

1992

## Wood Anatomy of *Hedyosmum* (Chloranthaceae) and the Tracheid-vessel Element Transition

Sherwin Carlquist

*Rancho Santa Ana Botanic Garden; Pomona College*

Follow this and additional works at: <https://scholarship.claremont.edu/aliso>



Part of the [Botany Commons](#)

---

### Recommended Citation

Carlquist, Sherwin (1992) "Wood Anatomy of *Hedyosmum* (Chloranthaceae) and the Tracheid-vessel Element Transition," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 13: Iss. 3, Article 4. Available at: <https://scholarship.claremont.edu/aliso/vol13/iss3/4>

WOOD ANATOMY OF *HEDYOSMUM* (CHLORANTHACEAE) AND THE  
TRACHEID-VESSEL ELEMENT TRANSITION

SHERWIN CARLQUIST

*Rancho Santa Ana Botanic Garden*  
and  
*Department of Biology, Pomona College*  
*Claremont, California 91711, USA*

ABSTRACT

Qualitative and quantitative data are presented for 22 collections of 14 species of *Hedyosmum*. Wood of the genus is primitive in its notably long scalariform perforation plates; scalariform lateral wall pitting of vessel elements; and the low ratio of length between imperforate tracheary elements and vessel elements. Pit membrane remnants are characteristically present to various degrees in perforations of vessel elements; this is considered a primitive feature that is related to other primitive vessel features. Specialized features of *Hedyosmum* wood include septate fiber-tracheids with much reduced borders on pits; vasicentric axial parenchyma; and absence of uniseriate rays (in wood of larger stems). Ray structure (predominance of upright cells) and ontogenetic change in tracheary element length are paedomorphic, suggesting the possibility of secondary woodiness in the genus. Wood structure is highly mesomorphic.

Key words: Chloranthaceae, *Hedyosmum*, primitive angiosperms, tracheids, vessel elements.

---

INTRODUCTION

The family Chloranthaceae consists of four genera: *Ascarina*, *Chloranthus*, *Hedyosmum*, and *Sarcandra* (*Ascarinopsis*, a Madagascan segregate of *Ascarina*, is not recognized by most authors: Jérémie 1980). Despite the small size of the family (about 75 species: Todzia 1988), Chloranthaceae have aroused great interest in recent years because of the apparent primitiveness of some features (combined with possible specialization in others) and the uncertain systematic position of the family. Floral anatomy of *Hedyosmum* has been interpreted as transitional between gymnosperms and angiosperms (Leroy 1983), although Endress (1971, 1987) has shown that several levels of reduction occur in flowers of Chloranthaceae and that the flowers are best interpreted as specialized.

Most wood features of Chloranthaceae qualify as primitive for dicotyledons according to the criteria most generally accepted (Bailey 1944; Frost 1930*a, b*, 1931; Kribs 1935, 1937). *Sarcandra* has been claimed to be vesselless (Swamy and Bailey 1950), and the genus has therefore been widely cited as a primitively vesselless dicotyledon. Vessels do occur, however, in the roots of *Sarcandra* (Carlquist 1987). Swamy (1953) presented a useful summary of wood features of Chloranthaceae, but only at the generic level, and no specimens were cited. The availability for the present study of numerous specimens of *Hedyosmum* wood permits a detailed survey of wood anatomy in the genus. The collections of Carol Todzia have been very helpful in this regard, and her courtesy in sharing materials with me is greatly appreciated. Wood samples from the MADw and SJRW collections of the Forest Products Laboratory, Madison, Wisconsin, have been very important to the present study (Table 1). A few collections from my 1982 field work in Peru, identified by Carol Todzia, have been included.

Study of chloranthaceous woods by means of scanning electron microscopy (SEM) has revealed characteristic presence of primary wall portions (pit membranes) in perforations of vessel elements (Carlquist 1987, 1988a, 1990a). Degree and kind of pit membrane presence in perforations are diverse in *Hedyosmum*. This phenomenon appears to be indicative of primitiveness of vessel elements (Carlquist 1988a), and to represent a structural stage transitional between tracheids and vessel elements. The examples thus far studied show pit membrane remnants in perforations to be indicative of primitiveness of vessel elements. Primary wall remnants in perforations have not been studied extensively in dicotyledons, but *Hedyosmum* provides ideal material for surveying the mode of occurrence of these remnants. Attention is paid here to variability in presence within a species and within a wood sample, as well as to various manifestations of wall presence ranging from nearly complete presence to occurrence only as strands.

The phylogenetic interest of Chloranthaceae is considerable, but comments can be made most effectively when woods of all of the genera have been studied. Comments on some issues will therefore be deferred until the woods of *Chloranthus* have been studied.

In the present account, attention is called to observations in particular species. That does not mean necessarily that these features characterize those respective species. The sampling of the genus is too small to permit assessment of any wood characters at the species level. The species represented in this study do represent extremes for the genus in terms of habit, ecology, and geographical distribution. Therefore, the range in wood features reported here is probably an accurate picture of what a more thorough exploration would reveal.

Quantitative wood features change with ontogeny in a given stem. This accounts for part of the range of figures in Table 1. This range requires interpretation, but comparisons cannot be precise. The diameter of stems collected by Carol Todzia and by me are known, but the diameter of xylarium samples is generally not available directly; one can guess the approximate diameter of boards from xylarium collections only approximately, by measuring divergence of rays as seen in a transverse section. Patterns of ontogenetic change in *Hedyosmum* wood are clear, even though quantification can only be approximate.

#### MATERIALS AND METHODS

Xylarium samples (Table 1) were supplied by the Forest Products Laboratory through the courtesy of Regis B. Miller and Donna Christensen. These samples were available in dried form. My collections and those of Todzia were available preserved in an ethyl alcohol solution. Herbarium specimens documenting Todzia collections are located at TEX-LL and MO, my collections are at RSA. Woods were sectioned, without softening, by means of a sliding microtome. Radial sections of each collection were dried between clean glass slides and examined by means of SEM according to the usual methods. Transverse, tangential, and radial sections of each collection were stained with safranin and fast green and examined with a light microscope.

Data presented in Table 1 are derived from 25 measurements per collection except for vessel wall thickness, fiber-tracheid diameter, and fiber-tracheid wall thickness, in which typical conditions were measured. Where too few intact cells were available (as in macerations of woods with long vessel elements and fiber-

Table 1. Wood characteristics of *Hedyosmum*.

Species	Collection	1 BP	2 VG	3 VD	4 VM	5 VL	6 VW	7 TL	8 TW	9 PD	10 MR	11 RW	12 FV	13 ME
<i>H. arborescens</i> Swartz	MADw-36349	142	1.32	80	19	2096	2.4	2316	5.8	0-5	9.2	2.3	1.10	8825
	MADw-36356	112	1.32	61	27	1872	3.8	2007	4.5	2-4	7.4	2.3	1.07	4229
<i>H. bonplandianum</i> HBK.	SJRw-20934	67	1.13	101	11	1523	3.2	1921	3.5	1-3	7.6	2.1	1.26	13,984
	SJRw-38401	114	1.13	89	11	1815	2.3	2330	4.2	0-5	9.1	1.3	1.28	14,685
	Todzia 2534	120	1.17	72	20	2039	2.4	2423	4.2	2-5	5.3	1.3	1.19	7340
<i>H. brasiliense</i> Miquel	Todzia 2371	79	1.17	48	42	1440	2.0	1882	4.1	0-3	4.1	1.2	1.31	1646
<i>H. brenesii</i> Standley	Todzia 2020	119	1.33	86	23	1404	1.6	1741	2.6	0-2	7.6	1.3	1.24	5250
<i>H. cumbalense</i> Karsten	Todzia 2904	119	1.20	62	43	1151	2.5	1647	4.1	0-3	6.8	2.0	1.43	1660
<i>H. domingense</i> Urban	MADw-36370	107	1.56	61	39	1282	2.8	1477	5.0	2-3	6.6	2.5	1.15	2005
<i>H. goudotianum</i> Solms	Carlquist 7060	134	1.16	106	17	1945	2.3	2177	6.7	0-3	5.6	2.0	1.12	12,117
	Todzia 2525	122	1.47	77	32	1771	2.4	2005	5.1	2-4	8.3	1.4	1.13	4261
<i>H. luteynii</i> Todzia	Todzia 2499	84	1.60	55	35	1038	4.2	1275	4.2	0-5	3.8	2.1	1.23	1631
<i>H. mexicanum</i> Cordemoy	MADw-23925	87	1.21	95	14	1569	2.6	1981	8.1	1-2	6.3	1.3	1.26	10,904
	Thorne 21137 (RSA)	47	1.40	80	11	1504	2.4	1643	7.0	0-4	11.0	2.0	1.09	10,934
<i>H. nutans</i> Swartz	SJRw-7272	55	1.03	73	19	1265	2.1	1395	6.1	2-4	5.9	2.4	1.10	4860
<i>H. peruvianum</i> Todzia	Carlquist 7091	64	1.16	120	11	1778	2.4	1882	6.0	0-4	7.0	1.8	1.06	19,396
<i>H. racemosum</i> (R. & P.) G. Don	Carlquist 7100	112	1.10	68	20	1761	2.4	1945	6.9	0-3	8.2	4.6	1.10	5987
	MADw-15325	101	1.12	95	6	1804	2.2	2021	7.3	0-4	8.4	1.8	1.12	28,563
	Williams 1562 (UC)	130	1.17	97	22	1920	2.8	2226	8.0	0-2	11.6	3.2	1.16	8465
<i>H. scaberrimum</i> Standley	SJRw-12228	116	1.10	68	9	1997	2.2	2161	4.6	0-5	11.4	2.1	1.08	15,088
<i>H. scabrum</i> (R. & P.) Solms	MADw-14623	91	1.03	119	10	1220	2.1	1432	3.0	0-2	8.2	1.1	1.17	14,518
	SJRw-28642	67	1.12	102	16	1235	1.8	1464	4.2	2-4	6.2	2.5	1.19	7873
All collections, averaged		100	1.18	83	18	1610	2.5	1880	5.7	—	7.5	2.3	1.17	8615

Key to columns: 1 (BP), mean number of bars per perforation plates; 2 (VG), mean number of vessels per group; 3 (VD), mean diameter of vessels at widest point,  $\mu\text{m}$ ; 4 (VM), mean number of vessels per  $\text{mm}^2$ ; 5 (VL), mean vessel element length,  $\mu\text{m}$ ; 6 (VW), mean vessel wall thickness,  $\mu\text{m}$ ; 7 (TL), mean fiber-tracheid length,  $\mu\text{m}$ ; 8 (TW), mean fiber-tracheid wall thickness,  $\mu\text{m}$ ; 9 (PD), diameter range of pit borders of fiber-tracheids,  $\mu\text{m}$ ; 10 (MR), mean width of multiseriate rays at widest point, cells; 11 (RW), mean ray cell wall thickness,  $\mu\text{m}$ ; 12 (FV), Ratio of lengths of fiber-tracheids to vessel elements; 13 (ME), Mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per  $\text{mm}^2$ ).

tracheids), means were based upon fewer than 25 measurements. Multiseriate rays are often more than 5 mm tall in *Hedyosmum*. Because few of these rays are entirely contained within the limits of a section, accurate measurements of multiseriate rays could not be obtained for most species and this feature is omitted from Table 1.

Vessels are measured as widest lumen diameter. Number of vessels per group is computed according to a simple scheme (a solitary vessel = 1, a pair of vessels in contact = 2, etc.). Terminology of most wood features follows that of the IAWA Committee on Nomenclature (1964). Ray terminology is according to the Kribs (1935) system as expanded in Carlquist (1988a).

Localities of collections studied are as follows: *Hedyosmum arborescens*, MADw-36348 (Howard 11662), St. Lucia, W. I.; *H. arborescens*, MADw-26356 (Howard 11811), Dominica, W. I.; *H. bonplandianum*, SJRW-20934, Colombia; *H. bonplandianum*, SJRW-38401, Costa Rica; *H. bonplandianum*, Todzia 2534, Del Valle, Cocle, Panama; *H. brasiliense*, Todzia 2371, Estado Rio de Janeiro, Brazil; *H. brenesii*, Todzia 2020, Parque Nacional Braulio Carillo, La Montura, Costa Rica; *H. cumbalense*, Todzia 2404, Parque Nacional Volcan Purace, Cauca, Colombia; *H. domingense*, MADw-36370 (Howard 12314), Dominican Republic; *H. goudotianum*, Carlquist 7060, Carpish, Huanuco, Peru; *H. goudotianum*, Todzia 2525, between Cosanga and Sarayacu, Napo, Ecuador; *H. luteynii*, Todzia 2499, Quichinchi on road to San Jose de Minas, Imabura, Ecuador; *H. mexicanum*, MADw-23925 (Breedlove 9727), Chiapas, Mexico; *H. mexicanum*, Thorne 23117, La Trinitaria, Chiapas, Mexico; *H. nutans*, SJRW-7272 (also USw-1961), San Francisco de Macordis, Dominican Republic; *H. peruvianum*, Carlquist 78091, Carpish, Huanuco, Peru; *H. racemosum*, Carlquist 7100, San Ramon, Junin, Peru; *H. racemosum*, MADw-15325 (Williams 7006), San Martin, San Roque, Peru; *H. racemosum*, Williams 1562 (UC), Peru; *H. scaberrimum*, SJRW-12228, Panama; *H. scabrum*, MADw-16623, Pinchincha, Ecuador; *H. scabrum*, SJRW-28642 (coll. Rimbach), Ecuador.

#### ANATOMICAL DESCRIPTIONS

##### *Perforation Plates*

The perforation plates of *Hedyosmum* are long (Fig. 1). Todzia states that "vessel elements have scalariform compound perforation plates on the lateral walls with 150–200 bars." These data are derived from Swamy (1953). By definition, perforation plates are always on end walls, but there is a possibility that some workers may have confused scalariform lateral wall pitting with scalariform perforation plates in *Hedyosmum*. In my material, no perforation plates with as many as 200 bars were found, and very few plates exceeded 150 bars. The average for the genus as a whole (Table 1), 100, falls well below the 150–200 range claimed by Swamy (1953). Longer perforation plates might be expected in the long vessel elements of main trunks from trees of maximal size for the genus, and these samples might be present in xylaria. In the present study, some woods are from shrubby species (*H. cumbalense*) or from branches of trees rather than from main trunks.

Swamy (1953) states that bars in perforation plates of *Hedyosmum* are thin and not bordered. When studied by light microscopy, some bars may not appear to be bordered. However, in none of the species studied here were borders on bars lacking. This can be most reliably demonstrated by SEM studies. Because face

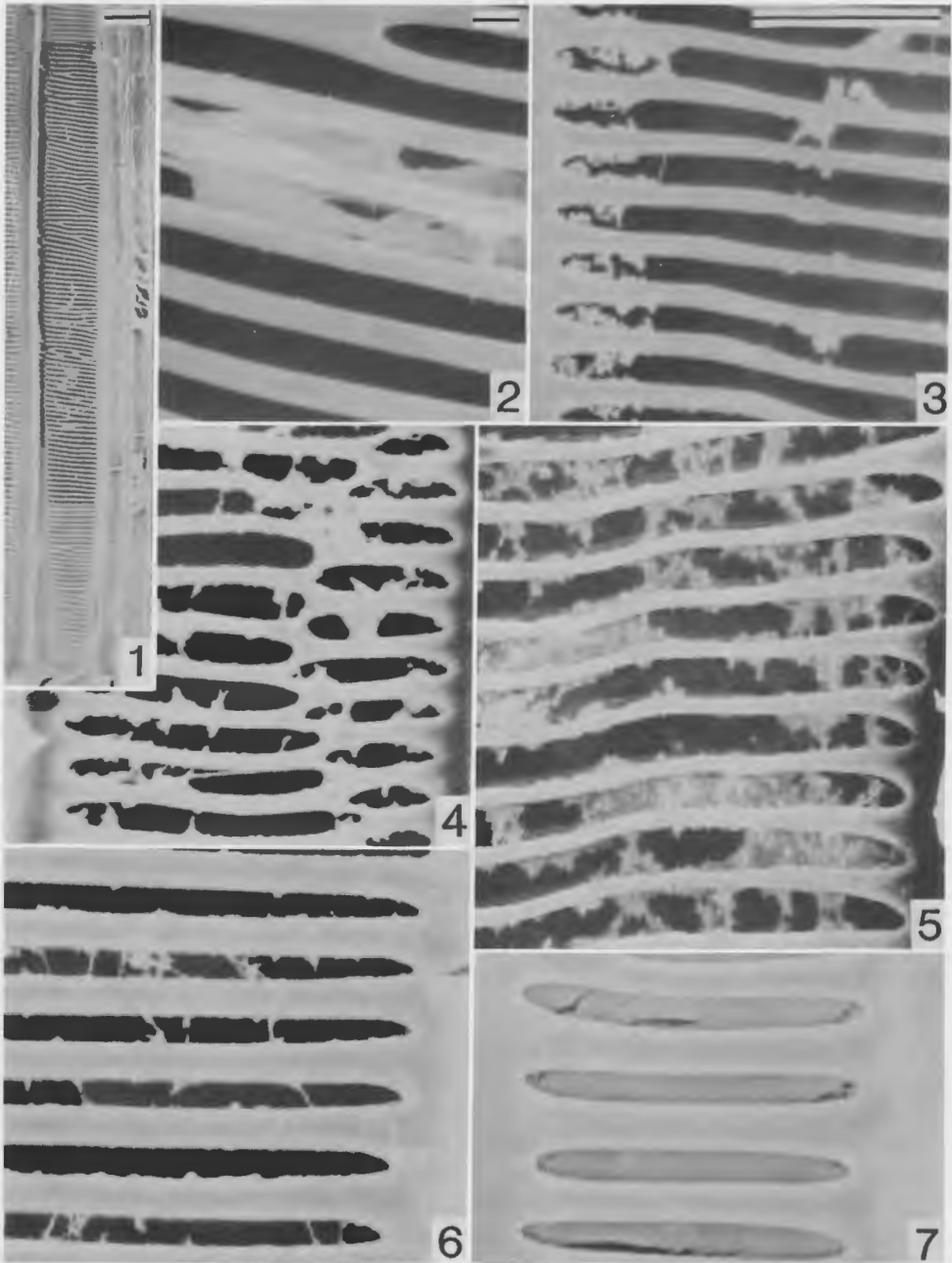


Fig. 1-7. SEM photomicrographs from radial sections of wood of *Hedyosmum goudotianum* (Carlquist 7060).—1. Approximately three quarters of a perforation plate.—2-6. Perforation plate portions, showing various types of primary wall remnants in perforations.—2. Pit membranes in some perforations but not in others.—3. Porose remnants, especially at ends of perforations.—4. Flakelike remnants.—5. Extensive remnants.—6. Occasional strands.—7. Lateral wall pitting of vessel, showing rupture of pit membranes due to preparation methods. (Fig. 1, bar = 10  $\mu\text{m}$ ; Fig. 2, 6, 7, bar = 1  $\mu\text{m}$ ; Fig. 3, 4, 5, bar = 5  $\mu\text{m}$ .)

views of perforation plates rather than oblique or sectional views are presented, borders are not illustrated in most of the SEM photographs here. Borders may be seen in one instance (Fig. 8, top right).

In a survey of primitive perforation plates (Carlquist 1988a), characteristic presence of fragments of primary wall material in perforations was noted for *Hedyosmum nutans*. Primary wall strands and other fragments were also noted for the genus *Ascarina* (Carlquist 1990a). Therefore, an effort has been made here to determine kinds and degree of presence of primary wall remnants in perforations. All of the specimens studied characteristically retain at least a few strands of primary wall material in perforations, but in at least half of the specimens, presence of remnants is above that minimal level. The mode of occurrence of pit membrane portions can be described in several ways: (1), in any given sample, some perforation plates retain more primary wall remnants than others; (2), some samples typically retain more primary wall remnants than do others; (3) the kinds of pit membrane remnants range from strands to extensive portions that can be likened to porose membranes. One must remember that only a small number of sections has been studied, so no reliable conclusions about the systematic distribution of pit membrane remnants in perforations can be reached.

The reader may wish to know if pit membrane remnants in *Hedyosmum* are altered by preservation or preparation methods. In order to clarify this, SEM photographs of lateral wall pitting were taken. One of these photographs is shown in Figure 7; this photograph shows rifts, likely the result of disturbance during sectioning, that represent about the most disturbance to normal structure observed. The photograph of lateral wall pitting (Fig. 7) can be contrasted with those of perforations of the same specimen, Figures 2 to 6. Similar comparisons could be offered for other species. For example, one can note minor rifts in vessel-to-vessel pitting in Figure 8 (bottom) and Figure 10 (bottom). Thus, preservation and preparation methods are of minimal significance, and the patterns shown for pit membrane remnants in perforation plates can be assumed to be intact.

Deposition of secondary plant products on vessel surfaces may result in failure of lysis of pit membranes in perforations. This possibility was noted and illustrated for *Ascarina* (Carlquist 1990a). In that study, the presence of secondary plant products that might prevent lysis of pit membranes is evident in SEM photographs as droplets or other amorphous deposits on wall surfaces. Such deposits were seen in a few cases in *Hedyosmum*. Failure of lysis in perforation plates is, in such instances, complete. The presence of pit membrane remnants in perforations characterizes species in about 20 families of dicotyledons, but such remnants are essentially absent in other dicotyledons. Both systematic distribution and presence of deposits in vessels are tests of artifact presence, and the results presented here are believed to be artifact-free.

Diversity in the presence of pit membrane remnants within a species is shown well in *H. goudotianum* (Fig. 2–6). In Figure 2, most perforations are clear, whereas most others contain nonporous portions of pit membranes. In Figure 3, one sees porous remnants of pit membranes at the ends of perforations, plus a few strands elsewhere in perforations. In Figure 4, strands and flakes of primary wall material are scattered throughout the perforations. In Figure 5, one sees greater abundance of the remnants, which represent strands, flakes, and unbroken portions; pores are visible in some membrane portions. In Figure 6, primary wall material is limited to strands and a few porous flakes.

The perforation plate of *H. cumbalense* shown in Figure 8 indicates that in a species with characteristic presence of pit membrane remnants in perforations, there is no clear demarcation between perforations and lateral wall pits. Instead, these categories grade into each other. This can also be shown by the perforation plates illustrated for *H. luteynii* in Figure 10. Thus, we should be skeptical of drawings for primitive perforation plates of dicotyledons that show a clear delineation between perforations and lateral wall pits.

The perforations of the *H. cumbalense* sample (Fig. 9) frequently contain strands or flakes of primary wall material. In *H. luteynii*, some perforation plates contain extensive portions of pit membranes (Fig. 11); these portions often are porose, corresponding to the porose pit membranes that may be seen on end walls of tracheids of vesselless dicotyledons such as *Tetracentron* (Carlquist 1988a: 113). A pair of photographs (Fig. 12, 13) for *H. brenesii* demonstrates the range that may be found within a species. In *H. brasiliense* (Fig. 14) and *H. bonplandianum* (Fig. 15), pit membrane remnants in perforations are minimal. Only a few strands characterize the *H. brasiliense* perforations (Fig. 14). In *H. bonplandianum* (Fig. 15), there are a few lumps or strands of primary wall material along the edges of perforations.

If one is acquainted with pit membrane presence in perforations on the basis of SEM studies, one can recognize such membrane portions in well-stained sections when they are studied by means of light microscopy. I was able to see such perforation occlusions in perforation plates of *H. brenesii* and *H. luteynii*, for example. For most species of *Hedyosmum*, I observed by means of SEM that most perforation plates are relatively free of remnants. The collections differed somewhat as to whether the plates with membrane remnants were few, as in *H. bonplandianum*, or many, as in *H. brenesii* or *H. luteynii*. Note should be made of the fact that samples from the latter two species were from smaller stems, but I am not able to conclude on the basis of my studies that pit membrane remnants in perforations are characteristic of juvenile wood—they appear approximately as common in wood from the periphery of older stems.

#### *Lateral Wall Pitting*

Vessels of *Hedyosmum* are characterized by scalariform or transition lateral wall pitting. Scalariform pitting is more abundant than transitional pitting in general (Fig. 7, 23). This is true equally in vessel to vessel, vessel to axial parenchyma (Fig. 23), and vessel to ray pitting.

#### *Quantitative Vessel Features*

Mean number of vessels per group is recorded in Table 1, column 2. The range from 1.03 to 1.60 is probably not very significant, but it does deserve mention because the figure is low compared to dicotyledons at large, and because figures in the vicinity of 1.60 indicate an appreciable degree of vessel grouping, which may be noticed in the photographs of Figures 19, 21, and 24.

Mean vessel diameter in *Hedyosmum* (Table 1, column 3) ranges from 48 to 120  $\mu\text{m}$ , a considerable span. This range is significant with respect to ecology, and will be interpreted in a concluding section of the paper. Vessel density (number of vessels per  $\text{mm}^2$ : Table 1, column 4) is generally thought to be inversely related to vessel diameter, and is, within limits, according to the data of Table 1.



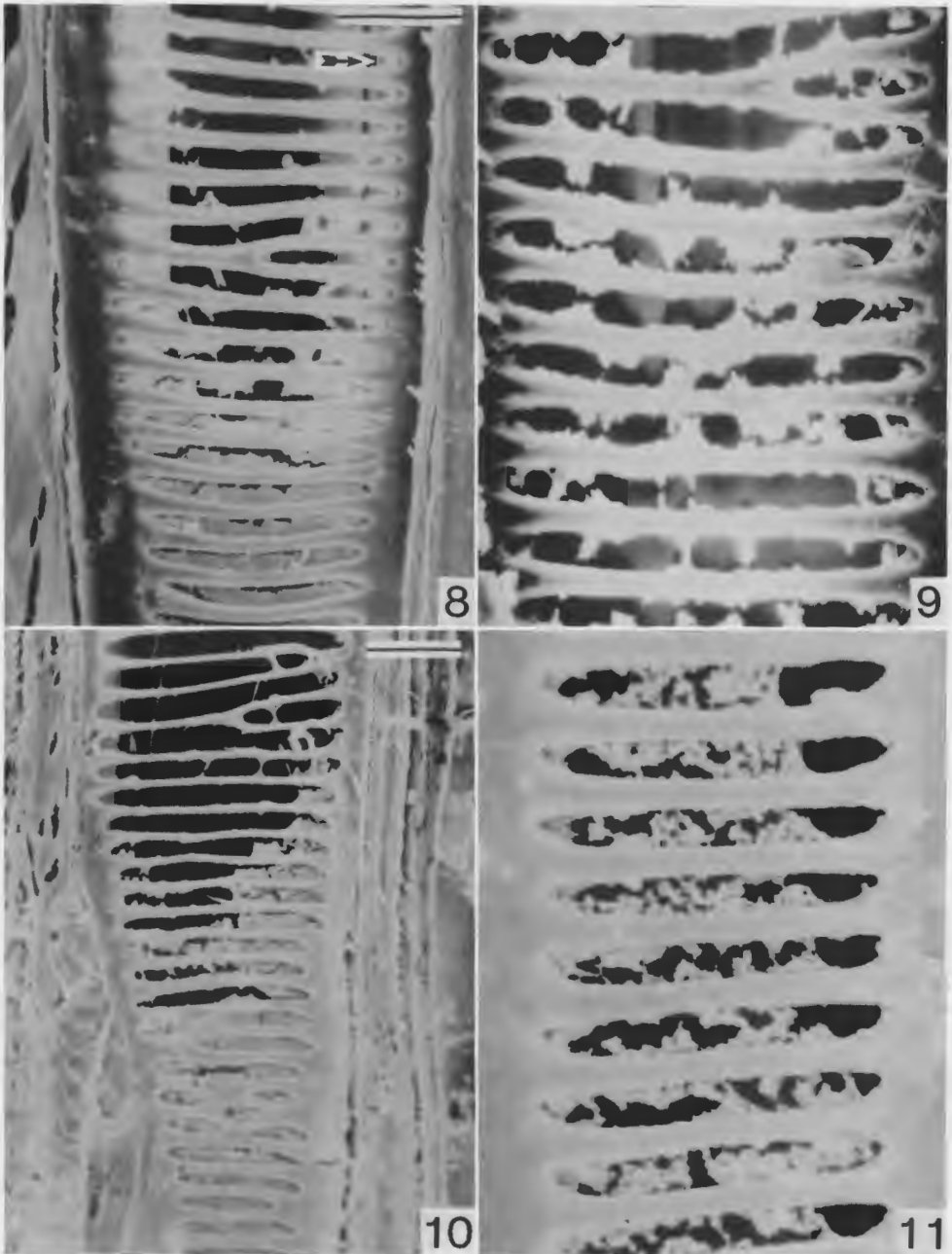


Fig. 8–11. SEM photomicrographs of perforation plate portions from radial sections of *Hedyosmum* wood.—8–9. *H. cumbalense* (Todzia 2904), perforation plates.—8. End of a perforation plate, transition to adjacent lateral wall pitting (below); pit remnants are present in perforations; arrow indicates pit border.—9. Extensive remnants of pit membranes in perforations.—10–11. *H. luteynii* (Todzia 2499), perforation plates.—10. End of a perforation plate, transition to adjacent lateral wall pitting (below).—11. Porose pit membrane remnants in perforations. (Fig. 8, bar = 5  $\mu\text{m}$ ; Fig. 9, scale in Fig. 3; Fig. 10, bar = 5  $\mu\text{m}$ ; Fig. 11, scale in Fig. 2.)

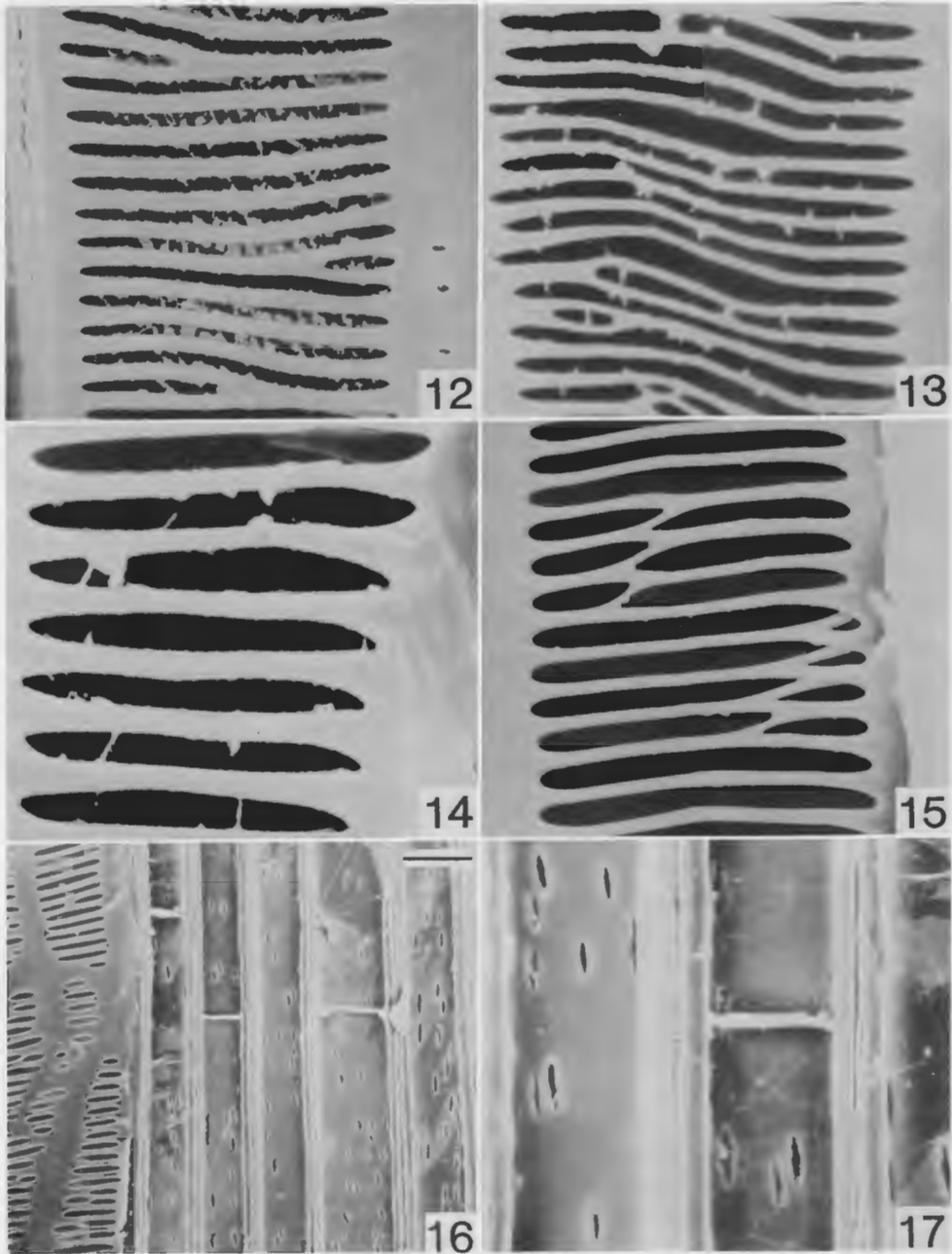


Fig. 12-17. SEM photomicrographs of radial sections of wood of *Hedyosmum*.—12-15. Portions of perforation plates to show degrees of pit membrane remnants.—12-13. *H. brenesii* (Todzia 2020).—12. Extensive flakelike remnants.—13. Limited strandlike remnants.—14. *H. brasiliense* (Todzia 2571), a few strandlike remnants.—15. *H. bonplandianum* (Todzia 2536), perforations nearly free of remnants.—16-17. *H. goudotianum* (Carlquist 7060), details of septate fiber-tracheids.—16. Several septate fiber-tracheids and, at left, mostly scalariform lateral wall pitting on vessel-axial parenchyma interface.—17. Slitlike pits and thin septum in fiber-tracheids. (Fig. 12, 13, 15, 17, scale in Fig. 8; Fig. 14, scale in Fig. 2; Fig. 16, bar = 10  $\mu\text{m}$ .)

Vessel element length tends to be great in dicotyledons with primitive wood (Bailey and Tupper 1918), so the rather long vessel elements of *Hedyosmum* (Table 1, column 5), which have a mean length ranging from 1038  $\mu\text{m}$  to 2096  $\mu\text{m}$  and a mean for the genus of 1610  $\mu\text{m}$ , are not surprising. The mean length given by Metcalfe and Chalk (1950) for dicotyledons as a whole (649  $\mu\text{m}$ ) is much less, but even that figure is probably not representative, because the Metcalfe and Chalk figures are based mostly on trees, whereas woods of shrubs and woody herbs typically have much shorter vessel elements than do woods of trees. Despite their great length, vessel elements in *Hedyosmum* have thin walls, which average 2.5  $\mu\text{m}$  in thickness for the genus (Table 1, column 6). Vessel walls in *Hedyosmum* vary in thickness within a vessel, often being only 1  $\mu\text{m}$  thick between the angles, but much thicker in the angles. This corresponds to the rather angular nature of the vessels (Fig. 19, 24) in some species. Vessels are more rounded in outline in other species, such as *H. scaberrimum* (Fig. 21). The thinness of walls of vessels in *Hedyosmum* is probably the primary reason for difficulty in wood sectioning. At least some collapsed vessels may be found in most of the sections prepared for this study.

#### *Imperforate Tracheary Elements*

The imperforate tracheary elements of *Hedyosmum* are termed fiber-tracheids because they have vestigial borders on pits, as mentioned by Swamy (1953). Fiber-tracheid diameter has not been presented in Table 1 because reliable dimensions are not readily obtained, nor would they be very meaningful. In *Hedyosmum*, as in other genera of dicotyledons, diameter of imperforate tracheary elements appears to parallel diameter of vessel elements. Fiber-tracheid length is given in Table 1, column 7. The range in mean fiber-tracheid lengths (1275 to 2330  $\mu\text{m}$ ) and the mean for the genus (1880  $\mu\text{m}$ ) are moderately high compared with lengths in dicotyledons as a whole (1318  $\mu\text{m}$ : Metcalfe and Chalk 1950).

Fiber-tracheid wall thickness in *Hedyosmum* shows an appreciable range (Table 1, column 8). Relatively thin-walled fiber-tracheids are illustrated for *H. luteynii* (Fig. 21), *H. scaberrimum* (Fig. 21), and *H. scabrum* (Fig. 24). Much thicker walls occur in *H. racemosum* (6.9–8.0  $\mu\text{m}$ ) and *H. mexicanum* (7.0–8.1  $\mu\text{m}$ ).

Pit apertures of fiber-tracheids are slitlike (Fig. 16, 17, 18). Most pits are located on radial walls (Fig. 18). Borders may be seen most clearly on fiber-tracheid to ray pits and fiber-tracheid to axial parenchyma pits. Borders are absent or apparently so in most (but not all) *Hedyosmum* species on fiber-tracheid to fiber-tracheid pits (Fig. 18). These different expressions account for the ranges (e.g., 0–4  $\mu\text{m}$ ) shown for diameter of pit borders in Table 1, column 9. This underlines the problem in defining terms that delineate segments of the continuum from tracheid to libriform fiber, not an easy situation terminologically. However, the separation proposed between imperforate tracheary elements with pit borders less than 2.5  $\mu\text{m}$  in diameter and those more than 2.5  $\mu\text{m}$  in diameter (Baas 1986) does not appear feasible in *Hedyosmum*, and continuation of the terminology of the IAWA Committee on Nomenclature (1964) is endorsed (see Carlquist 1986).

Throughout *Hedyosmum*, fiber-tracheids are septate at least once (Fig. 16, 17). Commonly two or three septa per fiber-tracheid were observed. In liquid-preserved material, nuclei were frequently observed in each segment of the septate fiber-tracheids, which are thus doubtless alive for prolonged periods.

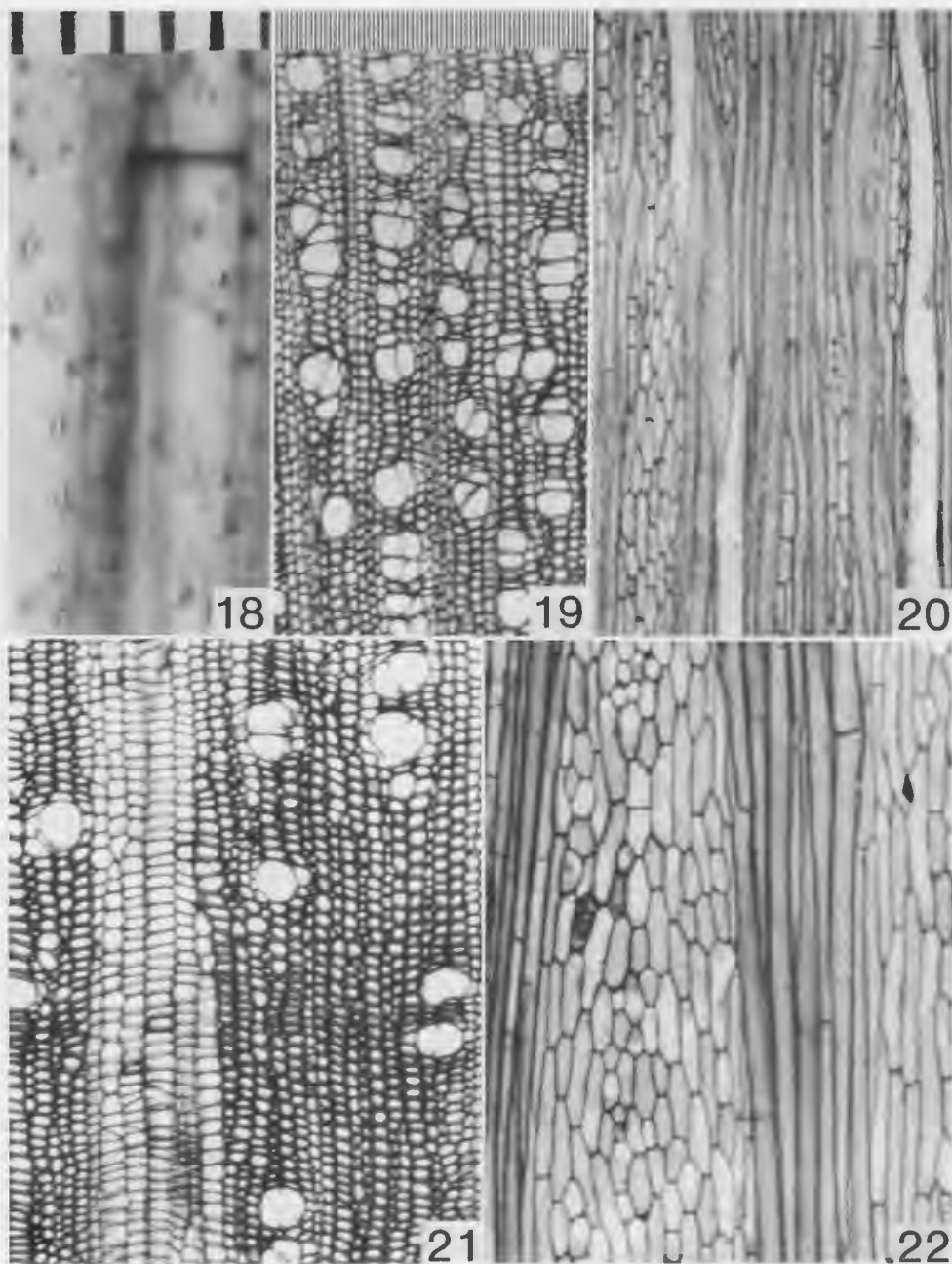


Fig. 18–22. Light photomicrographs of wood of *Hedyosmum*.—18. *H. arborescens* (MADw-16249), fiber-tracheids from radial section (septum, upper right) to show minimal border presence on pits.—19–20. *H. luteynii* (Todzia 2499).—19. Transection; about two thirds of the vessels are solitary.—20. Tangential section; uniseriate rays and uniseriate wings on multiseriate rays present.—21–22. *H. scaberrimum* (SJRw-12228).—21. Transection, showing low vessel density.—22. Tangential section; most cells in the two rays are upright cells. (Fig. 18, scale above Fig. 18 [divisions =  $\mu\text{m}$ ]; Fig. 19–22, scale above Fig. 19 [divisions =  $10\ \mu\text{m}$ ].)

### *Axial Parenchyma*

In *Hedyosmum*, scanty vasicentric parenchyma is present in all species. Usually the sheath of parenchyma cells around vessels or vessel groups is a single cell layer thick and often it incompletely sheathes the vessel. Axial parenchyma strands consist of about seven cells. Two species, *H. brasiliense* and *H. domingense*, had appreciable numbers of diffuse parenchyma cells in wood. Occasional diffuse axial parenchyma cells were observed in *H. goudotianum*, *H. mexicanum*, *H. scaberrimum*, and *H. scabrum*. Diffuse parenchyma cells were not observed in the species not listed above.

### *Rays*

Wood of most species of *Hedyosmum* has rays that must be termed Paedomorphic type II (Carlquist 1988a). Uniseriate rays are lacking, and procumbent ray cells are infrequent (Fig. 22, 26). Procumbent ray cells, where present, are in central portions of the multiseriate rays.

If one looks at rays in *Hedyosmum* stems of relatively small diameter, one sees that rays are transitional between Heterogeneous Type I and Paedomorphic Type II. Uniseriate rays are present, albeit less abundant than multiseriate rays, and procumbent cells are absent in rays of specimens with these transitional rays (Fig. 20). Uniseriate wings may be found on multiseriate rays in such stems (Fig. 20, 25).

Multiseriate rays are so tall that accurate dimensions cannot be determined from sectioned material. Many rays are not complete within a section (sections are usually about 1 cm in length). Figures on width of multiseriate rays at their widest point are given in Table 1, column 10. Lower figures for *H. brasiliense* and *H. luteynii* are correlated with smaller stem size. The stem diameter of the specimens with the widest rays could not be obtained because these specimens are mostly from trimmed xylarium specimens.

Ray cell walls are relatively thin (Table 1, column 11), as shown in Figures 20, 22, 25, and 26. Relatively thick cell walls were seen in two collections of *H. racemosum*. Occasional bordered pits were observed on ray cell walls (mostly tangential walls) in most species. Perforated ray cells were seen in *H. bonplandianum* (MADw-36356).

### *Tyloses*

Thin-walled tyloses occur in a portion of vessels in some species of *Hedyosmum* (the gray coloration seen in a few vessels of *H. luteynii*, Fig. 19, upper right). Tyloses of this sort were observed in *H. luteynii* and *H. scaberrimum*, but doubtless occur in other species also.

### *Crystals and Other Cell Contents*

Crystals were observed in only one specimen, *H. arborescens* (MADw-36356). In this collection, crystals were formed singly per ray cell, and occurred in only a fraction of the ray cells.

Dark-staining contents occur in all woods of *Hedyosmum*. In unstained preparations, the contents are yellowish to brownish. These contents take the form of droplets or more massive accumulations. These deposits usually occur not in

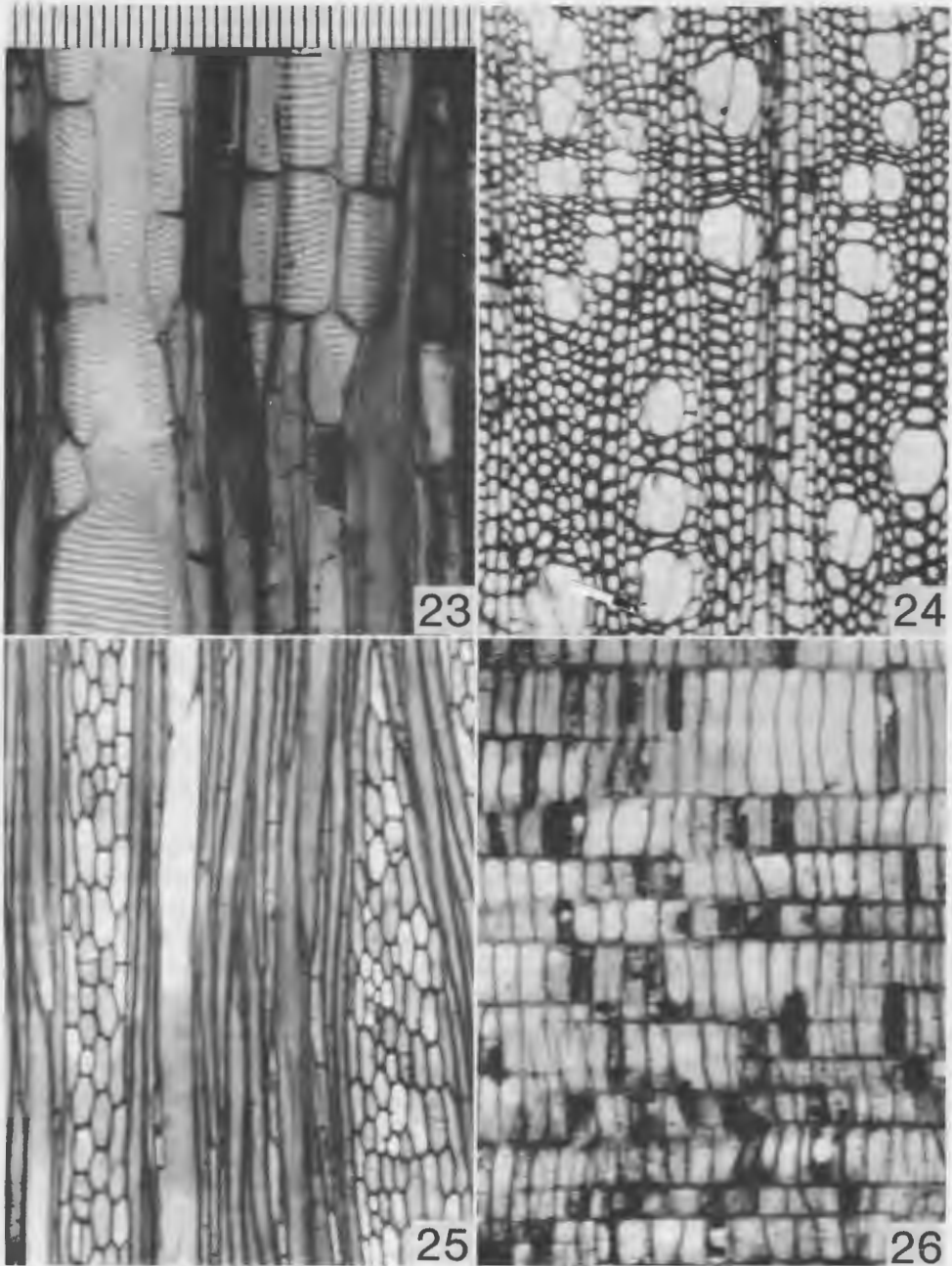


Fig. 23–26. Light photomicrographs of wood sections of *Hedyosmum scabrum* (SJRw-28642).—23. Radial section, showing vessel to axial parenchyma pitting (mostly scalariform) above; perforation plate portion, below left.—24. Transection; vessels mostly solitary.—25. Tangential section; uniseriate ray, below center.—26. Radial section; cells are square to upright, many have dark-staining contents. (Fig. 23, scale above Fig. 23 [divisions = 10  $\mu$ m]; Fig. 24–26, scale above Fig. 19.)

every parenchyma cell, but in about a third of the cells (*H. scabrum*, Fig. 26). When most abundant, these deposits may spread into vessels and fiber-tracheids. They are less common in two species illustrated: *H. luteynii* (Fig. 19, 20) and *H. scaberrimum* (Fig. 21, 22).

#### SYSTEMATIC AND PHYLETIC CONCLUSIONS

If one compares wood of *Hedyosmum* to that of *Ascarina* (Carlquist 1990a), one sees a contrast in perforation plates (shorter in *Ascarina*), imperforate tracheary elements (thicker walled, mostly nonseptate, and with more prominent borders in *Ascarina*), axial parenchyma (diffuse in *Ascarina*, vasicentric or rarely diffuse in *Hedyosmum*). Wood anatomy of the genera of the family will be summarized in a final paper in this series.

With respect to its position within Chloranthaceae, *Hedyosmum* would rank as primitive on the basis of number of bars per perforation plate, but specialized on the basis of axial parenchyma distribution and presence of septate fiber-tracheids with much reduced pit borders. In assessing the nature of the fiber-tracheids, one should keep in mind that formation of septa in imperforate tracheary elements hastens loss of pit borders phyletically (Carlquist 1988a, b). Borders on pits of imperforate tracheary elements should not be regarded as evolving gradually. Once these cells retain protoplasts for an indefinite period, the cells are no longer essential to the water-conducting system of the wood and therefore borders are of no selective value. Septa are an indication of protracted longevity of protoplasts in imperforate tracheary elements.

The ratio of length between imperforate tracheary elements and vessel elements has been considered an indicator of phyletic specialization, within limits (Carlquist 1975). A ratio around 1.00–1.20 is considered primitive, whereas a ratio above 2.00 is considered specialized. By these criteria, *Hedyosmum* wood is primitive (ratio for the genus as a whole, 1.17: Table 1, column 12). Very likely the evolution of vessels from a vesselless ancestry carries with it a difference in lengths between the two cell types of at least 10%, and one should not expect extremely primitive vessel-bearing woods to have extremely low ratios (e.g., 1.05).

The vessels of *Hedyosmum* are notably primitive in the frequency with which pit membrane remnants occur in perforation plates. This characteristic is found only in a few very primitive families of dicotyledons such as Cunoniaceae, Escalloniaceae, and Griselinaceae (Meylan and Butterfield 1978), Illiciaceae and Paracryphiaceae (Carlquist 1988a), and Ticodendraceae (Carlquist 1991). Similar primary wall remnants in perforations were figured in *Ascarina* (Carlquist 1990a). As discussed earlier, these pit membrane remnants are rarely artifacts (see also Carlquist 1990a). The distribution of this phenomenon within dicotyledons (Carlquist, unpublished) shows that pit membrane remnants in perforations occur in species with long scalariform perforation plates, just the vessel-bearing dicotyledons one would choose as having quite primitive wood. The presence of pit membrane remnants in perforations is a feature that should be added to other criteria of primitiveness in wood anatomy.

#### CONCLUSIONS ON HABIT EVOLUTION

The genus *Hedyosmum* ranges from shrubs of moderate size (1 m or more) to trees, some of which are small, but some of which may reach 30 m (Todzia 1988).



This habit range is atypical for Chloranthaceae: *Ascarina* consists of shrubs, rarely trees, whereas *Chloranthus* and *Sarcandra* can be called subshrubs or herbs. *Chloranthus* and *Sarcandra* produce innovations of limited duration; most species of *Chloranthus* have little cambial activity. The habitual range for the family does not suggest a primarily arboreal ancestry. The ray structure seems to confirm this. Rays of *Hedyosmum* correspond to Paedomorphic Type II, a type that has not been reported in typically woody groups. Rather, one finds it in groups that seem likely to be secondarily woody, such as the lobelioids (Carlquist 1969). This ray type does occur in *Lactoris*, which may have an herbaceous ancestry and very likely is more nearly related to Chloranthaceae than to Lauraceae, Myristicaceae, and other families that have been claimed to be related to it (Carlquist 1990b). Young stems of *Hedyosmum* have uniseriate rays in addition to multiseriate ones, but with no procumbent ray cells; such rays are referable to Paedomorphic Type I.

In paedomorphic woods, there is a decreasing rather than an increasing length of tracheary elements with development of a woody stem (Carlquist 1962). Comparisons within *Hedyosmum* indicate a paedomorphic curve for length against age for tracheary elements. In *H. bonplandianum*, the sample with the smallest diameter is *Todzia* 2534, whereas the widest diameter characterizes the sample *SJRw-20934* (judged on the basis of divergence angle of rays as seen in transection), yet the tracheary elements are longer in *Todzia* 2534.

Shorter tracheary elements characterize shrubs as opposed to trees (Carlquist 1975), and this proves to be true within *Hedyosmum*. The specimens with shortest vessel elements, *H. cumbalense* and *H. luteynii*, are from plants with shrubby rather than arboreal habit.

#### ECOLOGICAL CONCLUSIONS

Woods with long scalariform perforation plates come from mesic situations (Carlquist 1975), and *Hedyosmum* is no exception to this. The mesomorphy ratios for the genus (Table 1, column 13) confirm this: ratios above 100 could be called mesomorphic, whereas all of the species of *Hedyosmum* have Mesomorphy ratio values in excess of 1000. If one looks for low values within this range, one notes that figures for *H. brasiliense*, *H. domingense*, and *H. luteynii* are low (although certainly high by comparison with dicotyledons from Mediterranean-type areas). Habitats for the first two of these species may be slightly less mesic than those of other *Hedyosmum* species, judging from the data of *Todzia* (1988), but *H. luteynii* occurs in very wet Andean forests (*Todzia*, personal communication). Two of these species (*H. brasiliense*, *H. luteynii*) have a mean vessel grouping figure high for the genus, although the range is not great. A higher figure for vessels per group corresponds to greater wood xeromorphy (Carlquist 1975). One may conclude that *Hedyosmum* wood is definitely mesomorphic but that differences within the genus in quantitative wood features are not readily interpretable, at least not on the basis of the present sampling. Vessel grouping may confirm a slightly lesser degree of mesomorphy for shrubby species of *Hedyosmum* than for arboreal species, but one must stress that even the least mesomorphic species of *Hedyosmum* has wood highly mesomorphic by comparison with wood from dry areas. Note should be taken that samples for some of the species (particularly the *Todzia* collections) were relatively small stems. Small stems tend to have wood that is less mesomorphic in quantitative wood data than do main stems of large trees (Carlquist 1975).



## LITERATURE CITED

- Baas, P. 1986. Terminology of imperforate tracheary elements—in defence of libriform fibers with minutely bordered pits. *IAWA Bull.*, n.s., 7:82, 86.
- Bailey, I. W. 1944. The development of vessels in angiosperms in morphological research. *Amer. J. Bot.* 31:421–428.
- , and W. W. Tupper. 1918. Size variation in tracheary cells. I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms, and angiosperms. *Proc. Amer. Acad. Arts* 54:149–204.
- Carlquist, S. 1962. A theory of pedomorphosis in dicotyledonous woods. *Phytomorphology* 12: 30–45.
- . 1969. Wood anatomy of Lobelioideae (Campanulaceae). *Biotropica* 1:47–72.
- . 1975. Ecological strategies of xylem evolution. Univ. Calif. Press, Berkeley. 259 p.
- . 1986. Terminology of imperforate tracheary elements. *IAWA Bull.*, n.s., 7:168–170.
- . 1987. Presence of vessels in wood of *Sarcandra* (Chloranthaceae) and comments on vessel origins in angiosperms. *Amer. J. Bot.* 74:1765–1771.
- . 1988a. Comparative wood anatomy. Springer-Verlag, Berlin and Heidelberg. 436 p.
- . 1988b. Tracheid dimorphism: a new pathway in evolution of imperforate tracheary elements. *Aliso* 12:103–118.
- . 1990a. Wood anatomy of *Ascarina* (Chloranthaceae) and the tracheid–vessel element transition. *Aliso* 12:667–684.
- . 1990b. Wood anatomy and relationships of Lactoridaceae. *Amer. J. Bot.* 77:1498–1505.
- . 1991. Wood and bark anatomy of *Ticodendron*; comments on relationships. *Ann. Missouri Bot. Gard.* 78:96–104.
- Endress, P. 1971. Bau der weiblichen Blüten von *Hedyosmum mexicanum* Cordemoy (Chloranthaceae). *Bot. Jahrb. Syst.* 91:39–60.
- . 1987. The Chloranthaceae: reproductive structures and phylogenetic position. *Bot. Jahrb. Syst.* 109:153–226.
- Frost, F. H. 1930a. Specialization in secondary xylem of dicotyledons. I. Origin of vessel. *Bot. Gaz. (Crawfordsville)* 89:67–94.
- . 1930b. Specialization in secondary xylem of dicotyledons. II. Evolution of end wall of vessel segment. *Bot. Gaz. (Crawfordsville)* 90:198–212.
- . 1931. Specialization in secondary xylem of dicotyledons. III. Specialization of lateral wall of vessel segment. *Bot. Gaz. (Crawfordsville)* 91:88–96.
- IAWA Committee on Nomenclature. 1964. Multilingual glossary of terms used in wood anatomy. Verlagbuchanstalt Konkordia, Winterthur, Switzerland. 185 p.
- Jérémie, J. 1980. Notes sur le genre *Ascarina* (Chloranthaceae) en Nouvelle Calédonie et à Madagascar. *Adansonia*, sér. 2, 20:273–285.
- Kribs, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz. (Crawfordsville)* 96:547–557.
- . 1937. Salient lines of structural specialization in the wood parenchyma of dicotyledons. *Bull. Torrey Bot. Club* 64:177–186.
- Leroy, J.-F. 1983. The origin of angiosperms: an unrecognized ancestral dicotyledon, *Hedyosmum* (Chloranthales), with a strobiloid flower is living today. *Taxon* 32:169–175.
- Metcalfe, C. R., and L. Chalk. 1950. *Anatomy of the dicotyledons*. Clarendon Press, Oxford. 1500 p.
- Meylan, B. A., and B. G. Butterfield. 1978. The structure of New Zealand woods. *DSIR Bull.* 122. New Zealand DSIR, Wellington. 250 p.
- Swamy, B. G. L. 1953. The morphology and relationships of the Chloranthaceae. *J. Arnold Arb.* 34:375–411.
- , and I. W. Bailey. 1950. *Sarcandra*, a vesselless genus of the Chloranthaceae. *J. Arnold Arb.* 31:117–129.
- Todzia, C. A. 1988. Chloranthaceae: *Hedyosmum*. *Flora Neotropica Monograph* 48. New York Bot. Gard., N.Y. 139 p.