

Wood anatomy of Gentianaceae, tribe Helieae, in relation to ecology, habit, systematics, and sample diameter

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Twenty collections representing one species each of *Symbolanthus* and *Tachia*, and 17 species of *Macrocarpaea* were studied by means of light microscopy and scanning electron microscopy (SEM). Wood details show that the three genera form a coherent group; *Tachia* differs from the others in only a few minor characters. Because the species studied form a natural group, wood variations within Helieae offer the basis for correlations and interpretations with respect to habit and ecology. Diameter of stems studied proves to be an important variable that must be taken into account. Correlations with stem diameter include wider vessels in outer wood of wider samples. This would correspond to deeper penetration of reliable water tables by roots of helioid trees or large shrubs. Ray height decreases with increase in stem diameter, an indication of paedomorphosis. Rays of all species are paedomorphic in histology by virtue of relative paucity or even absence of procumbent cells in multiseriate rays. Pseudoscalariform lateral wall pitting of vessels is also a feature characteristic of paedomorphosis. The assemblage of paedomorphic features correlates well with the conclusion, reached by authors who used cladistic methods, that Gentianaceae other than Gentianeae are derived from suffrutescent perennials. The Mesomorphy Ratio, which incorporates three vessel features, correlates with leaf length and with stem diameter. All Helieae are mesophytic, but to various degrees. Septate fiber-tracheids, where present, are typically near vessels and form a substitute for or an addendum to vasicentric axial parenchyma as a mechanism for photosynthate storage. Vestured pits occur on lateral wall pits of vessels of all Helieae, but not on the fiber-tracheids. Vestured pits show diversity within *Macrocarpaea*, a feature of possible systematic significance.

Key words: comparative wood anatomy, ecological wood anatomy, fiber-tracheids, Gentianaceae, Helieae, *Macrocarpaea*, paedomorphosis, sample diameter, vestured pits.

Descriptions of wood anatomy of Gentianaceae s. s. are few: Gregory (1994) lists Carlquist (1984a), in which wood of two genera of Helieae (*Chelonanthus*, *Symbolanthus*) is described. If we follow an expanded definition of the family (Struwe et al., 2002), woods of genera of Gentianaceae

s.l. once put into Loganiaceae have been described by Mennega (1980). Vestured pits of several species of Helieae (all different from those in the present paper) were figured by Jansen and Smets (1998), who also presented photographs of pits of vessels of other Gentianaceae s.l. The chief reason for

lack of studies of wood of Gentianaceae is that, excepting genera formerly placed in Loganiaceae (*Anthocleista*, *Fagraea*, *Potalia*), most Gentianaceae are nonwoody. Woody Gentianaceae have been little collected by wood collectors, and the woods in the present study were collected expressly for a comparative study.

Study of this assemblage of woods reveals interesting patterns of diversification. Because the Helieae do not appear to be a series of relict genera, but are, rather, products of a radiation in northern South America and nearby lands, the patterns of diversification may be considered to be the action of evolution on a basic wood plan, so that relationships to ecology and habit are readily evident. This kind of pattern was earlier described for Asteraceae (Carlquist, 1966).

Habit in the genus *Macrocarpaea* ranges from branched shrubs (*M. wurdackii* and other species) to a minimally woody perennial herb (*M. rubra*) to several trees (*M. arborescens*, *M. bubops*, *M. gattaca*, *M. noctiluca*) up to 10 m tall (Ewan, 1948; Grant & Struwe, 2001; Struwe et al., 2002). *Symbolanthus* includes shrubs and trees. *Tachia guianensis* is a small tree. *Chelonanthus chelonoides* (L. f.) Gilg, included in the study of Carlquist (1984a), is an herb, woody at the base, that can reach 1 m. This range of habitats invites comparison with wood data and also ecology, because greater woodiness tends to characterize species of more mesic habitats. The material of *Macrocarpaea* permits us to see how woods of closely related herbs, shrubs, and trees, respectively, are different. Albert and Struwe (2002) concede that the family as a whole may be primitively woody, but that the tree habit in *Macrocarpaea* is derived, an interpretation Struwe et al. (2002) examine in detail.

The relationship between wood anatomy and habit is, to a certain extent, like the relationship between juvenilism and adulthood in wood anatomy characters. More juvenilism is to be expected in wood of families in which herbaceousness is the ancestral condition, as in lobelioids (Carlquist, 1969). Other families that appear thoroughly woody do, in fact, lack juvenilism in

wood features, as in Pittosporaceae (Carlquist, 1981).

If Helieae are derived from herbaceous ancestors, the diameter of the woody cylinder should relate directly to the degree of juvenilism (assuming a rather uniform rate of secondary xylem addition). In families that are ancestrally woody, adult wood patterns appear quickly and diameter of stem sample is not conspicuously related to juvenilism or adulthood. The diameter of stem samples is therefore an important consideration in this study, and is given for each collection studied in Table 1.

Macrocarpaea, the largest of the helioid genera, contains more than 100 species (see Grant; 2003, Grant & Struwe 2001, 2003). *Symbolanthus* comprises about 30, *Tachia* 10, and *Chelonanthus* eight (Struwe et al., 2002). All of the samples studied come from tropical latitudes of South America, mostly from highlands above 1000 m. Ecology of the species is not uniform, however. Although frost is probably not a factor of importance in ecology of the helioid species, differences in soil moisture certainly are demonstrable. The white sand road cuts where *Chelonanthus chelonoides* grows are much more likely to experience drought than the cloud forest areas of Loja Province, Ecuador, where about half of the species of *Macrocarpaea* sampled here grow. Differences among the species are doubtless reflected in wood anatomy, which is a very sensitive indicator of ecology. The fact that wood accumulation represents years of growth in the conditions in a given locality, makes wood a more reliable source of ecological information than a single day's visit to a particular locality.

There are other keys to ecology of the helioid species, however. Leaf size and texture are intimately related to ecology of Helieae, although measurements of these features that are truly representative may be difficult to obtain. Correlations between leaf area and vessel element length and diameter proved compelling in an asteraceous genus, *Dubautia* (Carlquist, 1974: 153). We have presented average leaf length within a species (Table 1) as a way of using foliar features as ecological indices.

The sampling here of woods of the tribe

TABLE I
WOOD CHARACTERISTICS AND OTHER DATA ON GENTIANACEAE, TRIBE HELIEAE^a

Species	1 VG	2 VD	3 VM	4 VL	5 FL	6 SF	7 MH	8 MW	9 RH	10 ME	11 LL	12 SD
<i>Macrocarpaea angel-liae</i>	1.72	30	43	420	627	nv	652	2.1	U	293	9	1.0
<i>M. apparata</i>	2.23	52	43	540	687	nv	457	2.9	Usp	652	37	5.7
<i>M. arborescens</i>	1.89	57	34	346	570	f	334	2.3	Usp	570	8	5.0
<i>M. bubops</i>	1.66	57	32	363	502	nv	459	5.0	USP	647	24	5.9
<i>M. gattaca</i>	1.83	40	77	509	613	nv	453	4.5	U	265	13	1.2
<i>M. harlingii</i>	1.39	50	18	586	728	0	737	2.0	Us	1625	15	2.2
<i>M. jensii</i>	1.60	47	57	512	771	0	1334	2.1	Usp	422	19	1.5
<i>M. lenae</i>	1.78	51	47	485	719	nv	985	2.1	U	526	24	2.0
<i>M. luna-gentiana</i> 4027	2.43	48	76	360	571	nv	416	2.4	Usp	228	11	3.0
<i>M. luna-gentiana</i> 4028	1.97	40	86	368	480	nv	375	2.7	USP	171	11	5.0
<i>M. micrantha</i>	1.30	40	39	308	617	nv	793	2.7	Usp	316	24	1.7
<i>M. noctiluca</i>	1.97	56	49	430	629	nv	307	2.1	USp	491	21	4.6
<i>M. pachystyla</i>	2.37	42	86	573	707	f	1982	3.6	Usp	280	19	1.4
<i>M. rubra</i>	1.72	27	93	327	806	nv	807	2.5	U	95	15	0.8
<i>M. sodiroana</i>	1.54	33	43	316	574	nv	1154	4.3	USp	245	32	2.9
<i>M. subsessilis</i>	1.97	39	92	447	648	0	1198	2.4	Us	190	8	2.5
<i>M. wallnoeferi</i>	2.33	31	103	477	582	0	818	2.7	Us	143	15	1.8
<i>M. wurdackii</i>	2.72	27	162	375	604	nv	2929	3.3	U	63	3	0.5
<i>Symbolanthus macranthus</i>	1.51	31	92	236	545	0	266	2.3	Us	80	12	1.3
<i>Tachia occidentalis</i>	1.90	36	67	661	814	ms	872	2.1	U	355	14	2.0
All collections, averaged:	1.90	42	67	432	640		862	2.8		368	17	2.6

^a Key to columns: VG (mean number of vessels per group); VD (mean vessel lumen diameter, μm); VM (mean number of vessels per mm^2); VL (mean vessel element length); FL (mean fiber-tracheid length); SF (septate fiber tracheids; 0 = no septa; f = few septate fibers present; ms = many septa per fiber present; nv = fiber-tracheids near vessels, nonseptate distal to vessels); MH (mean height of multiserial rays, μm); MW (mean width of multiserial rays at widest point, cells); RH (ray histology: u = upright cells; s = square cells; p = procumbent cells; capitals indicate abundance, lower case scarcity); ME (Mesomorphy ratio—vessel lumen diameter times vessel element length divided by mean number of vessels per mm^2); LL (average leaf length, cm); SD (sample diameter, cm). For collection data, see Materials and Methods.

Helieae falls well short of the ca. 184 species in 22 genera currently recognized. (Struwe et al., 2002). Nevertheless, the sampling of *Macrocarpaea* is very good, considering that wood anatomy has not hitherto been described for the genus. We recognize that conclusions can only be tentative, but to offer no interpretations because of sample size seems unwarranted.

Materials and Methods

All collections cited below were available in dried form. Samples of stem cylinders were preserved without any trimming, so that the diameter of the stem from which the sample was taken could be accurately determined. Detailed habit and habitat data can be found in Grant (2003, 2004, 2005), Grant and Struwe (2001, 2003), and Grant and Weaver (2003). Collections studied are

as follows: *Macrocarpaea angelliae* J. R. Grant & L. Struwe, Loja, Ecuador, J. R. Grant 4289 (NY); *M. apparata* J. R. Grant & L. Struwe, 28.8 km S of Yangana, Loja, Ecuador, J. R. Grant 4084 (NY, SBBG); *M. arborescens* Gilg, Loja, Ecuador, J. R. Grant 4084 (NY); *M. bubops* J. R. Grant & L. Struwe, Parque Nacional Podocarpus, Zamora-Chinchipe, Ecuador, J. R. Grant 4046 (NY, SBBG); *M. gattaca* J. R. Grant, Pichincha, Ecuador, J. R. Grant 4209; *M. harlingii* J. S. Pringle, Parque Nacional Podocarpus, Zamora-Chinchipe, Ecuador, J. R. Grant 4048 (NY, SBBG); *M. jensii* J. R. Grant & L. Struwe, Parque Nacional Podocarpus, Zamora-Chinchipe, Ecuador, J. R. Grant 4047 (NY, SBBG); *M. lenae* J. R. Grant, Loja, Ecuador, J. R. Grant 4013 (NY, SBBG); *M. luna-gentiana* J. R. Grant & L. Struwe, Loja, Ecuador, J. R. Grant 4027

(NY), 4028 (NY); *M. micrantha* Gilg, San Martin, Peru, J. R. Grant 3966 (NY); *M. noctiluca* J. R. Grant & L. Struwe, Parque Nacional Podocarpus, Zamora-Chinchipe, Ecuador, J. R. Grant 3994 (NY); *M. pachystyla* Gilg, S. Schunke V. 5298 (F, US); *M. rubra* Malme, BR 376 between Curitiba and Joinville, Paraná, Brazil, J. R. Grant 3449 (SBBG); *M. sodiroana* Gilg, Pichincha, Ecuador, Grant 4209 (NY); *M. subsessilis* R. E. Weaver & J. R. Grant, km 8.9 on road from Yangana to Cerro Toledo, Loja, Ecuador, J. R. Grant 4020 (NY); *M. wallnoeferi* J. R. Grant, Huánuco, Peru, Wolf 12269A (F); *M. wurdackii* R. E. Weaver & J. R. Grant, Peru, Smith 4793 (US); *Symbolanthus macranthus* (Benth.) Moldenke, 15 km S of Yangana, Loja, Ecuador, J. R. Grant and L. Struwe 3973 (NY); *Tachia occidentalis* Maguire & Weaver, Felix Woytkowski, Huánuco, Peru, USw-15885.

Collections studied for leaf measurements are the same as the above except for the following: *M. wurdackii*, San Martin, Amazonas, Peru, J. Wurdack 1071 (US); *Symbolanthus macranthus*, Zamora-Chinchipe, Loja, Ecuador, *Tachia occidentalis* Maguire & Weaver, Huánuco, Peru, F. Woytkowski (NY).

All wood specimens are from stems. Samples were boiled in water and stored in 50% aqueous ethanol. Although a range of textures was represented, all samples were of a hardness suitable for sectioning on a sliding microtome without special pretreatment. Sections intended for permanent slides were stained with a safranin-fast green combination. Unstained longisections were dried between clean slides, mounted on aluminum stubs, and examined with a Hitachi S2600N scanning electron microscope. Although well-preserved starch usually is not present in dried and boiled wood samples, starch remnants were present in some, the starch identified with polarized light. Macerations were prepared by means of Jeffrey's Fluid and stained with safranin. Stem diameter is based on the xylem cylinder without bark; drying of a stem does not appear to result in shrinkage of the xylem cylinder to any appreciable degree.

Terms are based on the IAWA Committee on Nomenclature (1964), although cer-

tain terms (fiber-tracheids, interxylary phloem, pseudoscalariform pitting, ray types) follow Carlquist (2001). Mean numbers of vessel per group are derived from an average where a solitary vessel = 1, a pair of vessels in contact = 2, etc. Vessel lumen diameter rather than outside vessel diameter is provided in Table 1 for reasons of physiological significance; diameter of vessels with non-circular outlines is based on an average of longest and shortest chords. Lengths of vessel elements and lengths of fiber-tracheids were determined from macerations of wood. The numerical comparisons given in the conclusions section are intended merely as illustrative of trends. True statistical significance in studies of wood anatomy is almost never attained, because that would require interplant comparisons as well as intraplant sampling (upper branches, outer main trunk, roots, etc.).

Results

GROWTH RINGS

No growth rings were observed in most of the species studied, as illustrated by Figures 1A, 2A, 2C, 3A, 3D, 4C. Weakly demarcated growth rings with vessels and fiber-tracheids wider in earlywood than in latewood were observed in *M. jensii*. Very weakly demarcated growth rings occur in *Symbolanthus macranthus* (Fig. 4C).

VESSELS

Solitary vessels are relatively common in *M. harlingii*, but even in that species the mean number of vessels per group is 1.39. In four species, the mean number of vessels per group exceeds 2.00 (Table 1, column 1). The predominant form of vessel grouping is radial multiples (Figs. 1A, 2A, 3A, 3D, 4A, 4C).

Vessel diameter ranges from 2 μm , as in *M. rubra* (Fig. 3A), to more than double that figure, as in *M. arborescens* (Fig. 1A). The mean for the family (Table 1, column 2) is close to halfway between the uppermost and lowermost means by species.

Vessel density ranges from 18 vessels per mm^2 in *M. harlingii* (Fig. 2C) to 162 in *M. wurdackii*. Although generally vessel di-

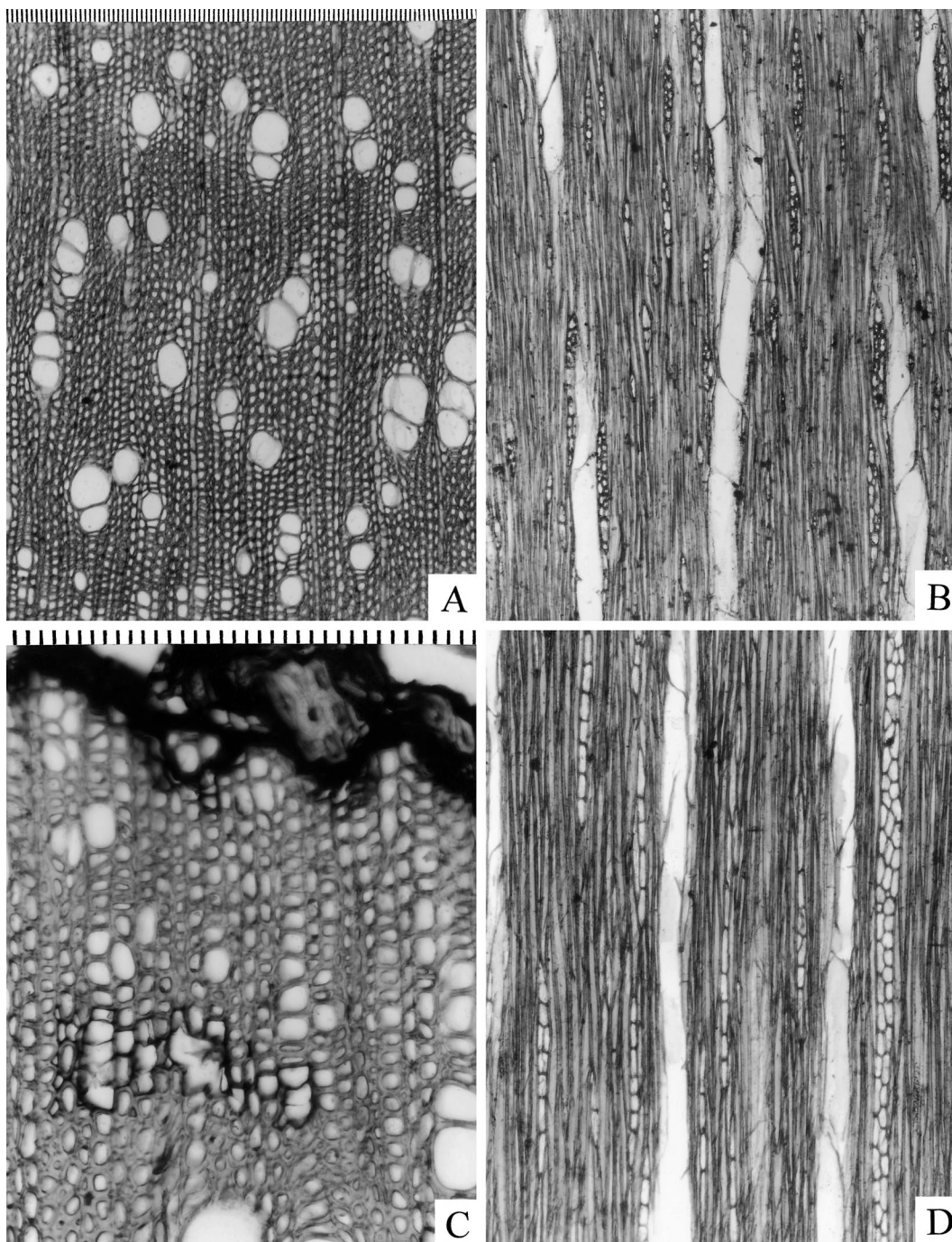


FIG. 1. Wood sections of *Macrocarpaea*. **A–C.** *M. arborescens*. **A.** Transverse section; vessels range widely in diameter. **B.** Tangential section; narrow multiseriate rays and uniseriate rays are about equally abundant. **C.** Portion of transverse section, bark at top; a tangentially broad strand of interxylary phloem is visible (dark, lower left). **D.** *M. lenae*. Transverse section; almost all ray cells shown are upright. Fig. 4A, B, D, scale above A (divisions = 10 μm); C, scale above C (divisions = 10 μm).

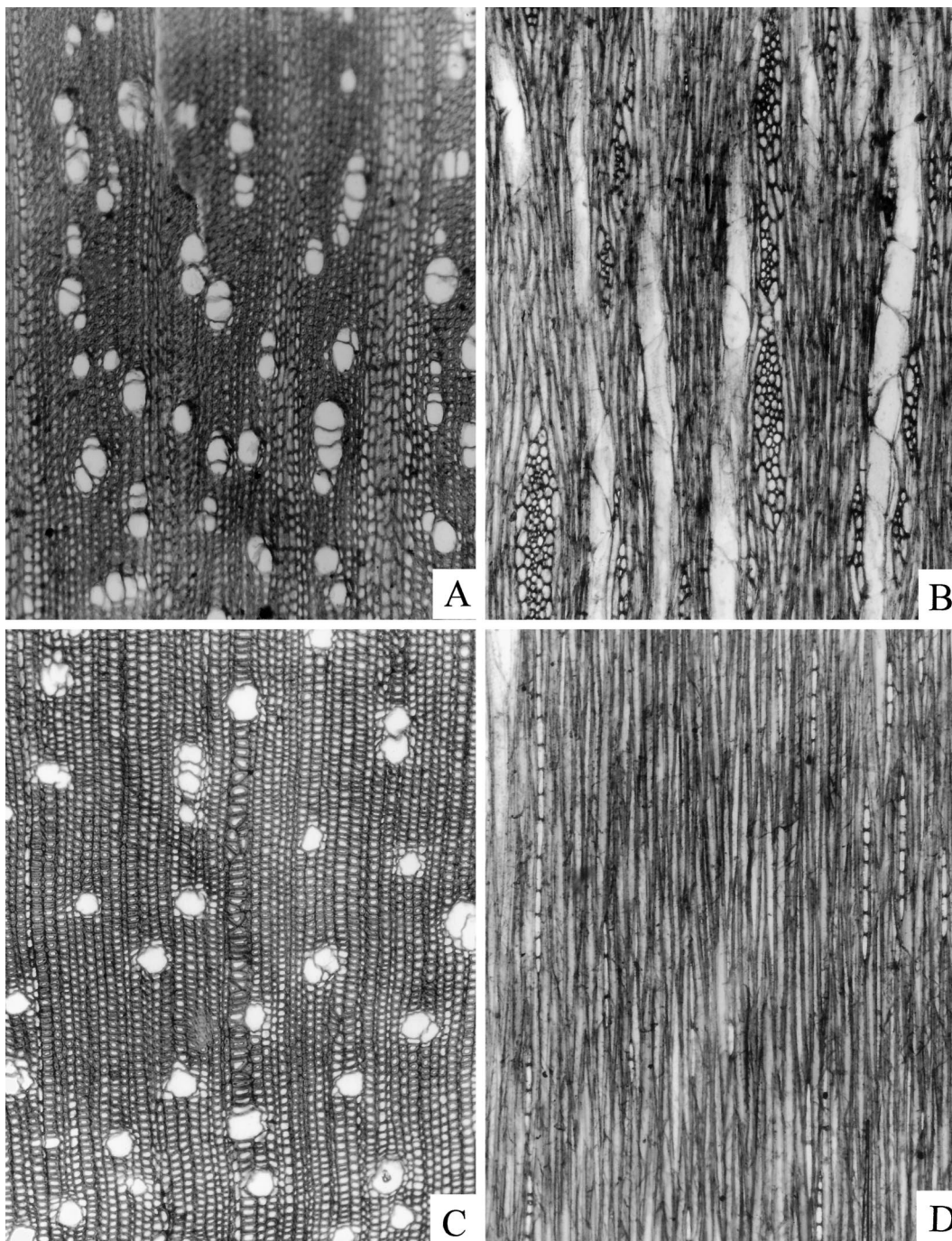


FIG. 2. Wood sections of *Macrocarpaea*. **A, B.** *M. bubops*. **A.** Transection; vessels are mostly grouped. **B.** Tangential section; Several wide multiseriate rays with procumbent cells in wider portions present. **C, D.** *M. harlingii*. **C.** Transection; vessels are mostly solitary. **D.** Tangential section; all rays shown are uniseriate, and composed of upright cells. Fig. 2A–D, scale above Fig. 1A.

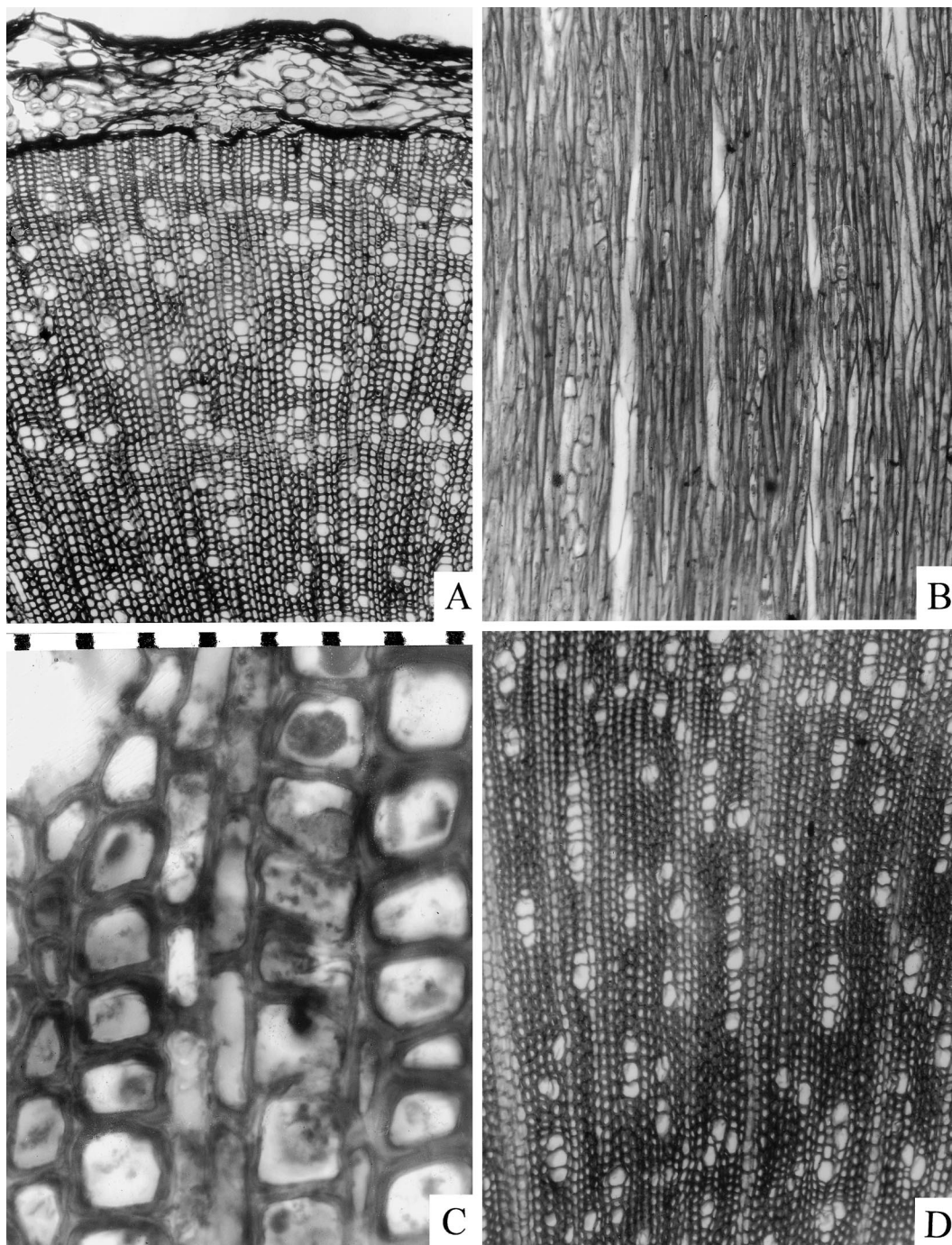


FIG. 3. Wood sections of *Macrocarpaea*. **A–C.** *M. rubra*. **A.** Transection, bark above; vessels are uniformly narrow in diameter. **B.** Tangential section; ray cells are upright; vague staining at lower right. **C.** Portion of transection (vessel, upper left, ray, middle) to show starch remnants and cytoplasm in fiber-tracheids. **D.** *M. subsessilis*. Transection; many vessels are in radial multiples. Fig. 3 A, B, D, scale above Fig. 1A; C, scale above C (divisions = 10 μm).

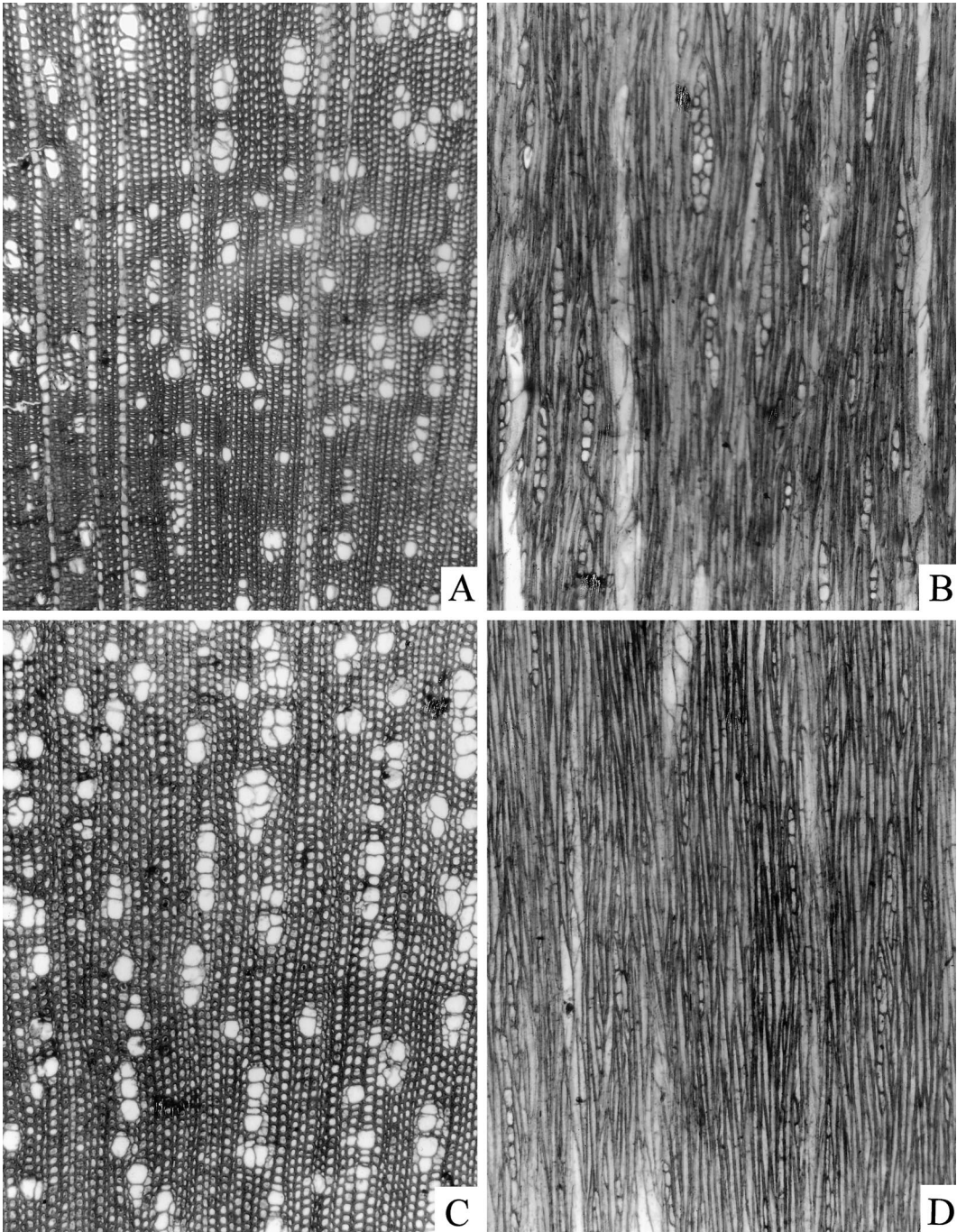


FIG. 4. Wood sections of Helieae. **A, B.** *Symbolanthus macranthus*. **A.** Transection; vessels narrow and solitary at bottom of photo, wider and grouped at top, suggesting an inconspicuous growth ring. **B.** Tangential section; rays are biseriate and uniseriate. **C, D.** *Tachia guianensis*. **C.** Transection; vessels mostly in radial multiples. **D.** Tangential section; rays are inconspicuous, composed wholly of upright cells. Fig. 4A–D, scale above Fig. 1A.

ameter and vessel density are thought to be reciprocals to each other, deviation from inverse proportionality is appreciable within the species studied.

Vessel element length (Table 1, column 4) is not uniform at all in the species studied. Such a pattern of variation demands comparisons with data on other wood dimensions, and Table 1 has been constructed to permit all possible comparisons.

Vessel wall thickness is not given in Table 1. For the species studied, mean thickness ranges from 1.5 to 2.5 μm , and averages 2.0 μm for the group. Vessel wall thickness is invariably lower than the wall thickness of the fiber-tracheids, for any given species.

Perforation plates are simple. Perforation plates are noteworthy in that in some collections of *Macrocarpaea*, occasional "constricted" plates are present. These plates are about half of the diameter of the vessel in which they are located; they were recorded for *M. apparata* and *M. arborescens*.

Lateral wall pits of vessels are 3–4 μm in axial diameter within *Macrocarpaea* (Figs. 5B–G, 6A–C) and in *Tachia*. They are about 5 μm in diameter in *Symbolanthus macranthus*. Lateral wall pitting is generally alternate (Figs. 5B–G, 6C–E). Despite the relatively uniform axial dimensions, lateral wall vessel pits show various degrees of lateral elongation. Marked lateral elongation of pits was observed to be common in *M. apparata*, *M. arborescens*, *M. gattaca*, *M. harlingii*, *M. pachystyla*, and *M. wurdackii*. This type of pattern is termed pseudoscalariform, and is easily distinguished from true scalariform by the fact that in scalariform pitting, lateral tips of pits terminate at cell angles rather than extending across two or more cell faces. Pseudoscalariform pitting in the Helieae is often but not always mixed with ordinary alternate pitting. Apparently true scalariform pitting was observed on vessel—ray and vessel—axial parenchyma contacts in *M. bubops*, *M. lenae*, and *Symbolanthus macranthus*. This trio of species has alternate pitting on vessel-to-vessel contacts.

Vestured pitting characterizes all of the species studied (Figs. 5, 6). Vestures range

from small (Fig. 5B, G) to larger (Fig. 6A, B, E, F). The vestures are more slender and coralloid in some collections (Fig. 5D), wider and blunter in others (Figs. 5E, 6A, 6B, 6C, 6E, 6F), and rounder and wartlike in yet others (Figs. 5C, 5F, 5G, 6C). These observations are intended to show a diversity within the material studied. A much more extensive series of observations on more numerous species would be required to establish correlations at the species level.

Lateral wall pits with rather wide ("gaping") pit apertures characterize a few species (Fig. 5D, E). Slitlike pit apertures are shown here (Figs. 5B, 5C, 5G, 6C–F).

IMPERFORATE TRACHEARY ELEMENTS

The imperforate tracheary elements of Helieae are fiber-tracheids, because bordered pits were observed on these elements (Fig. 5A) in all species. Borders (pit cavities) range in diameter from 2–3 μm . Figures for fiber-tracheid length are given in Table 1, column 5.

Septa were observed in fiber-tracheids in all species studied, except for *M. harlingii*, *M. jensii*, *M. subsessilis*, *M. wallnoeferi*, and *Symbolanthus macranthus* (Table 1, column 6). Septa are usually 1–3 per fiber-tracheid. Septate fiber-tracheids close to vessels, combined with nonseptate fibers distal to the vessels, were observed in *M. angelliae*, *M. apparata*, *M. bubops*, *M. lenae*, *M. luna-gentiana*, *M. micrantha*, *M. noctiluca*, *M. pachystyla*, *M. rubra*, *M. sodiroana*, and *M. wurdackii*. A high proportion of septate to nonseptate fiber-tracheids was noted in *Tachia guianensis*. Mean fiber-tracheid wall thickness for fiber-tracheids in the species studied is 3.4 μm .

AXIAL PARENCHYMA

Scanty vasicentric parenchyma was observed in all species studied, although it was noted to be infrequent in *M. angelliae*, *M. lenae*, *M. rubra*, and *M. wurdackii*. As seen in radial sections, strands of axial parenchyma consist mostly of two cells. The only exception to this is in *T. guianensis*, in which strands are composed of 2–5 cells.

RAYs

Multiseriate ray height (Table 1, column 7) shows an unusual distribution. The species mostly range between 300 μm and 900 μm in average multiseriate ray height. A scattering of species exceeds 1000 μm for this feature, however. Mean width of multiseriate rays at widest point, calculate in terms of number of cells, is given in Table 1, column 8. The figure for multiseriate ray width is relatively uniform, but species with notably wider rays include *M. bubops*, *M. gattaca*, and *M. sodiroana*.

In about half of the species studied, multiseriate rays are about as common as uniseriate rays in any given section (Figs. 1B, 1D, 3B, 4B). In other species, multiseriate rays are more common than uniseriate rays (Fig. 2B). Uniseriate rays outnumber multiseriate rays in *M. harlingii* (Fig. 2D). Uniseriate rays are present virtually to the exclusion of multiseriate rays in *T. occidentalis*. (Fig. 4D). In the present paper, biseriate rays are grouped with multiseriate rays in data categories.

Ray histology is summarized in Table 1, column 9. Readily apparent from the symbols used is the scarcity of procumbent cells, which are rare in most species, absent in some others. Where present, procumbent cells occur in the central portions of multiseriate rays. Because upright cells outnumber procumbent cells (Figs. 1B, 3B) or are at least as numerous as the procumbent cells, all of the Helieae studied should be designated as having Paedomorphic Type I rays (Carlquist, 2001). Multiseriate rays are rare in *M. harlingii* (Fig. 2D) and *T. guianensis* (Fig. 4D) and these species would have rays transitional between Paedomorphic Type I and Paedomorphic Type III. Upright, square, and procumbent cells are about equally frequent in *M. bubops* and *M. luna-gentiana* (Grant 4028), and thus these two species have ray conditions intermediate between Heterogeneous Type I and Paedomorphic Type I.

Mean ray cell wall thickness ranges from 1.5 μm to 2.5 μm in the species studied. Bordered pits are not common in species with thinner ray cell walls. Some bordered pits were observed on ray cells in species

with thicker ray cell walls, notably *Symbolanthus macranthus*.

TYLOSES

Thin-walled tyloses were observed in *M. arborescens* (tyloses abundant), *M. luna-gentiana* (tyloses scarce), *M. pachystyla* (with resinlike contents in tyloses), *M. wall-noeferi* (tyloses both with and without resinous contents), and *T. guianensis*.

INTERXYLARY PHLOEM

A few strands of interxylary phloem were observed at the periphery of stems of *M. arborescens* (Fig. 1C, lower left).

STORYING

Storying is vague at most in Helieae (Fig. 3B). The samples studied lack clearly storied structure with respect to any cell type.

CELLULAR CONTENTS

Starch is apparently often lost in preservation of wood samples or in processing them (fixation of living materials in ethanol tends to preserve starch). Thus, the absence of starch in most of the samples studied is not surprising. In the present study, starch was observed in fiber-tracheids of *M. arborescens* and *M. luna-gentiana*. Cytoplasm remnants plus starch remnants were seen in fiber-tracheids of *M. rubra* (Fig. 3C), *M. sodiroana*, and *T. occidentalis*. Starch was recorded in rays of *M. subsessilis*. No crystals or silica bodies were observed in any of the woods studied.

Conclusions

EFFECT OF SAMPLE DIAMETER

Before conclusions with relation to ecology, habit, and systematics can be addressed, the effect of the diameter of the stems studied (Table 1, column 12) should be addressed. Stem diameter is fortunately available for all specimens used in the present study, so that the effect of this factor can be taken into account. All too often, data on this factor are unknown (as with most xylarium samples, for example), and

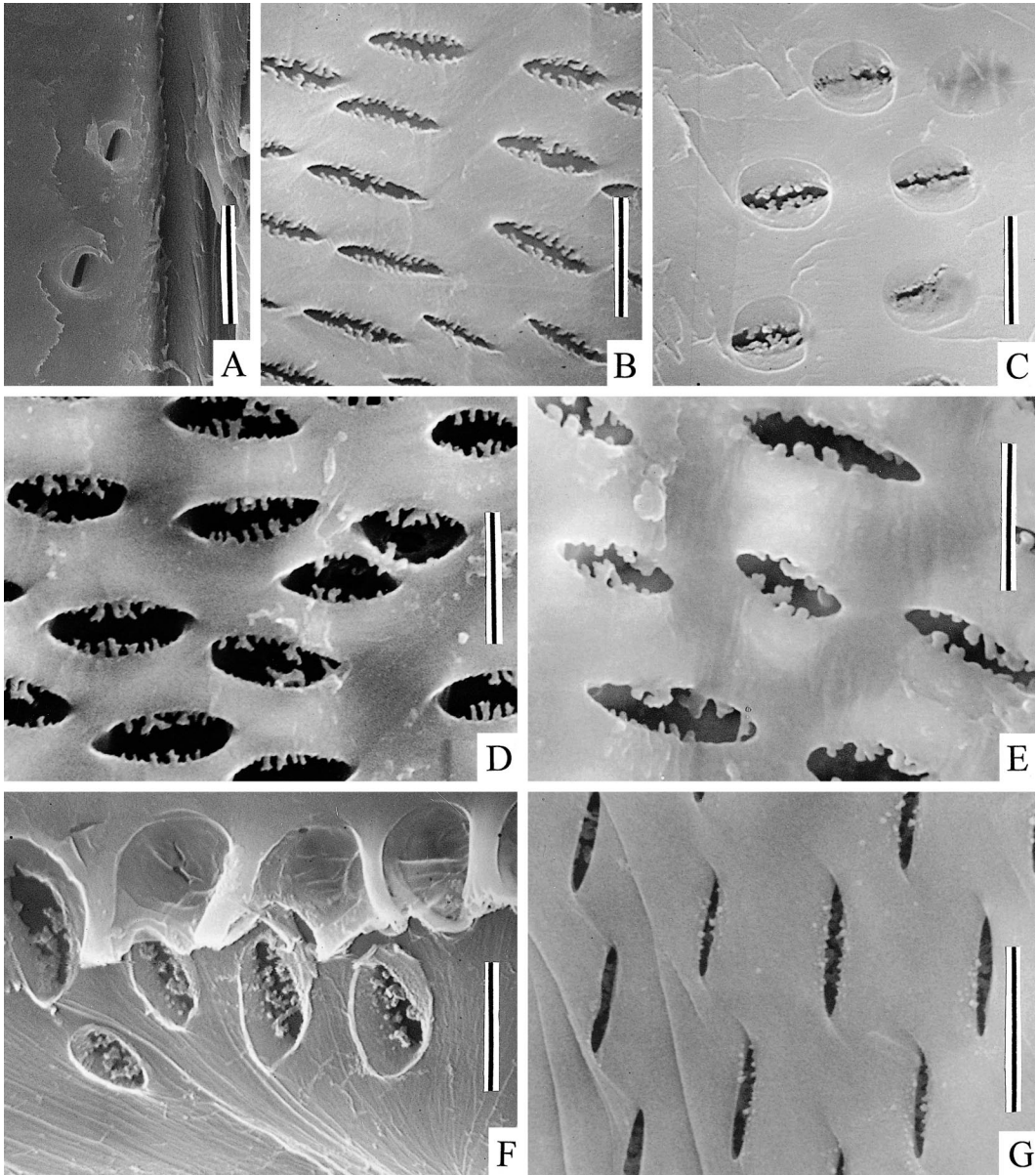


FIG. 5. SEM photographs of tangential wood sections of *Macrocarpaea*, showing vestured pits in B–G. **A.** *M. angelliae*. Outer surface of fiber-tracheid, showing two bordered pits. **B., C.** *M. apparata*. Lateral wall pitting of vessels. **B.** Inner surface of vessel, showing narrow pit apertures, **C.** Outer surface of vessel; vestures are wartlike. **D.** *M. bubops*, inner surface of vessel; vestures are coralloid. **E.** *M. gattaca*, inner surface of vessel; vestures are thick, rounded. **F.** *M. harlingii*, outer surface of vessel; vestures are wartlike. **G.** *M. jensii*, inner surface of vessel; vestures are notably small. Scale in A = 10 μm ; Scales in B–G = 5 μm .

thus there has been insufficient appreciation of changes in wood anatomy on a comparative basis. Barghoorn (1940, 1941) has called attention to changes in the cambium

as a stem increases in diameter, but only in selected examples.

A simple device is used here to develop ideas regarding the effect of sample size (as

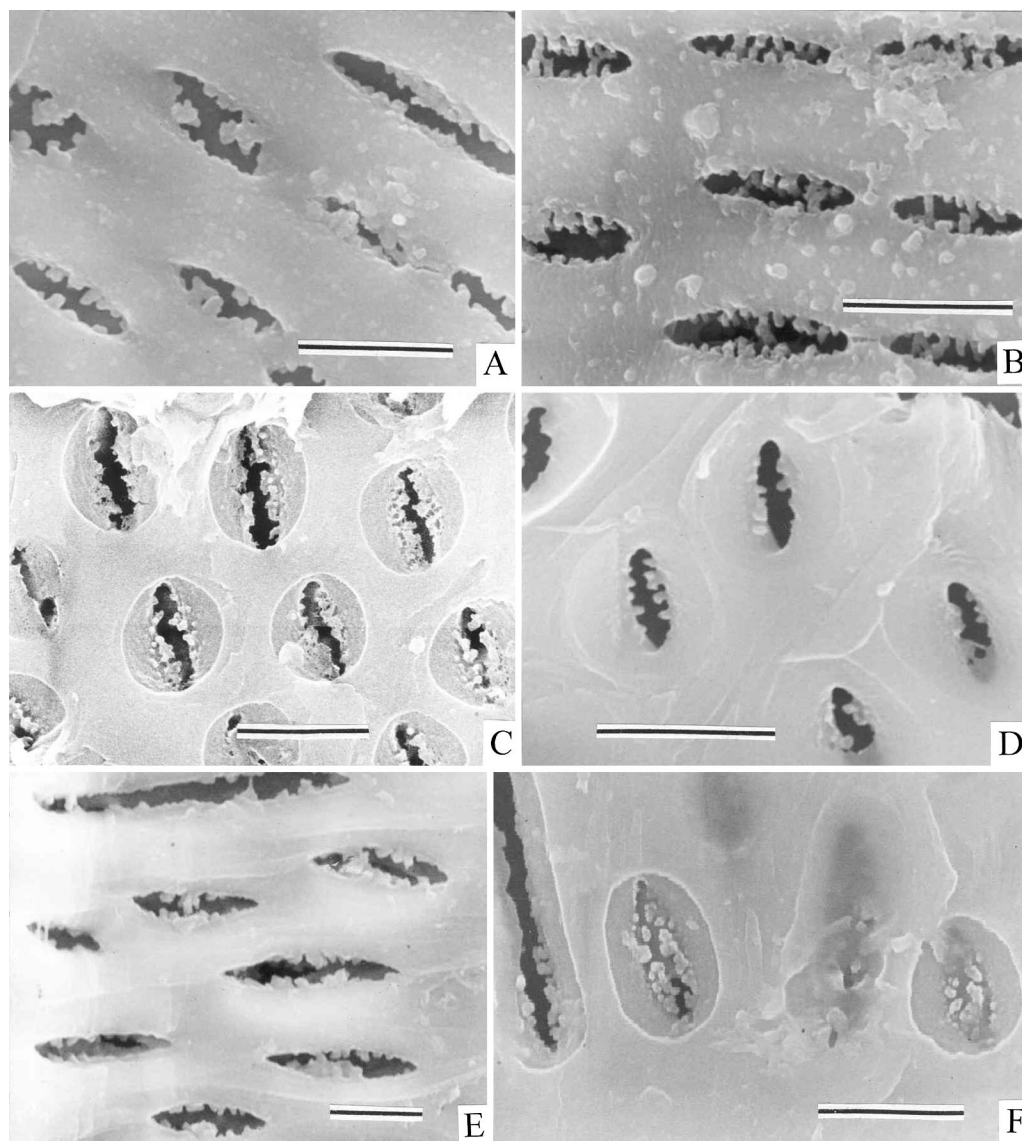


FIG. 6. SEM photographs of vestured pits in lateral walls of vessels from tangential sections. **A.** *Macrocarpaea micrantha*. Inner surface of vessel to show large, blunt vestures. **B.** *M. pachystyla*. Inner surface of vessel, showing rounded vestures in pit; droplets of a secondary compound are present on the vessel surface. **C.** *M. wallnoeferi*. Outer surface of vessel; vestures are varied in size. **D.** *Symbolanthus macranthus*. Outer surface of vessel; vestures are uniform, rounded. **E–F.** *Tachia occidentalis*. **E.** Inner surface of vessel; pit apertures are variously laterally elongate; **F.** Outer surface of vessel; vestures are varied in size, wartlike. Scales in A–F = 5 μm .

well as for discerning other correlations in wood features). Means for each quantitative feature in Table 1 have been presented and for each feature (bottom line) an average for the collections studied has been calculated. By dividing the figures for any fea-

ture that have values above the tribe average, taking those figures and obtaining figures for that same group of species, one can obtain a picture (supplemented by a similar procedure of figures below average for the tribe). For example:

Mean ray width for collections with below average (ave. = 2.6 cm) sample diameter = 3.1 cells.

Mean ray width for collections with above average (ave. = 2.6 cm) sample diameter = 2.5 cells.

The values for these two calculations are so similar that one may conclude that increase in ray width with increase in sample diameter does not occur here, and that in these collections, the considerations of Barghoorn (1940, 1941) do not apply.

RAYS AND PAEDOMORPHOSIS

Using the above format for a different feature, one obtains the following:

Mean sample diameter for species with above average (ave. = 862 μm) ray height = 1.8 cm.

Mean sample diameter for species with below average (ave. = 862 μm) ray height = 3.0 cm.

The figures 1.8 and 3.0 are sufficiently divergent to indicate a correlation between taller rays and narrower sample diameter. This is what one would expect if taller rays represent a juvenile condition. The decreased height of rays as stem diameter increases has been cited as a feature of paedomorphosis in dicotyledon woods (Carlquist, 1962, 1969, 1985).

A much more striking evidence of paedomorphosis in rays is the nature of ray histology (Carlquist, 1962, 2001). In Table 1, column 9, frequency abundance and presence of upright, square, and procumbent cells are characterized for each collection. If one selects the two collections designated by the formula USP (upright, square, and procumbent cells equally abundant), one finds a mean stem diameter of 5.4 cm. for those two samples. If, on the other hand, one selects the species with the designation U (only upright cells present in rays), one finds a sample size of 1.2 cm. Thus, in Helieae, when the amount of wood produced is more limited, the wood is highly juvenilistic in terms of ray histology. Moreover, the least juvenilistic woods with respect to ray histology (those designated USP) still can be considered more than ordinarily ju-

venilistic and thus paedomorphic (considering the great average sample diameter: these are trees, not mere twigs). In dicotyledons at large, the formula for rays with an adult ray structure would be usP, and Heterogenous Type I is based upon the usP formula. The wood of *Chelonanthus chelonoides* begins as rayless, after which multiseriate rays with upright cells only are produced. These characteristics meet the criteria of paedomorphosis (Carlquist, 1962).

Thus, all species in the present study have moderately to strongly juvenilistic rays, and paedomorphosis characterizes helioid woods. This would accord, under the theory of paedomorphosis (Carlquist, 1962) with an ancestry of minimally wood habit. Struwe et al. (2002: 209) concluded that the ancestor for Gentianaceae (excluding Gentianeae) was a suffrutescent perennial, and that arborescence has evolved in parallel several times within the family. Struwe et al. (2002) consider that arborescence has evolved from such a less woody ancestry in *Macrocarpaea* and *Symbolanthus*.

The pseudoscalariform pitting common on lateral walls of vessels of Helieae should probably be considered an indicator of paedomorphosis, in accordance with Carlquist (1962).

VESSEL FEATURES AND ECOLOGY

Comparisons like those above can be applied to quantitative data for vessels:

Mean sample diameter for species with above average (ave. = 42 μm) vessel lumen diameter = 3.7 cm.

Mean sample diameter for species with below average (ave. = 42 μm) vessel lumen diameter = 1.8 cm.

Comparison of these two figures shows striking divergence, indicating that narrower vessels are to be expected in samples with small diameter, and much wider diameter in samples with greater diameter. Note should be taken that wood anatomists typically take portions for sectioning from the outside of larger-diameter samples, as was done here. The phenomenon of production of vessels with increased diameter

as the stem increases in diameter is well known (e.g., Carlquist, 1987). There is no demonstrable correlation of juvenilistic features. Rather, the correlation seems to be that wider and therefore more efficient conduits in the xylem are produced when deeper, more relatively moist soil depths can be tapped by roots.

Grouping of vessels is a mechanism for producing conductive safety in dicotyledons with fiber-tracheids or libriform fibers as the ground tissue of a wood (Carlquist, 1984a). The average number of vessels per group in the helioids studied here is 1.90. This is not a notably elevated figure in dicotyledons at large. The mesic habitats of Helieae seem correlated with low degree of vessel grouping and low degree of vessel density (mostly <100 per mm²). Evidently, neither increased vessel grouping or greater vessel density is of much selective value in the relatively mesic habitats where Helieae grow.

Vessel diameter times vessel element length divided by number of vessels per mm² produces the so-called Mesomorphy Ratio; this Ratio has been shown to be a sensitive reflector of adaptation to moisture availability (Carlquist, 1981). Mesomorphy values are given for the collections studied in Table 1, column 10. Using this Ratio for Helieae:

Mean sample diameter for species with Mesomorphy Ratio above average (ave. = 368) = 3.8 cm.

Mean sample diameter for species with Mesomorphy Ratio below average (ave. = 368) = 2.0 cm.

The above correlation shows that increasing wood mesomorphy parallels increase in stem diameter.

Larger leaf size ought to be correlated with more mesomorphic woods, based upon the often-cited large leaf size (especially in understory plants) in wet forest. Figures for average leaf length (Table 1, column 14) are very imprecise, based as they are on herbarium specimens. Differing leaf textures among the species provide other sources of uncertainty where use of this dimension is concerned. Nevertheless, with the data available, we find that:

Collections with mean leaf length above average for the tribe (ave. = 17 cm) have a mean Mesomorphy Ratio value of 416. Collections with mean leaf length below average for the tribe (ave. = 17 cm) have a mean Mesomorphy Ratio value of 331.

The expectation that larger leaves are correlated with higher values in wood mesomorphy is fulfilled.

FIBER-TRACHEIDS

Helieae are interesting in possessing what should be called fiber-tracheids, as noted above and in Carlquist (1984a). The fiber-tracheids have distinct pit borders. However, because of sparseness of pits, small size of pit cavities, presence of septa, and presence of starch, any appreciable conductive function for these cells is unlikely. In confirmation of lack of conductive function of fiber-tracheids, the presence of vestured pits on lateral walls of vessels in Helieae stands in contrast with the absence of vesturing on bordered pits of the fiber-tracheids. Certainly the fiber-tracheids of Helieae do not deter vessel grouping, a correlation noted elsewhere in dicotyledons by Carlquist (1984b); in which a higher degree of grouping with heightened xeromorphy does not occur if tracheids are present. On the basis of these criteria, the imperforate tracheary elements of Helieae should be called fiber-tracheids, in conformity with earlier (IAWA Committee on Nomenclature, 1964) and more recent (Carlquist, 2001) usage.

A number of the species studied here were observed to have septate or living fiber-tracheids in close proximity to vessels, but nonseptate fiber-tracheids distal to vessels. This distribution suggests that living or septate fibers may be serving as a substitute for, or an augmentation of, paratracheal (vasicentric) axial parenchyma. Indeed, axial parenchyma is very scarce in *M. lenae*, *M. rubra*, and *M. wurdackii*. Thus, helioids appear to be a transition between possession of axial parenchyma as a photosynthate-rich tissue and conversion of imperforate tracheary elements to a tissue serving for photosynthate storage.

INTERXYLARY PHLOEM

The presence of interxylary phloem in *M. arborescens* is interesting, because it is the first report of this phenomenon in tribe Helieae. The fact that interxylary phloem is present only at the periphery of a rather large (for the tribe) stem is noteworthy in that this feature thus does not seem to be an expression of a juvenile condition. Metcalfe and Chalk (1950) reported the phenomenon in Gentianaceae for the genera *Blackstonia*, *Geniostemon*, *Gentiana*, *Nemothea*, *Schultesia*, and *Swertia*; it has also been reported and figured for the gentianaceous genus *Ixanthus* (Carlquist, 1984a).

VESTURED PITS AND OTHER SYSTEMATIC CRITERIA

Helioid Gentianaceae have not been sampled extensively with respect to wood anatomy. This circumstance limits the extent to which wood features can be cited as systematic criteria. Still, there are distinctive conditions that bear consideration. In *Symbolanthus macranthus*, the strands of axial parenchyma are composed of more numerous cells than in the other taxa, and the rather thick ray cell walls of this species bear more numerous bordered pits than are characteristic of other species of the tribe. In *Tachia occidentalis*, more numerous septa per fiber-tracheid are present in the remainder of the tribe.

Vestured pits characterize many Gentianaceae s.l. (Mennega, 1980; Jansen & Smets, 1998, 2000; Jansen et al., 1998). These papers clearly suggest that delimitation of Gentianaceae as a whole and of generic groupings within the family correspond to presence of vestured pits in lateral wall pitting of vessels. The data of the present paper suggest the possibility that coarseness and morphology of vestures may ultimately prove useful as systematic criteria within *Macrocarpaea* when more numerous species have been studied.

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