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## WOOD AND BARK ANATOMY OF MYRICACEAE: RELATIONSHIPS, GENERIC DEFINITIONS, AND ECOLOGICAL INTERPRETATIONS

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### ABSTRACT

Wood anatomy of the single species of *Canacomyrica* (hitherto not studied) shows that it belongs in Myricaceae, although it differs from other genera in several respects (axial parenchyma grouped in bands or columns as well as diffuse; Heterogeneous Type I rays; more numerous bars per perforation plate). The latter two features are primitive for the family. The four genera (*Canacomyrica*, *Comptonia*, *Morella*, and *Myrica* s.s.) differ from each other not only by qualitative features but by quantitative features (feature means in genera mostly non-overlapping). Wood of *Comptonia* and *Myrica* s.s. lacks chambered crystals in axial parenchyma and ray crystals. Wood of *Myrica* s.s. has tracheids in late-wood but fiber-tracheids in earlywood. Diagnostic generic summaries are presented. Features of Myricaceae such as scalariform perforation plates, presence of (true) tracheids, ray types, chambered encapsulated crystals in axial parenchyma, and bark anatomy correspond with character states and expressions in Betulaceae, Casuarinaceae, Corylaceae, Juglandaceae (including Rhoipteleaceae), Ticodendraceae and, to a lesser extent, Fagaceae and Nothofagaceae. This grouping of families can be found as Fagales in recent DNA trees. The predominance of tracheids in basal Fagales such as Myricaceae and Ticodendraceae suggests that origin of vasicentric tracheids which occur in combination with libriform fibers in Fagaceae is the product of tracheid dimorphism. Low imperforate tracheid length to vessel element length ratios (F/V ratios) in Myricaceae are a probable indication of wood primitiveness. Quantitative vessel features of Myricaceae, as combined in Mesomorphy Ratio values, characterize wood of Myricaceae as a whole, but at the species level such values correspond to respective habitats; notably high vessel density in *Comptonia* may represent greater conductive safety appropriate to relatively dry habitats.

Key words: *Canacomyrica*, ecological wood anatomy, eurosids, Fagales, *Morella*, systematic wood anatomy, tracheids, vasicentric tracheids, vessel grouping.

### INTRODUCTION

No monographic study of wood anatomy of Myricaceae exists, although details of wood of a scattering of species of Myricaceae can be found in a number of publications (see Gregory 1994). A condensed summary based on a small number of species can be found in Metcalfe and Chalk (1950). The present study is based on specimens of all species available in leading xylaria, plus collections by the writer. This monograph is intended to address particular questions about the systematics of Myricaceae and Fagales, but also to analyze the data in terms of ecology, habit, and particular anatomical modes of structure.

Definitions of genera in Myricaceae have varied considerably. The inclusion of *Canacomyrica* has been questioned (Thorne 1968, 1976), although no alternative placement has been proposed (Cronquist 1981; Thorne 2001). Wood anatomy of *Canacomyrica* has not been described hitherto. *Comptonia* seems universally recognized as a monotypic genus (Elias 1971; Cronquist 1981; Thorne 2001). Likewise, a number of workers have treated the species sometimes formerly known as *Gale hartwegii* A. Chev. and *G. palustris* A.

Chev. but more commonly under *Myrica* as a genus separate from the remainder of the family. The correct name for this small genus is not *Gale*, as assumed by Hylander (1945), who mistakenly thought that *Myrica cerifera* L. is the type species of *Myrica* (see Elias, 1971, p. 309), but *Myrica*, because the type of the genus is actually *Myrica gale* L. Elias (1971) recognizes sections *Gale* and *Morella* as sections of *Myrica*, but more recent workers have raised these sections to genera. *Morella* is being recognized by taxonomic workers (Knapp 2002), and in floristic treatments such as Killick et al. (1998) and Goldblatt and Manning (2000). Although in many families, wood features may follow ecological adaptations primarily, and relatively few criteria are present in wood features for generic distinctions, that proves not to be true in Myricaceae. The present study thus becomes an excellent example of systematic wood anatomy, in which all of the genera are amply distinguishable in terms of wood features. Unfortunately, all of the recognized genera have not been sampled for the purpose of constructing DNA-based phylogenetic trees, and such data is much needed. DNA data is available for only a tiny fraction

of the estimated 45 valid species of Myricaceae (Thorne 2001).

Myricaceae have been generally placed in Fagales or Juglandales, if recognized separately from Fagales (summary of treatment of 12 phylogeneticists in Goldberg 1986). Molecular data have confirmed this placement. Analyses offer trees that place Myricaceae in the rosoid line in a clade that corresponds to Fagales; closeness to Juglandaceae is indicated (e.g., Soltis et al. 2000), but some degree of proximity to Betulaceae and Casuarinaceae is also possible (Manos and Steele 1997). If floral morphology is a reliable indicator of relationships, female flowers of Juglandaceae are worthy of consideration. Just as the female flowers of Juglandaceae have inferior ovaries (Cronquist 1981), those of Myricaceae also appear to be epigynous (MacDonald 1989). In *Canacomyrica* (Fig. 1), this seems to be true, because a crown of five teeth, presumably calyx teeth, crown the fruit. Alternatively, these have been interpreted as a late-developing disc that envelops the ovary (Cronquist 1981). Three branched stigmas (dark in Fig. 1) tip the fruit of *Canacomyrica*. Between the calyx teeth and the stigmas are stamens, rendered visible in Fig. 1 by their covering of pale golden glandular trichomes (some of these trichomes are also seen on the bract below the ovary). MacDonald (1989) figures apparent apical bracts, like the putative calyx teeth of *Canacomyrica*, for *Myrica gale*. The apical androecium of *Canacomyrica* has a counterpart in the apical androecium figured for *Morella californica* (MacDonald 1989). The female flowers of *Canacomyrica* show at least superficial similarity to flowers of pomoid Rosaceae, if the above interpretation is correct. MacDonald (1989) interprets *Comptonia* as unique among Myricaceae in having a superior ovary. Developmental studies of myricaceous flowers are very much needed.

The notion that *Canacomyrica* does not have orthotropous ovules was corrected by Leroy (1949, 1957), who also demonstrated that what Guillaumin, in describing the genus, thought was an elongate funiculus is actually a prolonged integument (see Cronquist 1981, for a full account). Sundberg (1985) has concluded that pollen of *Canacomyrica* is compatible with that of other Myricaceae, although generically distinct.

Thus, comparisons of wood of Myricaceae with that of other Fagales, especially Juglandaceae, are appro-

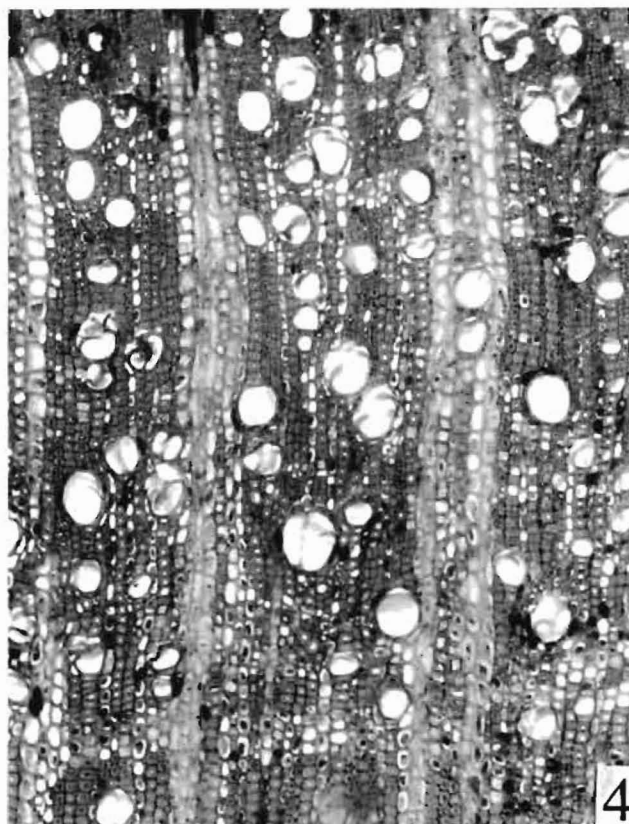
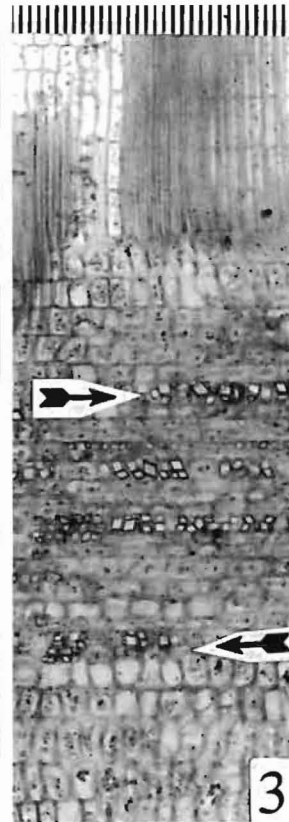
priate. The submersion of Rhoipteleaceae into Juglandaceae (e.g., Thorne 2001) suggests that *Rhoiptelea* must be included in comparisons also. Because the fagalean clade is a segment of the larger group now generally termed eurosids I (e.g., Soltis et al. 2000), Rosaceae might be expected to share some features with Fagales as a whole and Myricaceae in particular. The controversial matter of aggregate rays and compound rays, which are common in some Fagales (Metcalfe and Chalk 1983) must inevitably be considered in terms of whether Myricaceae offer any equivalents to such rays. Likewise, the relationship between tracheids in Myricaceae and vasicentric tracheids in Fagaceae needs examination.

Myricaceae occupy a range of habitats, apparently mostly mesic. Youngken (1919) claims swampy habitats for all eastern U.S. species except for *Comptonia*, which "thrives in dry sterile soil." *Morella californica* occurs in canyons and moist slopes, whereas *Myrica hartwegii* is found on montane stream banks (Munz 1959). The South African species (*Morella*) occur on sandstone or on sandy or limestone slopes (Goldblatt and Manning 2000), but those authors do not describe water availability in these localities. *Canacomyrica* grows in moist forest near the summit of the Montagne des Sources, New Caledonia (original observation). The range in quantitative vessel data within the family is considerable, indicating that adaptation to a range of habitats has occurred, so analyses like those of Carlquist and Hoekman (1985) are undertaken.

#### MATERIALS AND METHODS

Specimens documenting collections studied are as follows (xylaria abbreviated according to Stern 1988): *Canacomyrica monticola* Guillaumin, tree to 7 m, up to 12 cm in diameter at base, in *Araucaria humboldtensis* woodland, with *Balanops*, *Dacrydium*, and *Strasburgeria*, ridge near summit of Montagne des Sources, New Caledonia. Carlquist 15290 (RSA); *Comptonia peregrina* (L.) J. M. Coulter, barren flats adjacent to Logan Airport, Boston, Massachusetts, U.S.A., Carlquist 634 (RSA); *Morella californica* (Cham. & Schldl.) R. L. Wilbur, cultivated at Rancho Santa Ana Botanic Garden, Claremont, California, U.S.A.; *M. cerifera* Small, Yale-49459, Florida Keys, Florida, U.S.A., W. L. Stern 1955; *M. domingana* (C. DC.) Carlquist, comb. nov. [*Myrica domingana* C.

Fig. 1–5. *Canacomyrica monticola*.—1. Fruit on inflorescence axis, bracteole at base and anthers at apex are distinguished by their coverings of pale glandular trichomes; stigmas (dark gray) at summit of fruit; note pointed structures, which may be calyx teeth, below anthers.—2–3. Radial sections of wood.—2. Strands of axial parenchyma bearing rhomboidal crystals (above) and upright cells of uniseriate ray (below).—3. Radial files of crystal-bearing cells in multiseriate ray (arrows), separated from each other by cells that lack crystals.—4. Transection of wood, narrower latewood vessels near bottom.—5. Tangential section of wood; uniseriate rays have upright cells, multiseriate rays are composed of procumbent cells with some upright sheathing cells. Fig. 1, scale bar = 1 mm; Fig. 2, scale bar at top, divisions = 10  $\mu$ m; Fig. 3–5, scale bar at top of Fig. 3, divisions = 10  $\mu$ m.





DC.], Dominican Republic, USw-1929, in RSAw; *M. faya* (Ait.) R. L. Wilbur, adventive in forests of Kokee, Kauai, Hawaii, U.S.A., Carlquist 523 (RSA); *M. inodora* (W. Bartram) Small, SE U.S.A., Stearns 21, USw-160135; *M. javanica* (Blume) I. M. Turner, Java, SJRW-31834; *M. kraussiana* (Buchinger ex Meisn.) D. J. B. Killick, S. Carlquist 8067 (RSA), cult. Kirstenbosch Botanic Garden, South Africa; *M. microcarpa* Benth., Jamaica, USw-6105; ***Morella nagi*** (Thunb.) Carlquist comb. nov. [*Myrica nagi* Thunb., Nova Acta Soc. Sci. Upsal. 4:37. 1783], cult. Bot. Gard. Univ. Tokyo, S. Carlquist 7880 (RSA); *Morella pubescens* (Hunt. & Bonpl. ex Willd.) R. L. Wilbur, Peru, coll. Wurdack (US), USw-32525; *M. quercifolia* (L.) J. B. Killick, cult. Kirstenbosch Botanic Gardens, South Africa, Carlquist 8062 (RSA); *M. rubra* Lour., cloud forest surrounding Panar Laban Cabin, Mt. Kinabalu, 3800 m, Sabah, Malaysia, S. Carlquist 15495 (RSA); *M. salicifolia* (A. Rich.) B. Verdcourt & R. M. Polhill, Uganda, PRFW-26591; *Myrica gale* L., NE U.S.A., Pease 325 (RSA); *M. hartwegii* S. Watson, cult. Rancho Santa Ana Botanic Garden, Claremont, California, U.S.A. The genus *Myrica* as recognized here (*M. gale* and *M. hartwegii*, also the genus *Gale* of some authors) is termed *Myrica* s.s. (sensu stricto) here so as to distinguish it from the more inclusive *Myrica* of many earlier authors.

The wood and bark samples were all available in dried form. Samples were boiled and stored in 50% aqueous ethanol. Woods of Myricaceae are not exceptionally hard or soft, so they can be sectioned on a sliding microtome without pretreatment to mitigate hardness. Bark adhered to some wood sections and provided usable data on bark anatomy. Sections for permanent slides were stained with safranin and counterstained with fast green. Some sections were left unstained, dried between clean glass slides, mounted on aluminum stubs, sputter-coated, and examined with a Hitachi 2600N scanning electron microscope (SEM). Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Mean number of vessels per group is based on an average of counts in which a solitary vessel = 1, a pair of vessels in contact = 2, etc. (this can also be defined as number of vessels divided by number of vessel groups, solitary vessels in that case counting as a group). Because vessel tips overlap considerably, a transection of the overlapping region can appear as a pair of vessels, and care was taken to distinguish these instances from genuine pairs of vessels in contact. Vessel lumen diameter is measured rather than outside vessel diameter because the lumen diameter is significant hydrologically. Terms used are in accordance with the IAWA Committee on Nomenclature (1964), which distinguishes among tracheids, fiber-tracheids, and libriform fibers in dicotyledonous woods, but the

term vasicentric tracheid is used in accordance with Carlquist (2001), a usage that follows closely the usage of Metcalfe and Chalk (1950), and the term "apotracheal columns" is proposed for a grouping of axial parenchyma cells found in *Canacomyrica*. The arrangement of photographs (Fig. 1–45) is alphabetical by genus.

## RESULTS: WOOD ANATOMY

### Growth Rings

Most Myricaceae show growth rings, ranging from almost imperceptible, as in *Canacomyrica* (Fig. 4, latewood at bottom) to more pronounced, as in *Comptonia* (Fig. 8), *Morella californica* (Fig. 10), *M. inodora* (Fig. 14), *M. nagi* (Fig. 16), *M. rubra* (Fig. 38, 40), *M. quercifolia*, *Myrica gale* (Fig. 42), and *M. hartwegii* (Fig. 44). No appreciable growth ring formation was observed in *M. javanica* (Fig. 26), *M. kraussiana* (Fig. 30), or *M. pubescens* (Fig. 32). Growth rings, where minimal, feature a small change in vessel diameters between earlywood and latewood (Fig. 4, 12). In species of *Morella* with more pronounced growth rings, the latewood is brief, i.e., most of the growth ring contains vessels of moderate diameter and narrower vessels are formed only a short distance prior to the ends of the growth rings. In species with more pronounced growth rings, the latewood tracheids tend to be thicker walled and radially narrower than those in earlywood (Fig. 14, 16, 40).

*Myrica* s.s. is distinctive in having numerous vessels in the earlywood (Fig. 42, 44). These vessels are densely placed in earlywood, and therefore, the number of vessels per group is higher in *Myrica* s.s. than in other Myricaceae (Table 1, column 1). However, in the latewood, vessels are sparse (Fig. 44, center) or absent (Fig. 42, center). Thus, *Myrica* s.s. represents growth ring Type 5A or 5B (Carlquist 2001), whereas the remaining Myricaceae fall into Type 1D (vessels wider in earlywood, tracheids wider in earlywood) or Type 1C (vessels wider in earlywood, but tracheids about the same throughout the ring).

### Quantitative Vessel Features

Vessel grouping (Table 1, column 1) is minimal in Myricaceae. One must view reports of vessel grouping in dicotyledons with tracheids as the imperforate tracheary element type with care, because mistaking a transection of overlapping vessel ends as a pair of vessels is easy to do. Vessel grouping is as low as one finds in any family of vessel-bearing dicotyledons if one deducts the two species of *Myrica* s.s.

If one measures mean diameter of vessels as seen in transection (Table 1, column 2), narrower vessels characterize *Comptonia peregrina*, *Myrica gale*, and

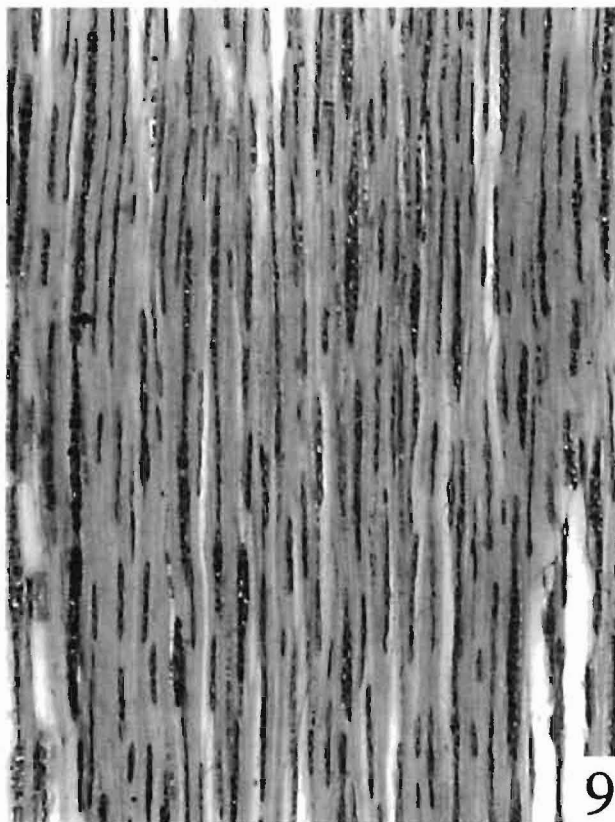


Fig. 6–9. Wood sections of Myricaceae.—6–7. *Canacomyrica monticola*.—6. Transection, vessel at bottom, axial parenchyma in bottom third of photo, and, in tracheids above, dark deposits outline the bordered pits.—7. Group of axial parenchyma strands (columnar apotracheal parenchyma) containing encapsulated rhomboidal crystals, from radial section.—8–9. *Comptonia peregrina*.—8. Transection of outer stem, bark at top (sclereid nests gray, parenchyma dark); secondary xylem below shows large vessels at the beginning of a growth ring.—9. Tangential section; rays are mostly uniseriate, and are distinguishable by their dark contents. Fig. 6, 7, scale above Fig. 6 (divisions = 10  $\mu$ m); Fig. 8, 9, scale above Fig. 3.

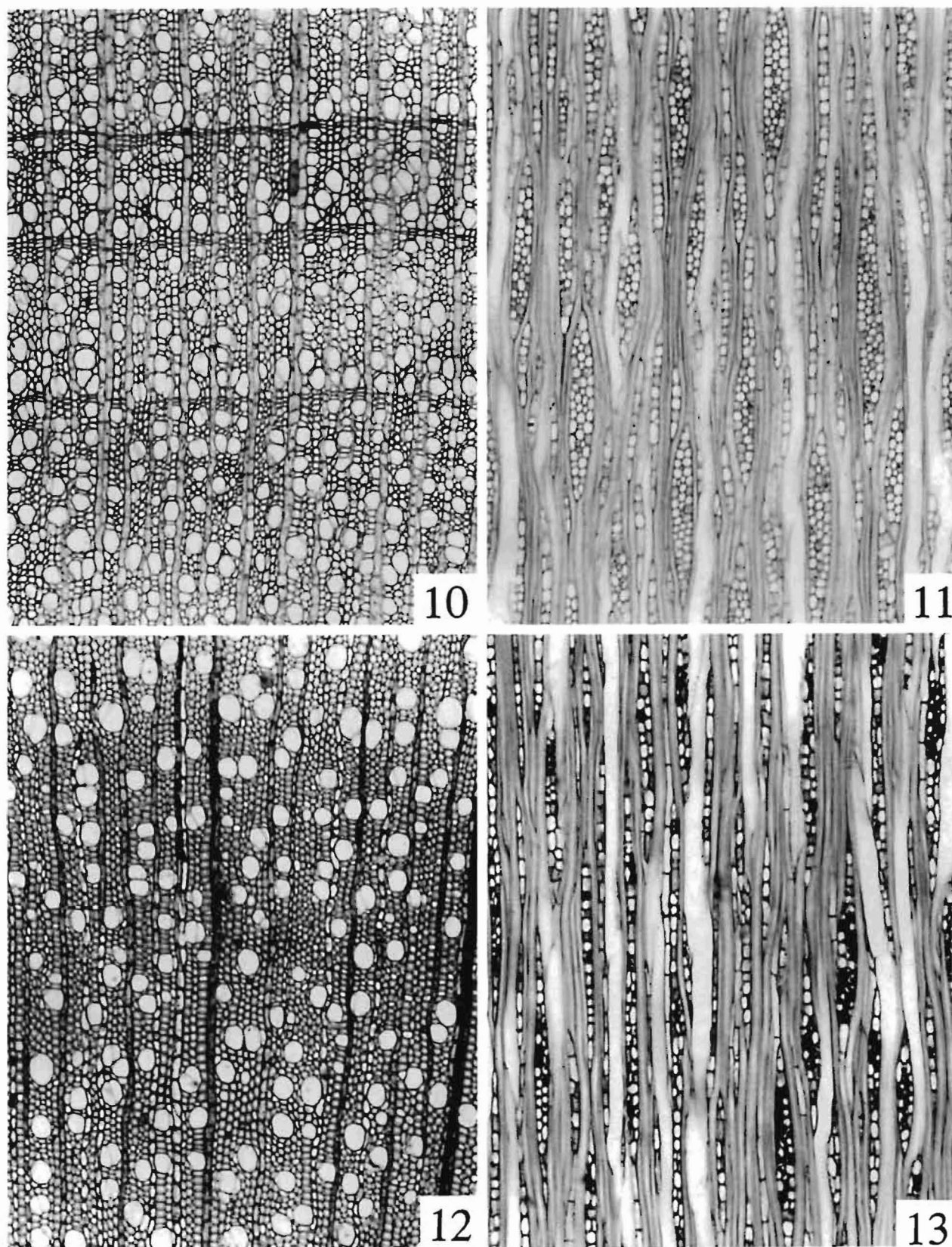


Fig. 10–13. Wood sections of *Morella*.—10–11. *M. californica*.—10. Transection; several growth rings evident, vessels relatively narrow.—11. Tangential section; dark-colored deposits essentially absent in rays.—12–13. *M. faya*.—12. Transection, no growth ring apparent.—13. Tangential section; multiseriate and uniseriate rays about equally frequent, some ray cells filled with dark-colored deposits. Fig. 10–13, scale above Fig. 3.



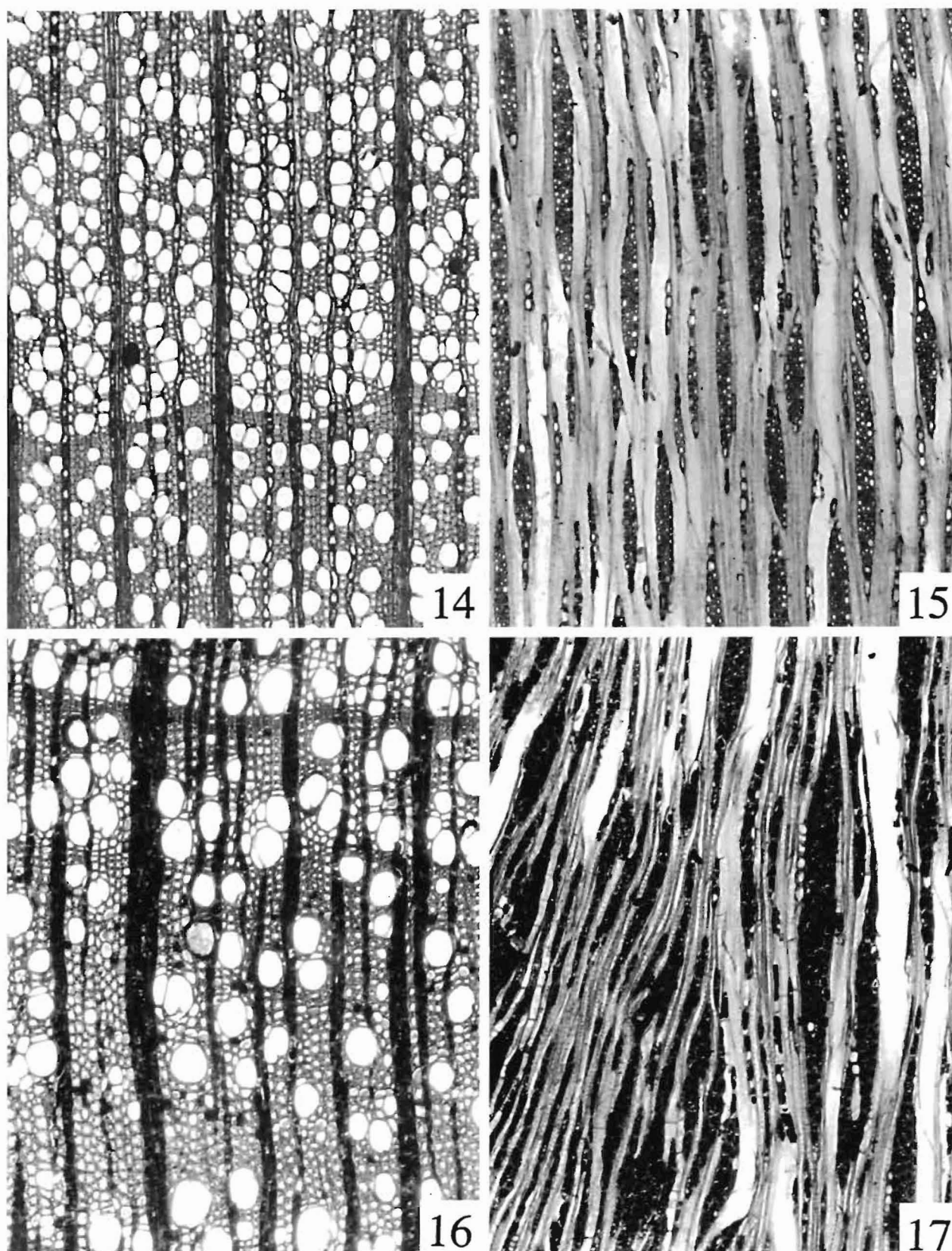
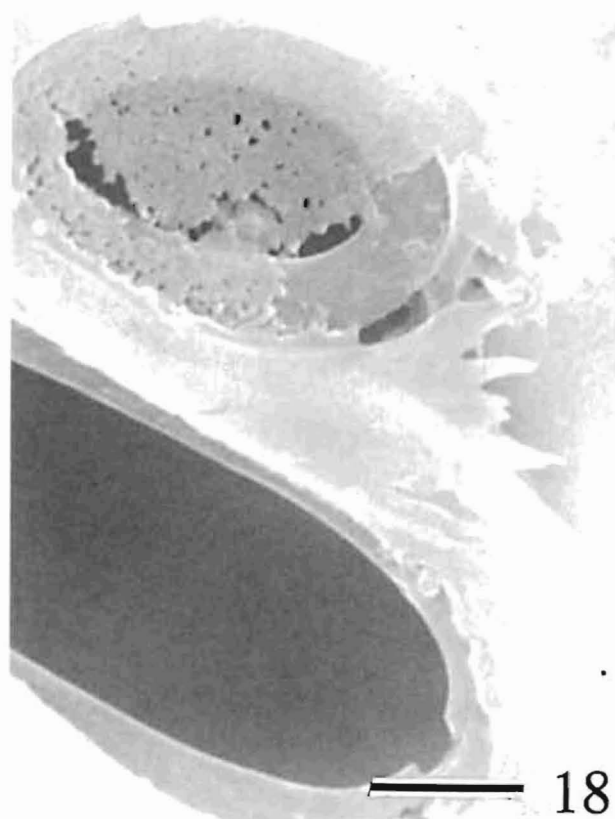
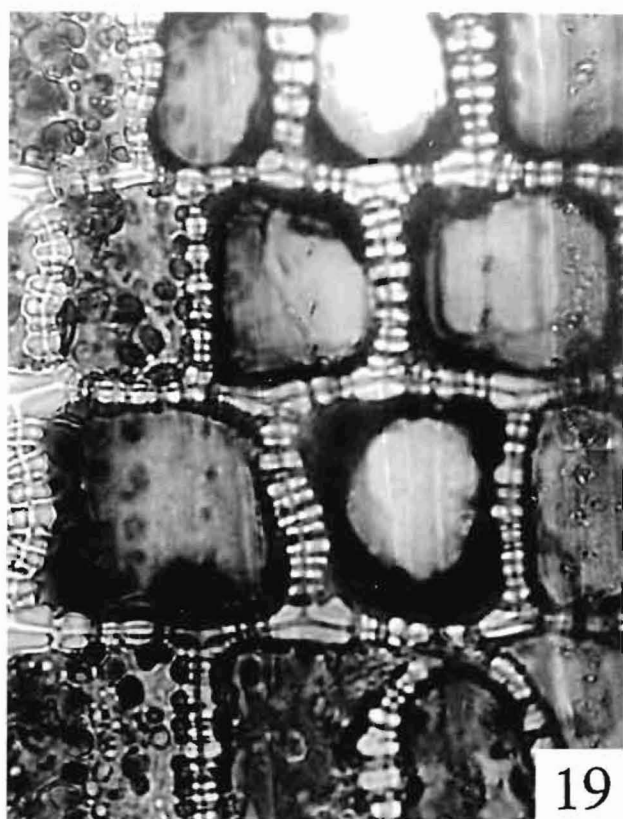


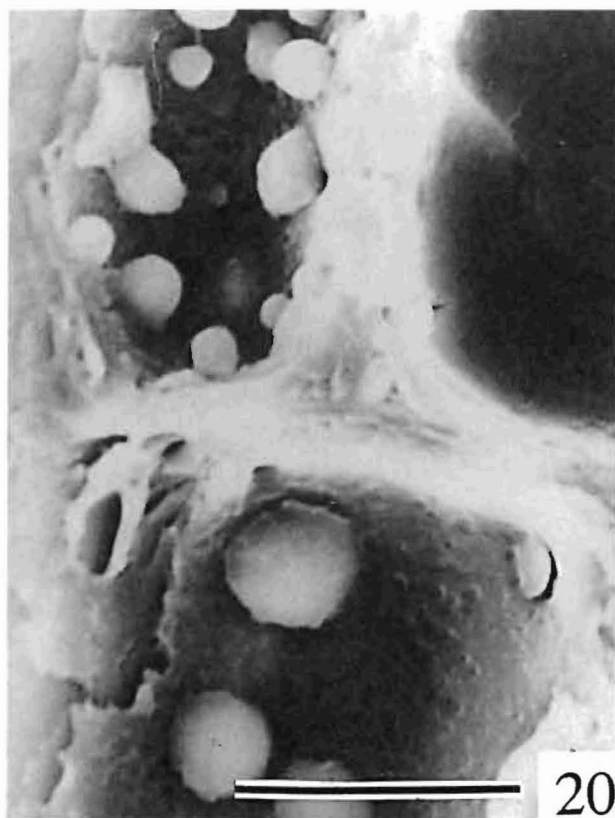
Fig. 14-17. Wood sections of *Morella*.—14-15. *M. inodora*.—14. Growth ring below middle, evident by band of tracheids; no marked change in vessel diameter evident.—15. Multiseriate rays abundant, relatively short, composed of cells mostly filled with dark-staining compounds.—16-17. *M. nagi*.—16. Transverse, growth ring near top distinguished by tracheid band; vessels relatively large in diameter.—17. Tangential section; uniseriate rays abundant at lower left; dark-staining deposits common in almost all ray cells. Fig. 14-17, scale above Fig. 3.



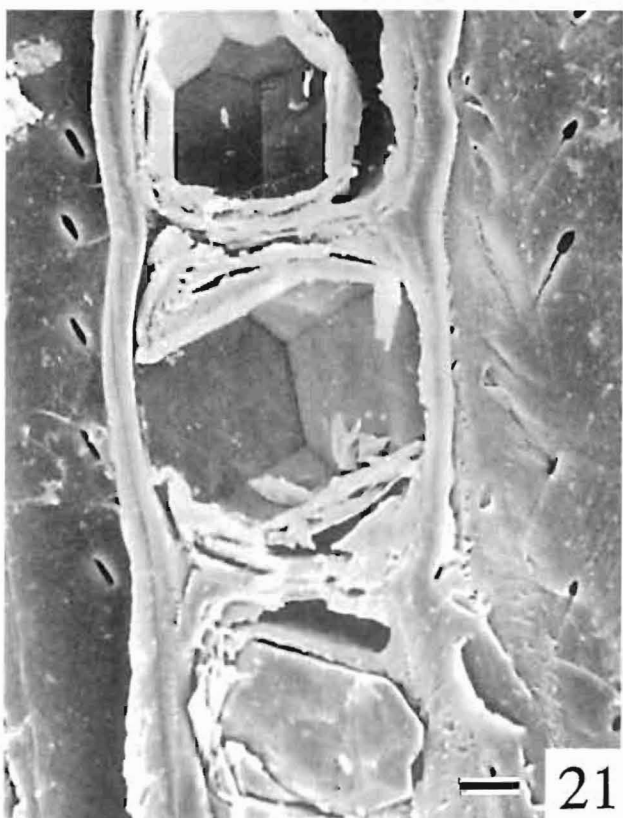
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Fig. 18–21. Wood details of *Morella*, shown by SEM (Fig. 18, 20, 21) and light microscopy (Fig. 19).—18–20. *M. inodora*.—18. Portion of perforation plate from radial section, with porose pit membrane transitional to lateral wall pitting above.—19. Ray cells as seen in radial section; dark-colored deposits outline lumina and pit cavities of ray cells, showing many of the pits to be bordered.—20. Droplets of dark-staining compounds in ray cells from radial section.—21. *M. kraussiana*; strand of encapsulated crystals of axial parenchyma strand from radial section; top two crystals intact, bottom crystal sheared off by sectioning; tracheids to left and right of axial parenchyma strand.—Fig. 18, 20, 21, scales = 2  $\mu$ m; Fig. 19, scale above Fig. 6.



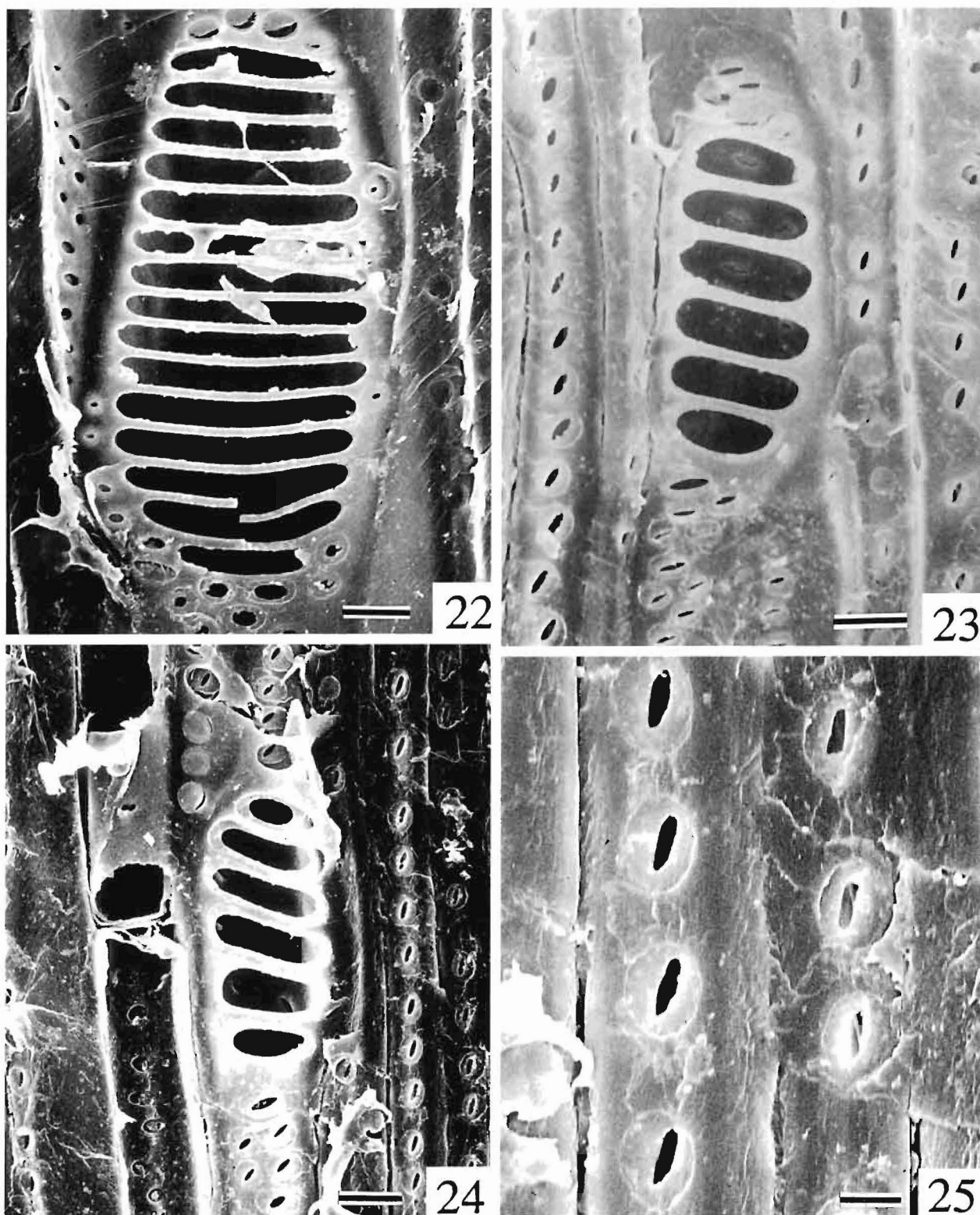


Fig. 22–25. SEM photographs of radial wood sections of *Morella*.—22. *M. kraussiana*. Perforation plate, with relatively narrow, numerous bars.—23–25. *M. nagi*.—23. Perforation plate with bars of typical thickness; bordered pits of tracheids are conspicuous to left and right of the vessel.—24. Perforation plate with relatively few, wide bars; prominent bordered pits of tracheids to the right of the vessel.—25. Portions of two tracheids, to show characteristic border diameters and pit aperture shapes. Fig. 22–24, scales = 10  $\mu\text{m}$ ; Fig. 25, scale = 2  $\mu\text{m}$ .

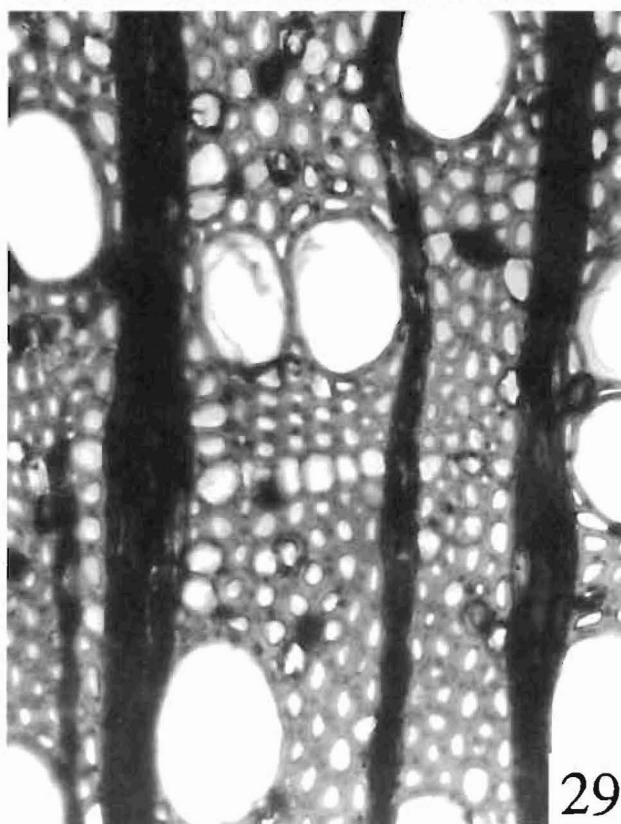
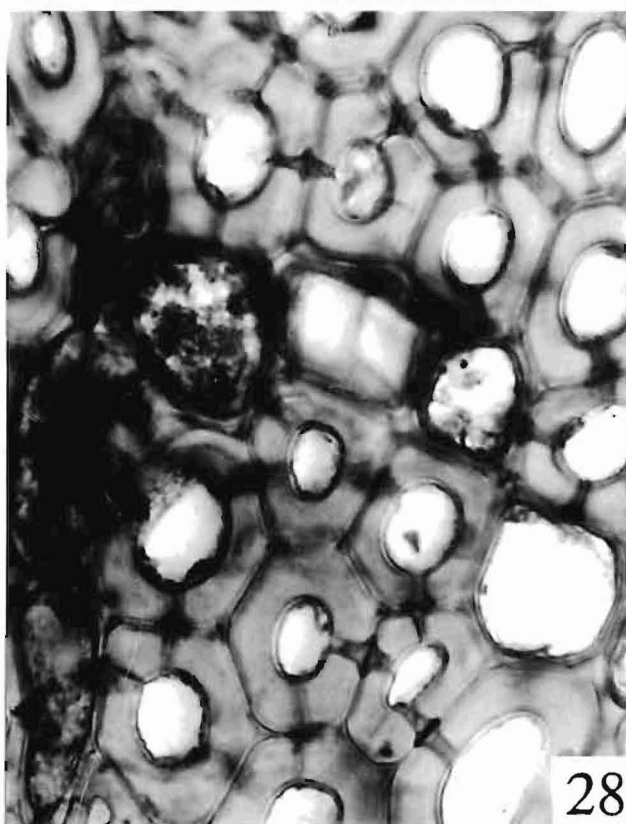
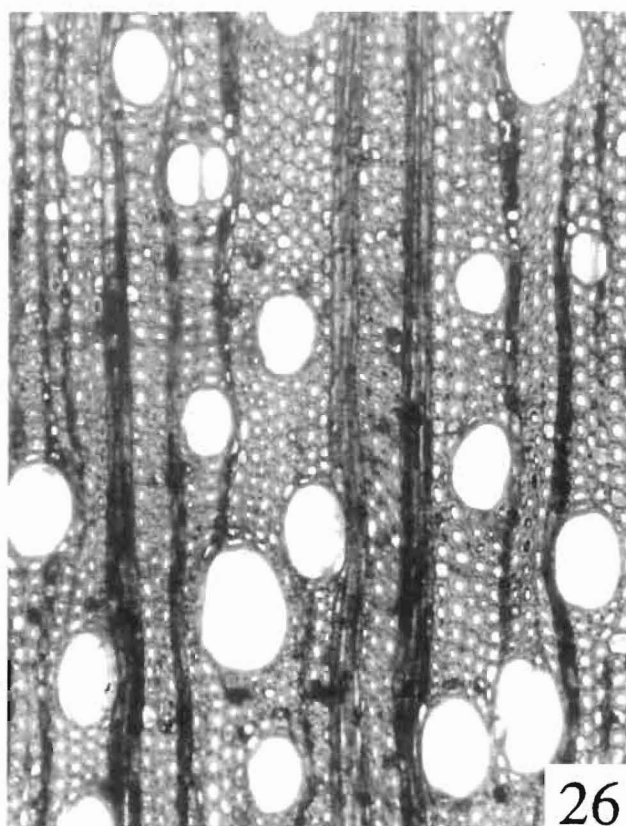


Fig. 26–29. Wood sections of *Morella*.—26–28. *M. javanica*.—26. Transection; growth rings absent, vessels notably wide.—27. Tangential section; wide as well as narrow multiseriate rays are present; both multiseriate and uniseriate rays contain dark-staining deposits.—28. Transection, showing thick-walled tracheids in which deposits of dark-staining material outline the bordered nature of the pits; a pair of rhomboid crystals, just above center, and, to right and left of the crystal-bearing cell, axial parenchyma cells.—29. *M. salicifolia*; transection; axial parenchyma is diffuse and, a little below center, a band of diffuse-in-aggregates axial parenchyma is present; dark deposits in rays and in a few of the axial parenchyma cells. Fig. 26, 27, scale above Fig. 3; Fig. 28, scale above Fig. 6; Fig. 29, scale above Fig. 2.

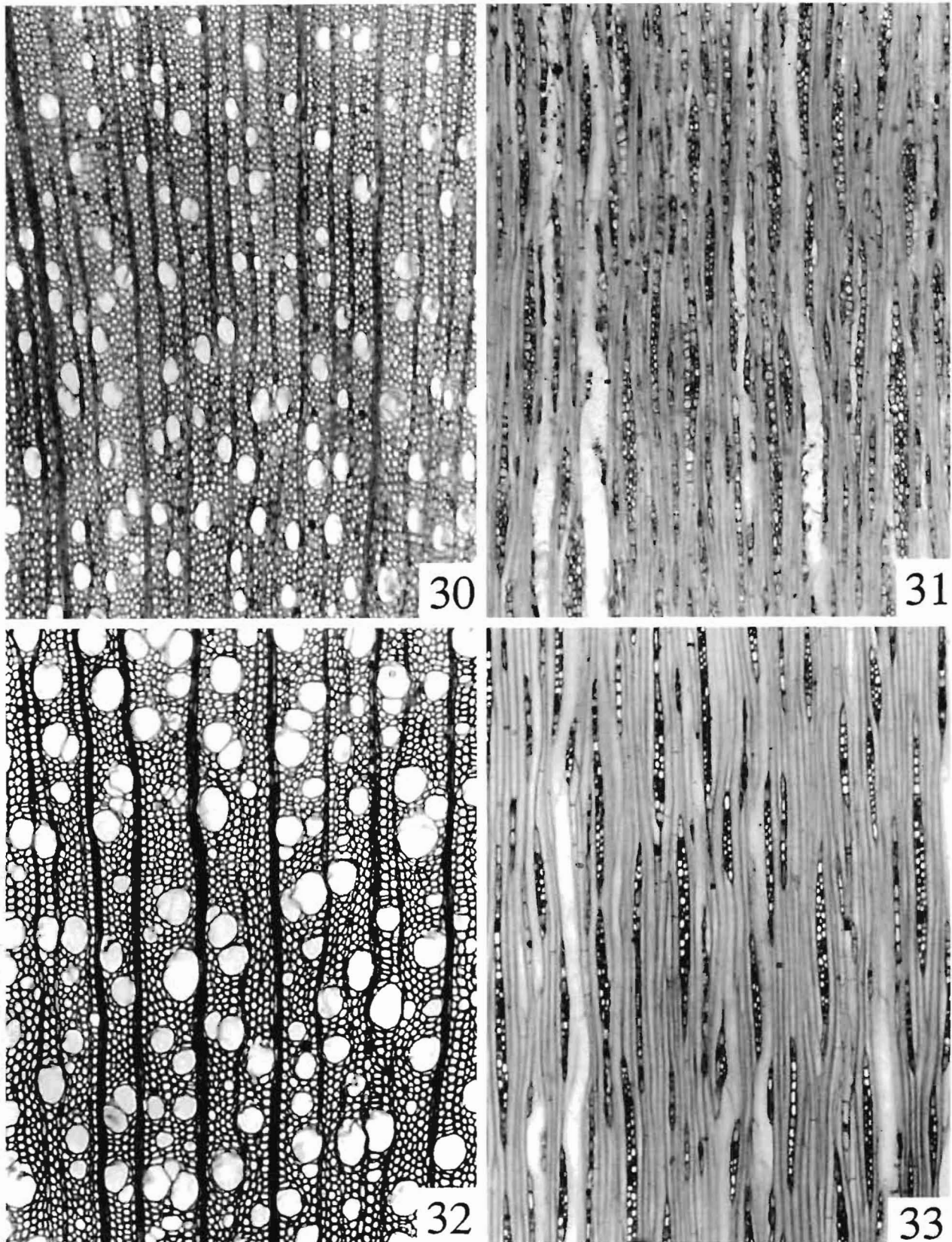


Fig. 30–33. Wood sections of *Morella*.—30–31. *M. kraussiana*.—30. Transection; relatively narrow vessels characteristic of a temperate species.—31. Tangential section; multiseriate rays are narrow; dark-staining deposits are sparse.—32–33. *M. pubescens*.—32. Transection; relatively wide vessels characteristic of a tropical species.—33. Tangential section with narrow multiseriate rays, but with dark deposits in many cells of both uniseriate and multiseriate rays. Fig. 30–33, scale above Fig. 3.



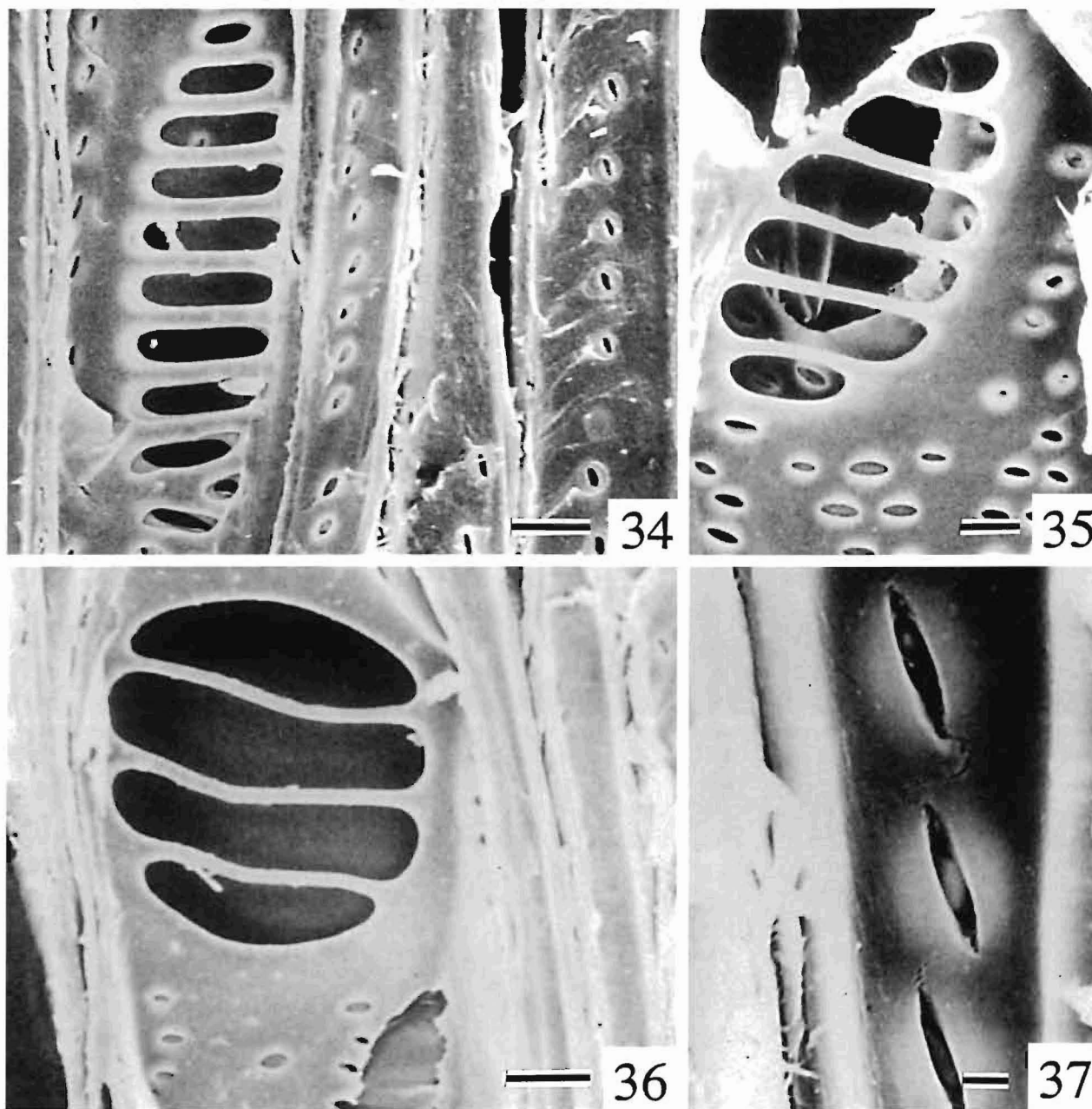


Fig. 34–37. SEM photographs of radial sections of wood of *Morella pubescens*.—34. Perforation plate with numerous bordered bars and, to right, three tracheids showing bordered pitting.—35. Perforation plate with an intermediate number of rather slender bars and, on the lateral wall, alternate pitting on a vessel face that probably was in contact with tracheids.—36. Perforation plate with few, narrow, minimally bordered bars; pitting sparse on lateral wall of vessel.—37. Pit apertures of three pits facing a tracheid lumen, to show narrowly elliptical pit aperture shapes. Fig. 34–36, scale = 10  $\mu\text{m}$ ; Fig. 37, scale = 2  $\mu\text{m}$ .

*M. hartwegii*. Narrow vessels were also observed in *Morella quercifolia*, although the small diameter (6 cm) of that wood sample and the fact that this species is shrubby rather than arboreal may account for this. The widest vessels observed in the study were those of *M. javanica* (Fig. 26). The transections of wood presented at the same scale (Fig. 5, 8, 10, 12, 14, 16, 26, 30, 32, 38, 42, and 44) show that there is an appreciable range in vessel diameters within the family, and these photographs accurately reflect the mean lumen diameters recorded in Table 1, column 2.

Mean vessel density (Table 1, column 3) shows an amazing range from 11 per  $\text{mm}^2$  (*Morella javanica*, Fig. 26) to 260 per  $\text{mm}^2$  (*Comptonia peregrina*, Fig. 8). This range is greater than one might expect from the span of vessel lumen diameters in the family. This circumstance will be examined below in terms of possible physiological significance.

Vessel element length (Table 1, column 4) ranges from relatively short in the shrubs *Comptonia peregrina* (477  $\mu\text{m}$ ) and *Morella quercifolia* (462  $\mu\text{m}$ ) to long in trees such as *M. javanica* (800  $\mu\text{m}$ ), *M. dom-*

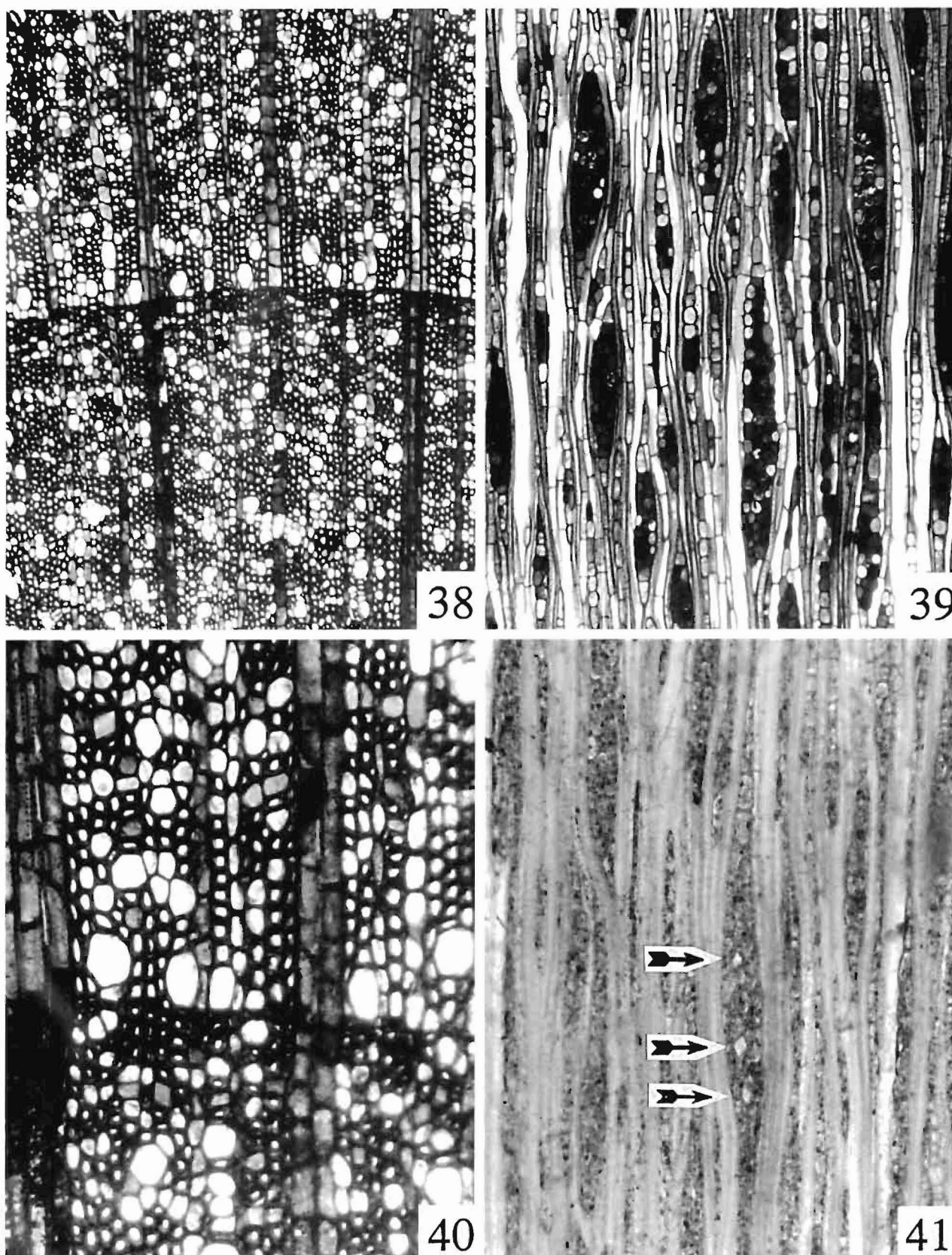


Fig. 38–41. Wood sections of *Morella rubra* (Fig. 38–40) and *M. quercifolia* (Fig. 41).—38. Transection; clearly demarcated growth ring present.—39. Tangential section; cells of rays are relatively large; many contain dark-staining deposits.—40. Transection; growth ring ends with narrow vessels, thick-walled tracheids.—41. Tangential section; rhomboidal crystals (arrows) occur in multiseriate rays. Fig. 38, 39, 41, scale above Fig. 3; Fig. 40, scale above Fig. 2.



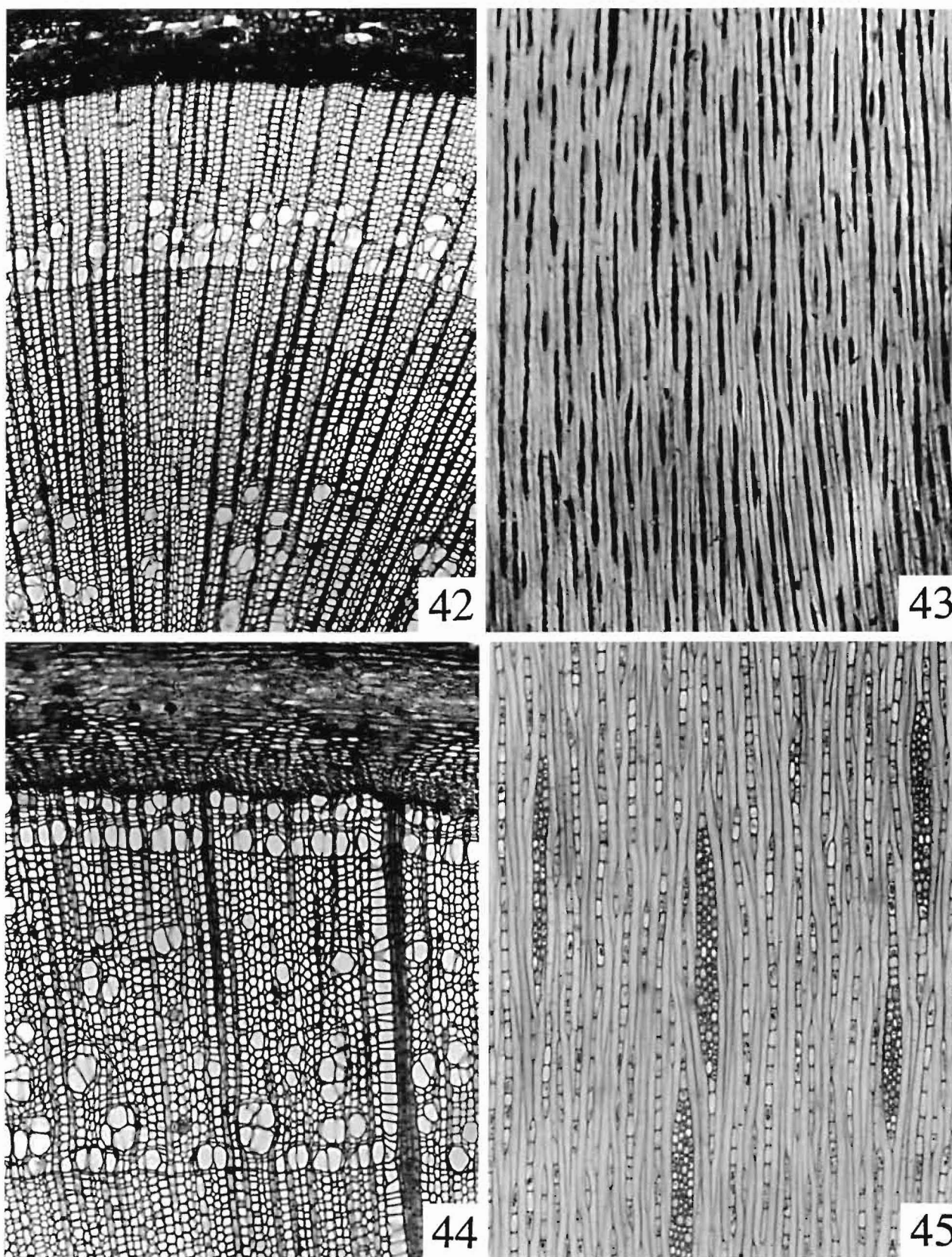


Fig. 42–45. Wood sections of *Myrica*.—42–43. *M. gale*.—42. Transection, bark above; vessels are absent in latewood of the two growth rings.—43. Tangential section; multiseriate rays are narrow, uniseriate rays abundant.—44–45. *M. hartwegii*.—44. Transection with bark at top; vessels are sparse in latewood, crowded at beginning of earlywood.—45. Tangential section; numerous uniseriate rays plus a few multiseriate rays are present. Fig. 42–45, scale above Fig. 3.

Table 1. Wood characteristics of Myricaceae.

Species	1 VG	2 VD	3 VM	4 VL	5 VW	6 BP	7 TL	8 TW	9 AP	10 MU	11 MW	12 MH	13 UH	14 FV	15 ME
<i>Canacomyrica monticola</i>	1.10	56	39	713	2.4	24.8 (17–32)	891	5.5	D, DA, AC, AB	M = U	4.7	1598	510	1.25	1024
<i>Campionia peregrina</i>	1.19	30	260	477	2.0	0.2 (0–3)	701	3.5	D, DA, VS	M < U	2.1	379	106	1.47	55
<i>Morella californica</i>	1.08	40	94	587	1.7	8.6 (0–13)	994	2.4	D	M > U	2.5	474	173	1.69	250
<i>M. cerifera</i>	1.10	42	151	647	2.9	7.9 (0–16)	914	4.7	D, DA, VS	M > U	2.6	527	228	1.41	180
<i>M. domingana</i>	1.04	48	51	801	1.8	8.8 (6–12)	1264	7.0	D, DA, VS	M = U	2.3	316	156	1.58	754
<i>M. faya</i>	1.03	54	34	669	1.2	9.0 (5–12)	958	2.5	D, DA, VS	M = U	3.0	429	239	1.43	1063
<i>M. inodora</i>	1.17	41	174	750	1.0	3.6 (0–12)	1028	3.5	D	M = U	3.5	433	140	1.37	177
<i>M. javanica</i>	1.03	133	11	800	4.0	6.6 (3–15)	1540	6.0	D, DA	M = U	3.7	447	287	1.93	9693
<i>M. kraussiana</i>	1.03	48	77	541	1.5	10.3 (0–17)	1075	2.4	D, DA	M = U	2.8	565	171	1.99	337
<i>M. microcarpa</i>	1.06	71	56	759	1.8	7.5 (3–15)	1323	5.2	D	M > U	3.4	385	185	1.74	962
<i>M. nagi</i>	1.08	60	56	560	1.1	6.6 (3–12)	825	5.4	D, DA	M > U	3.8	789	249	1.47	600
<i>M. pubescens</i>	1.10	59	68	605	2.1	9.2 (5–14)	929	2.7	D, DA	M = U	2.7	379	163	1.53	525
<i>M. quercifolia</i>	1.07	24	225	462	1.2	9.1 (0–15)	721	2.6	D, DA, VS	M = U	2.3	475	162	1.56	49
<i>M. rubra</i>	1.03	74	23	812	1.8	7.7 (6–10)	1243	5.0	D, DA, VS	M > U	2.5	492	195	1.59	2613
<i>M. salicifolia</i>	1.09	84	24	710	1.7	7.9 (0–18)	1602	3.5	D, DA	M > U	5.4	540	164	2.26	2485
<i>Myrica gale</i>	1.31	30	58	534	2.0	13.2 (5–17)	601	1.8	D, DA	M < U	2.1	384	262	1.13	276
<i>M. hartwegii</i>	2.17	35	76	466	1.3	12.0 (8–17)	493	2.3	D, DA	M < U	4.1	547	363	1.06	215
All species, averaged	1.11	55	87	641	1.8	9.3 (0–32)	1009	3.9			3.2	539	221	1.47	1250

Legends: 1 (VG), mean number of vessel per group; 2 (VD), mean lumen diameter of vessels,  $\mu\text{m}$ ; 3 (VM), mean number of vessels per  $\text{mm}^2$  of transection; 4 (VL), mean vessel element length,  $\mu\text{m}$ ; 5 (VW), mean vessel wall thickness,  $\mu\text{m}$ ; 6 (BP), mean number of bars per perforation plate (followed in parentheses by range observed); 7 (TL), mean tracheid length,  $\mu\text{m}$ ; 8 (TW), mean tracheid wall thickness,  $\mu\text{m}$ ; 9 (AP), types of axial parenchyma present (AB = apotracheal banded, AC = apotracheal columns, D = diffuse, DA = diffuse-in-aggregates, VS = vascentric scanty); 10 (MU), relative abundance of multiseriate and uniseriate rays; 11 (MW), mean width of multiseriate rays at widest point, cells; 12 (MH) mean height of multiseriate rays,  $\mu\text{m}$ ; 13 (UH), mean height of uniseriate rays,  $\mu\text{m}$ ; 14 (FV), mean F/V Ratio (vessel element length divided by tracheid length); 15 (ME), Mesomorphy Ratio (vessel diameter times vessel element length divided by mean number of vessels per  $\text{mm}^2$ ). For additional comments and for collection data, see Materials and Methods.

*ingana* (801  $\mu\text{m}$ ) and *M. rubra* (812  $\mu\text{m}$ ). The mean for the family as a whole (641  $\mu\text{m}$ ) is remarkably close to the mean given by Metcalfe and Chalk (1950) for dicotyledons at large, 649  $\mu\text{m}$ .

Vessel wall thickness (Table 1, column 5) is much less (family mean, 1.8  $\mu\text{m}$ ) than the thickness of tracheid walls, and varies relatively little within the family. The thinness of vessel walls is perceptible in the higher-scale photographs (Fig. 6, 29).

Pits on lateral walls of vessels are oval to circular and do not deviate much, throughout the family, from a diameter of 4  $\mu\text{m}$  (pit cavity diameter measured parallel to long axis of vessel element), as seen in Fig. 22–24. Pits are slightly larger, averaging about 5  $\mu\text{m}$  in diameter, in *Canacomyrica monticola* (Fig. 6), *Morella californica*, *M. javanica* (Fig. 28), *M. pubescens* (Fig. 35), and *M. salicifolia*. Species with pits approaching 3  $\mu\text{m}$  in diameter include *Morella cerifera*, *M. faya*, *M. kraussiana*, *M. quercifolia*, *Myrica gale*, and *M. hartwegii*.

Perforation plates of Myricaceae are generally scalariform, with a range of 1–32 bars (Table 1, column 6). One genus, *Comptonia*, has simple perforation plates almost exclusively, with a very small proportion of the plates bearing one to three bars. At the opposite extreme is *Canacomyrica*, in which the material studied averaged 24.8 bars per plate. Second to *Canacomyrica* is *Myrica* s.s., the two species of which together average 12.6 bars per plate. All of the species of *Morella* fall below *Myrica* in average bar number (Table 1, column 6; Fig. 22–24, 34–36). If one averages all species of *Morella* studied, one obtains the figure of 8.0 bars per plate. Thus, the four genera have notably different modes with respect to this feature.

Perforation plates with fewer bars per plate sometimes have wider bars (Fig. 24) than those with more numerous bars (Fig. 22, 23), but exceptions are easy to find. Notably wide but relatively numerous bars (Fig. 34) and notably slender bars in plates with few bars (Fig. 35, 36) may readily be found. Where wider, the bars have easily seen borders (Fig. 18, 34), and probably no bars lack borders entirely, at least if one looks at the lateral ends of the perforations.

### Qualitative Vessel Features

The limits between perforation plates and lateral wall pitting are not as clear as one might think if one studies the transitional pits with SEM. Transitional pits may bear porose pit membranes indicating only partial lysis of the pit membrane (Fig. 18). Pit membranes of pits on lateral walls of vessels do not bear these pores.

Vessels are typically circular or oval in outline, the radial axis slightly longer than the tangential axis as seen in transections (Fig. 4, 8, 10, 12, 14, 16, 26, 29, 30, 32, 38, 40). Even in the two species of *Myrica*,

there is only a slight tendency toward angular vessel outline where vessels are crowded in earlywood (Fig. 42, 44).

Pits on lateral walls of vessels are transitional, opposite, or alternate on vessel to vessel interfaces, and types vary greatly within species. Vessel to vessel interfaces occur mostly in the overlap areas between vessels, because degree of vessel grouping is so low. Vessel to ray pitting is scalariform (infrequently), transitional, opposite, or alternate, but rather frequently opposite. On vessel surfaces in contact with tracheids, pits are opposite or alternate (Fig. 35), quite sparse in some areas (Fig. 36). Opposite or alternate pits have pit cavities oval in face view, but the pit apertures facing the vessel lumen are narrowly elliptical (Fig. 35).

No helical thickenings or vesturing of any kind were observed in vessels of Myricaceae.

Thin-walled tyloses, often containing resinlike deposits, were observed in several Myricaceae; they were exceptionally common in material of *Canacomyrica* and *Myrica hartwegii*.

### Imperforate Tracheary Elements

With the exception of the two species of *Myrica*, all imperforate tracheary elements in Myricaceae are tracheids. This designation is easy to make because the pit cavities are large (“fully bordered pits”) and the pits are densely placed (Fig. 23, 24, 34, and especially Fig. 25). Pit cavities filled with dark-colored compounds show the bordered nature of the pits in tracheids (Fig. 6, 28). The apertures facing the lumina of tracheids are slitlike (Fig. 37).

In the two species of *Myrica*, a curious and subtle difference between earlywood and latewood occurs with respect to imperforate tracheary elements. In addition to vessels, the earlywood contains fiber-tracheids with sparsely distributed pits that have reduced pit borders (pit cavities ca. 1–2  $\mu\text{m}$  in diameter). In latewood of both species, vessels are sparse or absent, depending on the growth ring, and imperforate tracheary elements are clearly tracheids. Fiber-tracheids in earlywood plus tracheids in latewood have also been reported in *Carpinus*, *Corylus*, and *Ostrya* of the Corylaceae or Betulaceae (Metcalfe and Chalk 1950). Note should be taken that the concept of vascular tracheids, in which extremely narrow vessels grade into tracheids (which are, in effect, vessels lacking perforation plates) in the last few layers of latewood, is quite a different concept.

Mean lengths of imperforate tracheary elements in the family (Table 1, column 7) range from 493  $\mu\text{m}$  to 1602  $\mu\text{m}$ , a considerable range. The species with the shortest mean imperforate tracheary element length are *Myrica gale* (601  $\mu\text{m}$ ) and *M. hartwegii* (493  $\mu\text{m}$ ).

Mean wall thickness of imperforate tracheary elements follows a pattern similar to the lengths. The means for *Myrica gale* and *M. hartwegii* are 1.8  $\mu\text{m}$  and 2.3  $\mu\text{m}$ , respectively, whereas the range in species means for the three other genera is from 2.4  $\mu\text{m}$  to 5.5  $\mu\text{m}$  (Fig. 6, 29). In species with moderately to strongly demarcated growth rings, differences in wall thickness between earlywood and latewood occur. For example, in *Comptonia* (Fig. 8), earlywood tracheid wall thickness is about 2.3  $\mu\text{m}$ , whereas latewood wall thickness is about 4.7  $\mu\text{m}$ . The claim by Metcalfe and Chalk (1950) that *M. gale* has imperforate tracheary element walls thicker than those of other Myricaceae is not confirmed here; the reverse was observed.

Mean pit cavity diameter of tracheids is essentially the same as the pit cavity diameter of lateral wall pits of vessels for any given species of Myricaceae (see data for vessel pits above). Contrary to what one sees in conifers and in many dicotyledon families, pitting is denser on tangential walls of tracheids in Myricaceae, sparser on radial walls.

#### Axial Parenchyma

Axial parenchyma in Myricaceae is basically diffuse; diffuse parenchyma can be found in all species (Table 1, column 9). In most species, diffuse-in-aggregates (tangential aggregates of two to about five cells) is commonly present in addition (Fig. 29). The type "diffuse" implies random distribution of parenchyma throughout the fascicular secondary xylem. Diffuse-in-aggregates is recognized because it is a departure from randomness. In *Comptonia peregrina*, *Morella cerifera*, *M. faya*, *M. quercifolia*, and *M. rubra*, axial parenchyma cells adjacent to vessels seem a little more numerous than randomness would dictate, so scanty vasicentric parenchyma is said to be present in these species.

In addition, *Canacomyrica* possesses axial parenchyma distributions not seen in the other Myricaceae: apotracheal bands and apotracheal groupings circular in transection. The latter type is infrequent enough in dicotyledons so that it has not been recognized with a term, so "apotracheal columns" is proposed here for groups composed of about five to ten cells as seen in transection. Longisections of these types are seen in Fig. 2 (upper left, crystal-containing cells) and Fig. 3 (upper left). Arrows indicate apotracheal strands in Fig. 4, and in Fig. 5, a strip of apotracheal parenchyma runs down the center of the photograph (about  $\frac{1}{4}$  the width of the photograph).

Axial parenchyma strands, as seen in longisection, range from 3–8 cells. Varying numbers of these cells may be subdivided into cuboidal crystal-containing cells (Fig. 21). Thus, a strand might consist of three or four undivided cells plus the equivalent of two more

such cells subdivided into cuboidal crystal-containing cells ("chambered crystals"). No subdivision into crystal-containing cells was observed in the two species of *Myrica* s.s. or in *Comptonia*, and the lack of such crystal strands is apparently a diagnostic feature of these two genera. Crystal-containing strands of cuboidal cells were observed in *Canacomyrica* and in all of the species of *Morella*, although these strands are scarce in some of the *Morella* species and abundant in others. The nature of crystals in these strands is discussed further below under "Crystals."

#### Vascular Rays

As shown in Table 1, column 10, multiseriate rays are more abundant than uniseriate rays, or approximately equal in abundance in *Canacomyrica* (Fig. 5) and in *Morella* (Fig. 11, 13, 15, 17, 27, 31, 33, 39, and 41). Biseriate rays are considered multiseriate here for purposes of comparisons. In contrast to those two genera, uniseriate rays are more common than multiseriate rays in *Comptonia* (Fig. 9) and *Myrica* s.s. (Fig. 43, 45). The two species of *Myrica* s.s. differ, however, in that multiseriate rays are scarce and narrow in *M. gale* (Fig. 43), in which the mean multiseriate ray width (at the widest point) is 2.1 cells (Table 1, column 11). Multiseriate rays are more common in *M. hartwegii* (Fig. 45), in which mean multiseriate ray width is 4.1 cells. However, this comparison may be misleading because the specimen of *M. gale* was from a narrower stem—the wood of a more juvenile character, therefore—than that of *M. hartwegii*. Rays tend to increase in width as woody stems increase in diameter (Barghoorn 1940). The widest multiseriate rays in the family were observed in *Canacomyrica* (Fig. 5) and *Morella salicifolia* (Table 1, column 11). In *Morella*, greater width of multiseriate rays was observed in *M. inodora* (Fig. 15), *M. javanica* (Fig. 26) and *M. nagi* (Fig. 17), but narrower rays characterize *M. californica* (Fig. 11), *M. cerifera*, *M. domingana*, *M. faya* (Fig. 13), *M. kraussiana* (Fig. 31), *M. pubescens* (Fig. 33), *M. quercifolia* (Fig. 41), and *M. rubra* (Fig. 39). Of these, narrower rays might be related to small sample diameter in *M. kraussiana* and *M. quercifolia*, although not in the other species.

With respect to ray histology, the rays of most Myricaceae qualify as Heterogeneous Type IIA, in which multiseriate ray tips are typically more than a single cell tall (Fig. 45; most rays of Fig. 13), or Heterogeneous Type IIB, in which multiseriate ray tips are usually a single cell tall (Kribs 1935; Carlquist 2001). Rays of the latter type can be seen in all species of *Morella*, and are shown here in Fig. 27. Where multiseriate rays are very scarce (Fig. 43), one can say that the ray type is transitional between Heterogeneous Type II and Heterogeneous Type III, and closer to the



latter (in which all rays are uniseriate), These assignments for rays in Myricaceae agree with those of Metcalfe and Chalk (1950). However, Metcalfe and Chalk (1950) state that in Myricaceae, the multiseriate portions of multiseriate rays are "sometimes with sheath [= upright] cells." Such sheath cells are, in fact, very scarce in most species, but are relatively common in rays of *Canacomyrica* (Fig. 5), which also has elongate uniseriate tips on multiseriate rays and therefore is referable to Heterogeneous Type I of Kribs (1935). In Myricaceae as a whole, the multiseriate portions of multiseriate rays consist almost wholly of procumbent cells (except in *Canacomyrica*) and the uniseriate tips of multiseriate rays consist of upright cells. Uniseriate rays consist of upright cells (Fig. 2, lower  $\frac{2}{3}$  of photograph). Occasional square cells may be observed in radial sections, but they are much less common than either upright or procumbent cells (Fig. 3).

Mean height of multiseriate rays in Myricaceae is relatively low and relatively uniform, 379  $\mu\text{m}$  to 784  $\mu\text{m}$  (Table 1, column 12) except in *Canacomyrica* (Fig. 5), which has a mean ray height of 1598  $\mu\text{m}$ . The mean multiseriate ray height for the family as a whole is 539  $\mu\text{m}$ , and this figure is reflected visually in the rays shown in Fig. 9, 11, 13, 15, 17, 31, 33, 39, 41, and 45. Metcalfe and Chalk (1950) report ray height exceeding 1000  $\mu\text{m}$  for *M. nagi*, but these rays must be infrequent and probably in wood from the base of a relatively large tree. Metcalfe and Chalk (1950) did not study wood of *Canacomyrica*.

So-called aggregate rays (clustering of uniseriate or biseriate rays into larger units: IAWA Committee on Nomenclature 1964) are reported most commonly in Fagales, but occasionally in other families (Carlquist 2001). Aggregate rays have not been reported in Myricaceae, apparently. A phenomenon that some might refer to this phenomenon is visible in some Myricaceae. In transection, one can see multiseriate rays that abruptly break into uniseriate or biseriate rays; these slender rays, in large stems, become wider toward the outside of the stem, in agreement with the increase in ray width with age noted by Barghoorn (1940). The association of uniseriate rays into groupings (perhaps represented in Fig. 17, lower left) decreases rapidly with age, and certainly does not increase as the stems increase in diameter, as the term "aggregate," indicating a kind of "coming together," suggests. The terminology for the rapid breakup of wide primary rays as secondary growth begins in Myricaceae is problematical, therefore. The idea that aggregate rays are large multiseriate rays in the process of disintegration is a generalization offered by Bailey and Sinnott (1914) and Barghoorn (1941), but the reverse (progressive clustering or union of uniseriate rays with age of stem) has been demonstrated repeatedly (see Carlquist 2001). The existence of multiseriate rays near the pith of Myr-

icaceae might be considered an example of disintegration of multiseriate rays to form aggregate rays, but the abruptness of the process in Myricaceae probably disqualifies them from this designation.

Uniseriate ray height is given in Table 1, column 13. As with multiseriate rays, relatively great mean uniseriate ray height was observed in the material of *Canacomyrica*, but uniseriate rays in *Morella*, *Myrica* s.s., and especially *Comptonia* are shorter.

Ray cells have secondary walls in all Myricaceae. Bordered pits are common in most species, especially on tangential walls, but simple pits are more common in some species. Bordered pits are shown very clearly in sectional view in rays of *Morella inodora* (Fig. 19).

### Crystals

Rhomboidal crystals occur abundantly in cuboidal cells of the axial parenchyma strands of all types of axial parenchyma groupings of *Canacomyrica* (Fig. 2, 7). These cuboidal crystal-containing cells ("chambered crystals") contain rhomboidal crystals covered with a layer of secondary wall material ("encapsulated crystals"). Similar strands of cuboidal crystal-containing cells occur in some sheathing cells on multiseriate portions of multiseriate rays of *Canacomyrica*. Crystals are also abundant in the central portions of multiseriate rays of *Canacomyrica*, in which they occur in radial series of procumbent cells (Fig. 3). Many such crystals occur in vertically or horizontally subdivided procumbent ray cells. Crystals are so abundant in wood of *Canacomyrica* that wood sectioning inevitably produces imperfect results.

Outside of *Canacomyrica*, crystals in rays were observed only in *Morella quercifolia* (Fig. 41) and *M. rubra*.

All species of *Morella* were observed to have chambered crystals in axial parenchyma strands. Some of these crystals are so heavily covered (encapsulated) with secondary wall material that virtually no lumen space remains in the cell. This covering can be seen on the lower two crystals in Fig. 21. The crystals in Fig. 21 are more complicated in shape than simple rhomboids. Crystals in axial parenchyma can be seen in transections (e.g., Fig. 28). Crystal strands are common in some species of *Morella*, rare in others. However, a careful search revealed at least a few chambered crystals in all species of *Morella*. Complete absence of chambered crystals from the genus cannot be claimed in any species of *Morella* in the present study.

No crystals were observed in wood of *Comptonia* or *Myrica* s.s.

### Starch and Resinlike Deposits

Starch grains were observed in axial parenchyma of *Morella californica* and *M. nagi*, and in the axial pa-



renchyma and rays of *M. salicifolia*. Doubtless starch is more widely present in wood of the family, but was not observed because some methods of preservation tend to promote loss of starch (e.g., bacterial action during slow drying). Some objects I interpret as starch remnants were observed in several species of Myricaceae.

Dark-colored resinlike deposits are common in axial and ray parenchyma cells, and account for the darkness of these tissues in Fig. 5, 9, 12, 13–33, 38–41, and 43. These deposits may be in the form of droplets (Fig. 19, left; Fig. 20), a thin layer lining cells (Fig. 6), or more massive accumulations filling all or part of a cell (Fig. 13, 19, 27, 31, 33, 39, 43). Although most common in rays, dark-colored deposits occur also in axial parenchyma (Fig. 29). Deposits even spread into tracheary elements (Fig. 6, 28).

#### RESULTS: BARK

In *Comptonia* bark, there is a band of sclereids separating outer from inner cortex (not shown in Fig. 8). Scattered druse-bearing parenchyma cells and strands of fibers occur in secondary phloem of *Comptonia* (Fig. 8, top).

In *Myrica gale* (Fig. 42), druses are present in the outer cortex. A layer of sclereids is present in the inner cortex. In *M. hartwegii* (Fig. 44), numerous druses occur in the outer cortex along with a few fibers, but no sclerenchyma layer was observed.

In *Morella quercifolia*, rhomboidal crystals occur in idioblasts in the outer cortex and a sclerenchyma layer encircles the stem in the central cortex. Fiber bands and rhomboidal crystal-containing idioblasts are present in secondary phloem.

Where the band of sclereids (forming a cylinder in three dimensions) occurs in the cortex of Myricaceae, it is continuous around the stem regardless of the age of the sample (at least in the present study). Breaks inevitably occur in the cylindrical band of sclereids as the xylem cylinder increases in diameter, but as in other dicotyledons with such a sclerenchyma cylinder in bark, parenchyma cells adjacent to the sclerenchyma band doubtless divide, intrude into the break, and become converted into sclereids.

In all species of Myricaceae for which bark was available, periderm is present outside of the cortex and consists of cells much narrower radially than tangentially. There is a tendency for phellem to exfoliate as thin sheets. The stem specimens of species for which bark was available were relatively small in diameter, so persistence of the cortex by means of tangential stretching and radial subdivision of cortical cells was observed. In bark of older stems, loss of cortex is to be expected.

#### SYSTEMATIC AND PHYLOGENETIC CONCLUSIONS

The four genera of Myricaceae are so different on the basis of wood anatomy that diagnostic summaries, given below, can be developed. These summaries, however, could eventually be expanded more precisely in terms of quantitative features if wood samples of similar degrees of maturity were available. Some quantitative estimates are included in these summaries in the form of terms such as "short" and "intermediate," and these designations can be translated into more precise numerical terms by reference to Table 1.

1. *Canacomyrica*. Vessels scattered among tracheids. Vessel elements long. Mean number of bars high. Tracheid length long; tracheid walls thick. Parenchyma diffuse, diffuse-in-aggregates, in apotracheal bands, and in apotracheal columns; strands composed of 3–4 long cells plus long cells subdivided into cuboidal cells each containing an encapsulated rhomboidal crystal (chambered crystal). Multiseriate rays about as abundant as uniseriate rays; crystals common in procumbent ray cells that are usually subdivided. Multiseriate rays tall, the multiseriate portion with sheathing cells; ray type Heterogeneous Type I. Crystals present in procumbent (and usually subdivided) ray cells of multiseriate rays.
2. *Comptonia*. Vessels narrow, scattered among tracheids. Vessel elements short. Perforation plates mostly simple, mean number of bars very low. Tracheid length intermediate. Tracheid wall thickness varies with position in growth rings. Apotracheal diffuse, diffuse-in-aggregates, occasionally scanty vasicentric; strands composed of about four long cells, none subdivided into cuboidal cells. Multiseriate rays few, short, lacking sheath cells, Heterogeneous Type IIB. Uniseriate rays more common than multiseriate rays. Crystals absent.
3. *Morella*. Vessels moderately wide, scattered among tracheids. Vessel elements intermediate in length. Perforation plates with bars fewer than in *Canacomyrica* or *Myrica* (when given in terms of means). Simple perforation plates infrequent. Tracheid length intermediate to long. Tracheid wall thickness, intermediate, less than that of *Canacomyrica*, more than that of *Myrica* s.s. Apotracheal parenchyma diffuse or diffuse-in-aggregates, composed of strands of 2–6 long cells intercontinuous with chains of cuboidal cells each containing one crystal. Multiseriate rays more abundant than uniseriate rays. Sheathing cells lacking on multiseriate portions of multiseriate rays, rays Heterogeneous Type IIA or Heterogeneous Type IIB. Crystals present in rays of a few species.
4. *Myrica* s.s. (*Gale* of some authors). Vessels narrow, crowded in earlywood (number per group higher than in other genera), sparse or absent in latewood.

Perforation plates with bar number means intermediate between that of *Canacomyrica* and those of *Morella*. Imperforate tracheary elements shorter than in *Canacomyrica* or *Morella*; the elements are tracheids in latewood but fiber-tracheids in earlywood; wall thickness of imperforate tracheary elements is uniformly thin. Axial parenchyma diffuse or diffuse-in-aggregates. Axial parenchyma strands composed of 3–4 long cells, no chains of chambered crystals present. Multiseriate rays fewer than uniseriate rays, sheath cells lacking, rays Type heterogeneous Type IIA and IIB. Crystals absent in rays.

The above comparisons support the classification of Elias (1971) who, however, recognized *Morella* and *Myrica* s.s. as subgenera rather than as genera; the diagnostic features above support recognition of these as genera. The ray type Heterogeneous Type I and the relatively large number of bars per perforation plate found in *Canacomyrica*, a genus not considered by Elias, are features that are primitive within the family. Aggregation of axial parenchyma into bands and columns may, however, be an autapomorphy in *Canacomyrica*. These features are compatible with a myricaceous placement for *Canacomyrica*. The similarity between *Canacomyrica* and *Morella* with respect to crystals in rays and chambered crystals in axial parenchyma is striking. The absence of crystals in *Comptonia* and *Myrica* s.s. contrasts with their presence in *Canacomyrica* and *Morella*.

Presence of scalariform perforation plates and diffuse axial parenchyma (and variations on diffuse parenchyma) are doubtless symplesiomorphies for the family, although reduction in number of bars per perforation plate (most notable in *Comptonia*) is a probable apomorphy. The presence of dark-colored deposits in the wood, although not a striking feature, unites Myricaceae; Heterogeneous Type IIA or IIB rays are characteristic of all genera but *Canacomyrica*. Tracheid dimorphism and the thin-walled nature of tracheary elements in *Myrica* s.s., in which earlywood contains numerous vessels but latewood consists of tracheids into which few or no vessels are interspersed, are distinctive features that separate *Morella* from *Myrica* s.s. and are likely an autapomorphy in *Myrica* s.s. Other features of *Myrica* s.s. that differentiate it from *Morella* include greater grouping of vessels, shorter vessel elements, more numerous bars per perforation plate, presence of tracheids in latewood but fiber-tracheids in earlywood, predominance of uniseriate rays, and absence of crystals. These two genera are amply justified on the basis of wood features. *Comptonia* is distinctive with respect to its large number of narrow vessels, change in tracheid wall thickness with respect to position in growth rings, and ex-

tremely low mean number of bars per perforation plate. Thus, the recognition of four genera is supported. Sampling of *Morella* here is insufficient to judge whether subgenera proposed within *Morella* (see Elias 1971) receive any support from wood anatomy, however.

Inclusion of Myricaceae in Fagales (near Juglandaceae, Casuarinaceae, and Betulaceae) is proposed by recent phyletic studies that utilize DNA analysis (Manos and Steele 1997; Soltis et al. 2000). Fagaceae form a clade adjacent to the clade formed by the preceding four families by Soltis et al. (2000); Corylaceae are frequently included in Betulaceae and are close to Betulaceae even if recognized at the familial level. Rhoipteleaceae are now indicated as optionally included in Juglandaceae (APGII 2003). Nothofagaceae and Ticodendraceae are clearly in Fagales (APGII 2003), but were not included in the tree of Soltis et al. (2000). Assuming that these families are the ones most relevant for comparison to Myricaceae, distribution of features found also in Myricaceae can be listed as follows (data from Moseley 1948; Metcalfe and Chalk 1950; Miller 1976; Meylan and Butterfield 1978; and Carlquist 1991).

1. Scalariform perforation plates: Betulaceae (scalariform with more numerous bars in *Alnus*, fewer in *Betula*; Casuarinaceae (mostly simple plates, but scalariform with up to 20 bars in sect. *Leiopitys*); Corylaceae (predominantly scalariform in *Ostrya* and *Ostryopsis*, fewer than 20 bars in *Corylus*); Fagaceae (occasionally scalariform in *Fagus*, otherwise characteristically simple); Juglandaceae (mostly simple except for a few bars in *Alfaroa* and *Engelhardtia*, and typically several bars per plate in *Rhoiptelea*); Nothofagaceae (plates simple and scalariform within particular species, bars sometimes numerous in the scalariform plates); Ticodendraceae (scalariform with many bars in the single species).
2. Presence of tracheids as imperforate tracheary elements: Betulaceae (tracheids, fiber-tracheids); Casuarinaceae (tracheids, or fiber-tracheids plus vasicentric tracheids); Corylaceae (tracheids in latewood of *Carpinus*, *Corylus*, and *Ostrya*, but fiber-tracheids similar to the tracheids in earlywood); Fagaceae (vasicentric tracheids plus libriform fibers in all genera except *Fagus*, which has fiber-tracheids); Juglandaceae (tracheids plus libriform fibers in *Platycarya*, fiber-tracheids in other genera); Ticodendraceae (*Ticodendron*, tracheids).
3. Chains of cuboidal crystal-containing cells (chambered crystals) in portions of axial parenchyma strands: Casuarinaceae (*Casuarina*); Fagaceae (*Castanopsis*, *Quercus*); Juglandaceae (shorter chains or single cells in *Carya* and *Engelhardtia*,

but long chains of chambered crystals in tropical black walnuts); Nothofagaceae (some species of *Nothofagus*).

4. Diffuse and diffuse-in-aggregate axial parenchyma (other types may be present as well): Betulaceae (*Alnus*, *Betula*); Casuarinaceae (*Casuarina*); Corylaceae (*Carpinus*, *Corylus*, and *Ostrya*); Fagaceae (all genera); Juglandaceae (*Juglans*, some *Engelhardtia* species); Ticodendraceae (*Ticodendron*).
5. Rays Heterogeneous Type I: Juglandaceae (some species); Ticodendraceae (*Ticodendron*). Heterogeneous Type IIA: Juglandaceae (some species). Heterogeneous Type IIB: Casuarinaceae (*Casuarina*); Juglandaceae (some species). Families other than those listed above have rays that are homogeneous (or nearly so).
6. Crystals in ray cells: Casuarinaceae (*Casuarina*); Juglandaceae (*Carya*, *Engelhardtia*, and *Platycarya*) have crystals in enlarged and subdivided ray cells as well as in ordinary ray cells).

Myricaceae contain more primitive character states than any other fagalean family mentioned above except for Ticodendraceae, which are more primitive only in the scalariform perforation plates (which have more numerous bars and which retain pit membrane remnants in many perforations). Thus, Myricaceae are rich in symplesiomorphies for Fagales. Most of the features listed above are generally considered by wood anatomists as indicative of primitive wood structure, and are thus symplesiomorphies, which are not considered by cladists as indicative of relationship. The distinctive modes of crystal occurrence shared by Myricaceae and Juglandaceae probably represent synapomorphies, underlining the alliance of the two families indicated in recent DNA analyses.

The retention of tracheids in many of the families of Fagales listed above is interesting because the feature occurs in Rosaceae also (Metcalf and Chalk 1950), and thus is a symplesiomorphy including eurousids other than Fagales. From an ancestry based on an all-tracheid background of imperforate tracheary elements in secondary xylem, instances of vasicentric tracheids have developed in Fagaceae (vasicentric tracheids plus libriform fibers in all genera except *Fagus*), *Casuarina* (vasicentric tracheids plus fiber-tracheids in a few species), and chaparral species of *Prunus* (e.g., *P. ilicifolia*, *P. lyoni*) in Rosaceae (Carlquist 1985; Carlquist and Hoekman 1985). These are interesting instances of tracheid dimorphism (Carlquist 1988). Thus, libriform fibers (and in *Casuarina*, fiber-tracheids) are apomorphic in the species listed above as instances of vasicentric tracheid presence. As will be shown in a study in progress, this pathway is more common than innovation of tracheids in a group with an axial wood background of libriform fibers as a basic

condition, although that pathway does occur (e.g., *Rosmarinus* of Lamiaceae, S. Carlquist, unpublished data).

The F/V ratio (see Table 1, column 14 for values and definition) can be seen as an index of phyletic advancement, because primitive imperforate tracheary elements (tracheids) are only a little longer than the vessel elements they accompany. Specialized imperforate tracheary elements (libriform fibers) are much longer than the vessel elements they accompany (Carlquist 1975). Judged by this interpretation, Myricaceae have rather primitive wood, an interpretation reinforced by the presence in the family of features 1, 2, 4, and 5 cited earlier in this section. The F/V ratio is not, however, a precise measure of phyletic specialization, because other factors can be involved in this ratio (e.g., succulence).

#### ECOLOGICAL CONCLUSIONS

The degree of vessel grouping in Myricaceae is very low (Table 1, column 1). The only exceptions of note are in the two species of *Myrica* s.s., especially *M. hartwegii*. Myricaceae are one more clear demonstration of the principle that in those dicotyledon families with tracheids in wood, vessel grouping is minimal, whereas more appreciable grouping occurs (to a progressively greater degree with greater xeromorphy) in woods with fiber-tracheids or libriform fibers around vessels (Carlquist 1984). The earlywood of *Myrica gale* and of *M. hartwegii* contains fiber-tracheids, so that grouping of vessels is an advantageous conductive safety device in earlywood. Latewood in these two species has tracheids, and thus, vessel grouping does not occur in latewood. Indeed, there are few vessels in latewood of these species: the tracheid is the conductive cell type with optimal safety (resistance to embolism formation and to spread of embolisms). This is the physiological significance of the Type V growth ring (Carlquist 1980, 2001).

The range in vessel density might be expected to be approximately inverse to vessel diameter because of packing considerations. Deviations from such an inverse relationship do occur, however, as in lianas, in which greater vessel density probably is related to the relative paucity of mechanical tissue in this growth form, in which stems are not self-supporting. In Myricaceae, notable departure from the inverse relationship occurs in *Comptonia peregrina*, in which vessels are more numerous per mm<sup>2</sup> than would be expected (e.g., the mean vessel diameter in *C. peregrina* is the same as that in *M. gale*, which has about a quarter as many vessels per mm<sup>2</sup>). The elevated vessel density in *C. peregrina* may relate to its habitats, which are probably among the driest for Myricaceae. Although tracheids in *Comptonia* offer conductive safety, presence of a very high number of vessels offers another form

of conductive safety by providing a redundancy of vessels that would insure that some of them (presumably mostly latewood vessels) would resist embolism in times of drought and frost.

The family Myricaceae as a whole characterizes moist habitats, including those where water stands for prolonged periods, resulting in low nitrate conditions. Nitrogen fixation in roots of Myricaceae by actinomycetes has been repeatedly observed (Van Ryssen et al. 1970; Turner and Vitousek 1987; Sprent et al. 1978). Certainly Myricaceae have wood features that qualify as mesic. The Mesomorphy Ratio (see Table 1, column 15, for values and definition) value for all studied Myricaceae, averaged, is 1250. This figure is higher than those for all but a few southern Californian plants (Carlquist and Hoekman 1985). Because the habitats most commonly occupied by Myricaceae (swamps with fluctuation of water level; streamsides; slopes or flats with steady subsurface water availability) are not easy to define in terms of rainfall, but do exemplify various kinds of moisture availability, comparison of the rather high Mesomorphy Ratio values of species of Myricaceae with those in other habitats is difficult. Such high values, however, would be expected in tropical cloud forest shrubs and trees (e.g., moist forest species of the Hawaiian genus *Dubautia*, Carlquist 1998).

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