crystal-containing cells occur as sheath cells of the rays. In *Chasmanthera welwitschii* (Fig. 20), these sheath cells contain one crystal each, and the ray cell wall facing the fascicular tissue is thick and lignified, whereas the other walls of these ray cells are thin and nonlignified. In *Tinospora funifera* (Fig. 23), ray cells adjacent to fascicular tissue have several crystals each, but have the wall facing fascicular tissue thick and lignified, as in *Chasmanth-*

era welwitschii. These crystal-containing cells are reminiscent of the cristarque cells, except that cristarque cells contain druses rather than single crystals (see Metcalfe and Chalk 1950, Fig. 77F). Cristarque cells occur on leaf veins in a trio of related families, Ochnaceae, Quinaceae, and Scytopetalaceae (Metcalfe and Chalk 1950), and have also been reported in Balanopaceae (Carlquist 1980).

Bands of sclerenchyma form the outer portion of each increment of conjunctive tissue in most species (Fig. 1–4, 5, 6, 8). In some species such as *Abuta racemosa*, the sclerenchyma of the conjunctive tissue may extend inward radially as plates that occur within rays. Sclereids seen in rays of Menispermaceae should be referred to this phenomenon unless there is no connection between the conjunctive tissue sclerenchyma and the ray sclerenchyma.

Because the duration of each cambium is relatively brief, very few new rays originate during the functioning of a cambium. However, in *Tinospora caffra* (Fig. 10, top), one can see the origin of large multiseriate rays. In most dicotyledons, large secondary rays originate by widening, over time, of narrower rays—even uniseriate rays may represent a point of origin. Aggregate rays represent an alternative mode of origin of a wide multiseriate ray. However, in *Tinospora caffra*, the origin is abrupt, with no antecedent ray. Abrupt origin of multiseriate rays has also been demonstrated in lianoid Aristolochiaceae (Carlquist 1993) and in the scandent genus *Clematis* of the Ranunculaceae (Carlquist 1995a).

Tyloses

Tyloses were observed in *Abuta racemosa*, *Anamirta cocculus*, *Epinetrum excelsum*, *Hypserpa decumbens*, *Pycnarrhena* sp. (Fig. 9), *Telotoxicum krukovii*, and *Tiliacora funifera*. In *Epinetrum excelsum* and *Hypserpa decumbens*, some of these tyloses have thick, lignified cell walls. Tyloses that originate via the enlarged pits at the ends of vessel elements were observed in *Pycnarrhena* sp.

Storied Structure

Where tangential sections of secondary phloem were visible on tangential sections of stems of Menispermaceae (e.g., *Anamirta cocculus*, *Tiliacora funifera*), sieve-tube elements are invariably storied. Tracheids as seen in tangential sections rarely appear storied, although storied tracheids were observed in *Anamirta cocculus* (Fosberg 53137). The storied nature of secondary phloem is explained by the presence of a storied cambium (storied fusiform cambial initials), combined with lack of elongation of sieve-tube elements as they mature. Tracheids elongate greatly during maturation—they average 3.2 times the length of

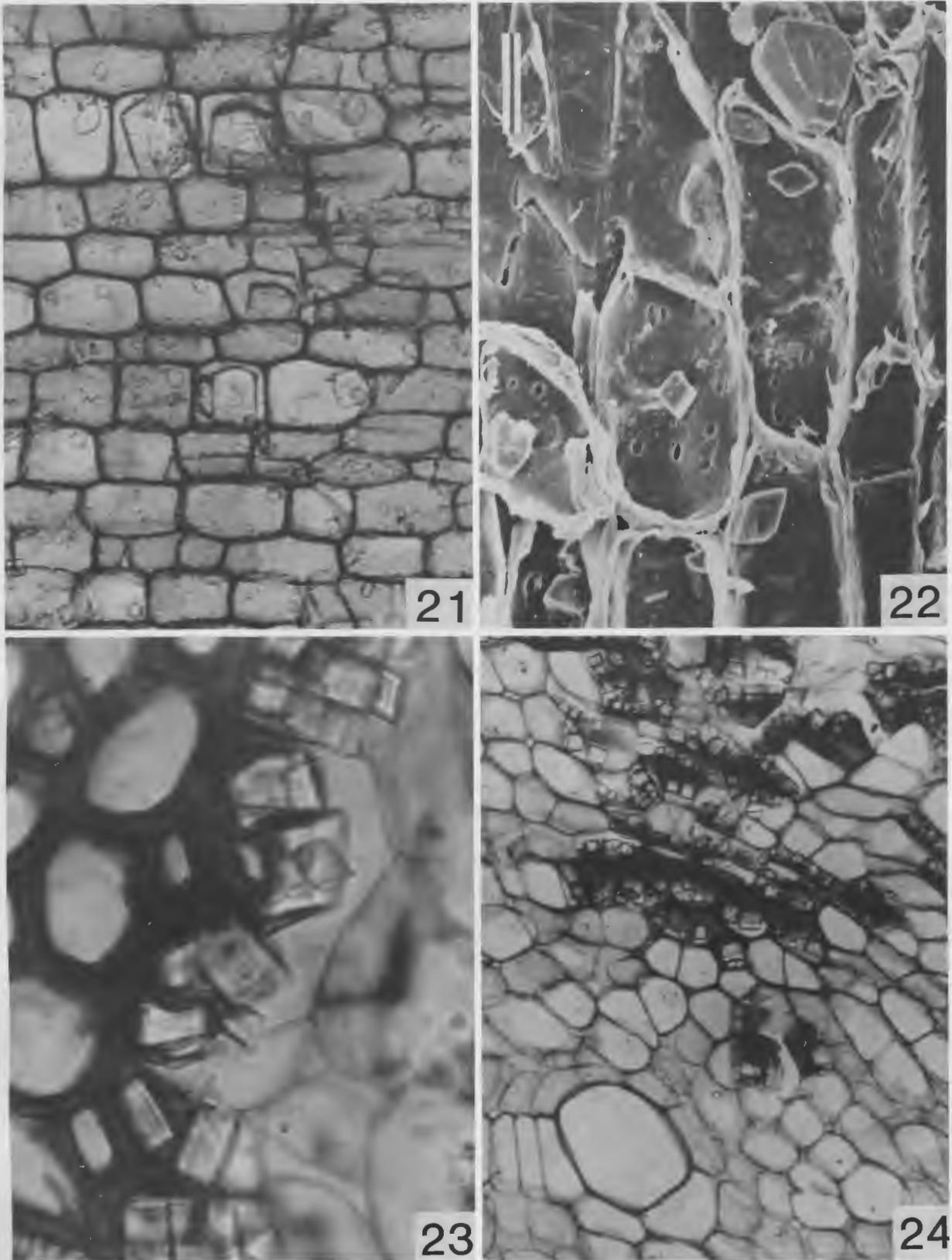


Fig. 21–24. Sections of stems of Menispermaceae to show crystals.—21. *Pachygone ovata*, radial section; ray cells contain crystals of various sizes.—22. *Tiliacora funifera*, SEM photograph of ray in tangential section; relatively small rhomboidal crystals are present.—23–24. *Tinospora caffra*, stem transections.—23. Crystal-containing cells (likened to cristarque cells in the text) form a single layer on outer surface of ray; fascicular cells in transection (tracheids) at left.—24. Cortex (bark tissue); laticiferlike secretory cell, lower left; upper right, extensive nest of crystal-containing cells in which some walls are thin, but in which one or more wall is thick and lignified. (Fig. 21, 24, scale above Fig. 2; Fig. 23, scale above Fig. 11; Fig. 22, 10 μ m scale bar at upper left.)

vessel elements in lianoid Menispermaceae. Vessel elements are approximately the same length as fusiform cambial initials, and show relatively little elongation during maturation. If the average elongation of a tracheid is 3.2 times the length of a fusiform cambial initial, there is considerable deviation—different tracheids will elongate to different degrees. Therefore, even though fusiform cambial initials are storied, tracheids rarely show storying. Because vessel elements do not elongate appreciably during maturation, one would expect that they should show storying, as they often do in Lardizabalaceae (Carlquist 1984a), Papaveraceae (Carlquist and Zona 1988; Carlquist et al. 1994), Ranunculaceae (Carlquist 1995a) and Berberidaceae (Carlquist 1995b). However, vessel density in Menispermaceae is relatively low: in tangential section, one sees individual vessels separated by rays or by fascicular tissue, one almost never sees several files of adjacent vessels. If there were files of adjacent vessels in menispermaceous woods the way there are files of adjacent sieve-tube elements in secondary phloem of Menispermaceae, we would likely be able to see storying in vessel elements. Very possibly, some species of Menispermaceae have numerous narrow vessels that would reveal storying.

Crystals and Other Cellular Contents

Crystal distribution is summarized in Table 1, column 14. The diversity of crystal distribution is clearly evident. Very likely, patterns other than those reported occur. The crystals may be in virtually all ray cells (R), or only in some of them (r), or lacking in rays. If crystals are large (they may be at least half the diameter of the cells that contain them), they tend to occur singly; if smaller, several per cell may occur (Fig. 21, 22). Crystals may be restricted to the margins of rays (M), and, if so, may be enclosed in cells with one thick lignified wall facing fascicular cells (C), likened to cristarque cells above (Fig. 20, 23). In one species, *Abuta racemosa*, crystals were observed only in latewood cells of rays. Small and numerous crystals were observed in axial parenchyma cells (A) of several species (see Table 1, column 14). In one species, crystals were observed in tyloses (T). In several species, large crystals were observed in the sclerenchyma of outer conjunctive tissue (S). In one species, *Cocculus laurifolius*, crystals were seen in the thin walled cell layers formed innermost in each increment of conjunctive tissue (I). Although no species list was assembled with respect to presence of crystals in parenchyma of secondary phloem (because good preservation was not available for phloem of all species), small crystals were characteristically observed in phloem parenchyma of Menispermaceae. In dicotyledons at

large, crystals are more common in phloem than in wood in any given species.

Nests of the crystal-containing cells were observed in bark of *Tinospora coffra* (Fig. 24). *Tinospora coffra* bark also contains cells that have been termed “secretory sacs” (Fig. 24) by Metcalfe and Chalk (1950). These sacs do not occur in conjunctive tissue or in secondary xylem. The nature of contents of these sacs has evidently not been determined yet.

Ray cells of all Menispermaceae studied contain either starch grains or remnants of starch grains. Starch grain remnants were observed in axial parenchyma of *Pachygone ovata*, *Pycnarrhena* sp., and *Tiliacora funifera*, but are likely to be found in more species in the family. Starch was observed in thin walled conjunctive tissue of *Tiliacora funifera* (Tw-31260).

CONCLUSIONS

Habit and Ecology

Lianas have a higher proportion of species with successive cambia than do other growth forms (Carlquist 1975). Lianas and vines also have relatively less mechanical tissue but more conductive area per unit transactional area than do other growth forms, but vessel elements are of average length for dicotyledons (Carlquist 1975). In addition, lianas tend to have a high proportion of species with true tracheids, wide rays (as well as other forms of parenchymatization such as conjunctive tissue), and starch storage. All of the above generalizations are exemplified by lianoid Menispermaceae. The figures for quantitative features of lianoid Menispermaceae (Table 1, last line of table) are remarkably close to figures reported in Carlquist (1975) for a sampling of vines and lianas at large. Figures for lianoid Menispermaceae, with figures for categories from the Carlquist (1975) sampling in parentheses are as follows: mean vessel diameter, 149 μm (157 μm); mean number of vessels per mm^2 , 22.2 (19.1); conductive area per mm^2 , 0.387 mm^2 (0.359 mm^2); mean vessel element length, 318 μm (334 μm). The presence of tracheids in lianoid Menispermaceae is in accord with the concept that they are of great selective value in cases where the conductive flow in large and vulnerable vessels is interrupted (Carlquist 1985). To be sure, one shrubby species, *Cocculus laurifolius*, also has tracheids. However, the subshrub *C. trilobus* has septate libriform fibers rather than tracheids, indicating that shift from tracheids to libriform fibers is readily accomplished, and that species of Menispermaceae are retaining them not because of inertia of a primitive character state, but because there is a selective advantage to tracheids in lianas, and evidently the shrub *Cocculus laurifolius* as well. That shrub may be relatively close to scandent species such as *C. hirsutus* (L.) Diels and *C. pendulus* (Forst.) Diels, so there is also

a possibility that time has been insufficient for tracheids to have altered evolutionarily.

The short duration of stems of *Cocculus trilobus* probably accounts for lack of successive cambia in that species. The short duration of stems in that species may also account for the juvenilistic ray tissue, which consists wholly of upright cells. The subshrub habit of *C. trilobus* seems related to the narrower, shorter rays in *C. trilobus* in comparison to the taller, wider rays of the lianas. The presence of libriform fibers, rather than tracheids, in *C. trilobus*, accounts for the fact that this is the only species of the family with a high proportion of grouped vessels, in accord with an earlier hypothesis (Carlquist 1984b). Grouped vessels afford a degree of conductive safety; in a species with tracheids, tracheids would be so effective a subsidiary conductive system that vessel grouping would be of little selective value.

The Mesomorphy ratio (Table 1, column 15; definition of ratio in legend for table) is exceptionally high for lianoid Menispermaceae (mean = 6245). The figures for *Cocculus laurifolius* (31) and *C. trilobus* (52) are more typical for shrubs, and fall in the same order of magnitude as the figure for southern Californian chaparral shrubs (67) in the survey of Carlquist and Hoekman (1985).

Phylogeny and Systematics

The outstanding xylary feature that separates Menispermaceae from other families of Ranunculiflorae is the presence of successive cambia. Successive cambia are not universal in the family—they are lacking in reduced subshrubs like *Cocculus trilobus* and *Menispermum canadense*. Only single cambia have been found in some species of large lianas, but failure to find successive cambia in those species may be an artifact of study of relatively small stems, such as those on herbarium specimens. One is tempted to say that because the successive cambia are so widespread in Menispermaceae, the feature is plesiomorphic for the family. Examination of larger stems and roots of as many species as possible is urged in order to assess this possibility, and to see if successive cambia truly are lacking in any species that forms large stems. As the family becomes better known through cladistic analysis of macromorphic and molecular features, very likely we will be able to identify phylads within the family likely to be more nearly basal, and search in these phylads for systematic distribution of successive cambia will likely be more important than search throughout the family at large.

Although storying was observed only in terms of tracheids in one species and in terms of sieve-tube elements in two others, the clear nature of storying in the sieve-tube elements in species that do not show

storying in fibers seems a clear indication that storying of fusiform cambial initials is likely widespread in the family, perhaps universal except for those species in which there is only a limited production of xylem and phloem. The reasoning by which storying in sieve-tube elements can be used as a strong indicator that storying is widespread in the family is described above. In addition, one of the samples in which storying in sieve-tube elements was observed was only 1 cm in diameter. Because storying tends to increase with the increase in diameter of a stem, occurrence in a small stem suggests the feature is deep-seated rather than systematically local, and expressed only in some species that have large stems. Storying has been found in wood of all five major families of Ranunculiflorae (see wood studies cited in the Introduction), so storying appears likely a feature of ancestral Ranunculiflorae.

Menispermaceae have rays that are very wide and very tall, and that originate suddenly as multiseriate rays if they originate during the activity of a particular cambium. These rays are sheathed with one or two layers of upright cells, but the remainder of the ray cells are procumbent in most species. All of the ray features just mentioned may be found in Lardizabalaceae, Papaveraceae, Ranunculaceae (*Clematis*) and Berberidaceae (Carlquist, 1984a, 1995a, 1995b; Carlquist and Zona 1988). Rays of this description are not widespread in dicotyledons, so their occurrence throughout Ranunculiflorae (with some modifications in genera with more juvenilistic wood) seems a significant link among the genera, and likely a plesiomorphy. Very similar (but often more juvenilistic) rays have been found in "paleoherb" families such as Aristolochiaceae (Carlquist 1993). The paleoherb families will be compared to the families of Ranunculiflorae in a concluding paper of this series.

A concluding paper in this series will also summarize the various phyletic levels of wood character states (e.g., vessel element length; axial parenchyma type) for the various families of Ranunculiflorae. These features are not discussed at the present juncture, therefore. One can say as a generalization at present that phyletically relevant characters of wood anatomy in Menispermaceae tend to exhibit a level above Lardizabalaceae but below Berberidaceae. This parallels the cladistic picture presented by Qiu et al. (1993), with the exception that Papaveraceae are given a basal position in the ranunculoid clade of Qiu et al. (1993). The small number of ranunculoid genera incorporated in the study of Qiu et al. (1993) likely limits the reliability and resolution of their cladogram. The fact that all of the families of Ranunculiflorae emerge in a single clade in the scheme of Qiu et al. (1993) (admittedly together with a family that was not previously included with Ranunculiflorae, Eupteleaceae) under-

lines the usefulness of the *rbcL* evidence that Qiu et al. (1993) employ.

The great diversity of the Menispermaceae woods studied in such respects as crystal distribution suggests that study of more numerous genera and species is likely to be rewarding. The distinctive character states of quantitative and qualitative features in two non-lianoid species in the present study, *Cocculus laurifolius* and *C. trilobus*, as compared to features of the lianoid species, suggests that study of species with diverse habits and sizes is likely to yield interesting correlations with wood features. There is a scattering of upright shrubs in the family, even a few trees, as well as lianas that begin as shrubs (Diels 1910). Some of the lianas in Menispermaceae have adventive roots (Diels 1910), but to my knowledge, the anatomy of these remains unstudied. We also have no idea if the products of successive cambia at the periphery of large stems are similar, quantitatively and qualitatively, to those at the inside of small stems. The many opportunities that remain for anatomical studies of woods in Menispermaceae are a byproduct of the paucity of samples that have been collected thus far. Few families of such size and such potential interest with respect to wood anatomy remain so poorly represented in dried or liquid preserved wood collections.

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