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Sherwin Carlquist

Santa Barbara Botanic Garden, Santa Barbara, California

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WOOD ANATOMY OF CROSSOSOMATALES: PATTERNS OF WOOD EVOLUTION WITH RELATION TO PHYLOGENY AND ECOLOGY

SHERWIN CARLQUIST

*Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, California 93105, USA
(s.carlquist@verizon.net)*

ABSTRACT

The seven families hypothesized by Sosa and Chase to comprise Crossosomatales possess relatively long vessel elements with scalariform perforation plates and scalariform to opposite vessel-ray pitting; tracheids; diffuse axial parenchyma; and heterogeneous rays. These and other primitive character states do not indicate relationships, but they do not offer any evidence against the idea that Crossosomatales are a natural order. Departures from the primitive character states are related to ecological adaptations. Crossosomataceae have simple perforation plates (scalariform briefly at the beginning of the secondary xylem), a feature correlated with the seasonal aridity of habitats occupied by the family, the sole family of the order to exhibit such an ecological shift. Presence of tracheids (which confer embolism resistance to a wood) in ancestors of Crossosomataceae probably pre-adapted the family for entry into highly seasonal habitats. Minimal vessel grouping in all other genera shows that tracheid presence deters vessel grouping; tracheid presence also deters shortening of vessel elements. Autapomorphies are shown by Aphloiaceae (tracheid dimorphism, rays of two distinct widths); Crossosomataceae (perforation plates predominantly simple, lateral wall pitting of vessels alternate); Geissolomataceae (wide rays); Ixerbaceae (fiber-tracheid tendency); Staphyleaceae (adjacency of axial parenchyma to vessels); Stachyuraceae (simplification of perforation plates); and Strasburgeriaceae (large cell size). Although tracheid presence seems plesiomorphic in Crossosomatales, a degree of lability in density and size of bordered pits on imperforate tracheary elements probably occurs within this order and in other dicotyledon groups.

Key words: Aphloiaceae, Crossosomataceae, Geissolomataceae, Ixerbaceae, Stachyuraceae, Staphyleaceae, Strasburgeriaceae, tracheids, vessel grouping, wood evolution, xeromorphy.

INTRODUCTION

The order Crossosomatales is a remarkable assemblage of seven families (Aphloiaceae, Crossosomataceae, Geissolomataceae, Ixerbaceae, Stachyuraceae, Staphyleaceae, Strasburgeriaceae). Evidence supporting the idea that the order is monophyletic came to light very recently, as a result of DNA studies (Savolainen et al. 2000; Soltis et al. 2000; Cameron 2001; Sosa and Chase 2003). The novelty of Crossosomatales derives from the fact that the seven component families were assigned to remarkably disparate places in frequently consulted phylogenies. A detailed history of the development of the concept of Crossosomatales, and citations of the relevant literature on the group are offered by Matthews and Endress (2005), and need not be repeated here. The diversity of orders to which the component families were assigned by earlier workers is indeed astonishing.

The focus of the present study is not, however, application of wood anatomical data to clarify systematics. That approach characterized much 20th century work on systematic anatomy, but has now been clearly supplanted by DNA-based phylogenies, which have statistical likelihood that renders contributions to natural phylogeny by wood anatomy essentially obsolete. The powerful nature of DNA evidence now has the

effect of showing how wood anatomy evolves. The net effect of comparing DNA phylogenies to wood anatomy databases is to demonstrate greater and more rapid evolution in wood anatomy within orders or superorders than had been suspected hitherto. The 21st century is proving to be the century during which tendencies, modes, and degrees of wood evolution are elucidated by using DNA-based phylogenies as a matrix for interpretation of wood features. Wood anatomy is no longer a building block of importance for the natural system; wood data studied in terms of molecular phylogenies reveal kinds of structure change in wood and help in the analysis of those changes (e.g., ecological shift of a phylad to drier habitats).

Some wood data for the seven families are available in the following publications: Aphloiaceae (Miller 1975); Crossosomataceae (DeBuhr 1978); Geissolomataceae (Carlquist 1975a); Ixerbaceae (Patel 1973; Meylan and Butterfield 1978; Cutler and Gregory 1998); Staphyleaceae (Carlquist and Hoekman 1985a); and Strasburgeriaceae (Dickison 1981; Cameron 2003). Summaries of wood data for some genera of the families may be found in Metcalfe and Chalk (1950), and papers that describe the wood for a few species are listed by Gregory (1994). The present study presents new data, especially for Crossosoma-

Table 1. Wood features of Crossosomatales.

Taxon	1 VG	2 VD	3 VM	4 VL	5 BA	6 TL	7 MW	8 MH	9 FV	10 ME
Aphloiaceae	1.10	77	33	1169	22	1752	18.0	3267	1.36	2752
<i>Aphloia myrtifolia</i>	1.10	74	32	1105	27	1465	16.4	3138	1.33	2555
<i>A. theiformis</i>	1.10	79	33	1232	16	1724	19.6	3377	1.40	2949
Crossosomataceae	1.10	14	42	7281	0	456	2.7	469	1.63	17
<i>Apacheria chiricahuensis</i>	1.15	10	771	249	0	324	2.0	553	1.30	3
<i>Crossosoma bigelovii</i>	1.12	17	180	258	0	488	4.0	765	1.89	24
<i>C. californicum</i>	1.06	20	122	342	0	598	2.9	648	1.75	56
<i>Glossopetalon meionandrum</i>	1.12	14	416	265	0	411	2.7	368	1.55	9
<i>G. nevadense</i>	1.03	15	345	258	0	494	2.2	298	1.91	11
<i>G. stipuliferum</i>	1.20	17	567	237	0	384	3.0	464	1.62	7
<i>Velascoia recondita</i>	1.08	15	587	358	0	491	2.0	772	1.37	9
Geissolomataceae										
<i>Geissoloma marginatum</i>	1.04	32	26	902	19	1224	5.8	578	1.3	1110
Ixerbaceae										
<i>Ixerba brexioides</i>	1.06	36	80	1200	39	1469	2.0	549	1.22	540
Stachyuraceae	1.06	40	129	1073	42	1276	3.1	1889	1.20	415
<i>Stachyurus himalaicus</i>	1.10	50	89	776	59	908	3.9	1468	1.17	436
<i>S. macrocarpus</i> stem	1.03	36	75	1213	38	1439	2.8	1413	1.19	582
<i>S. macrocarpus</i> root	1.03	43	125	977	33	1407	3.5	1245	1.44	336
<i>S. praecox</i> 'gracilis'	1.10	30	265	804	29	889	2.5	744	1.11	91
<i>S. praecox</i> 'matsuzaki'	1.06	45	92	1442	55	1537	3.5	776	1.00	705
<i>S. praecox</i> subsp. <i>praecox</i>	1.06	36	130	1225	39	1473	2.3	888	1.20	339
Staphyleaceae										
<i>Euscaphis</i>	1.07	69	52	1110	31	2100	4.7	1077	1.89	1558
<i>Staphylea</i>	1.12	46	148	697	22	1140	4.1	687	1.64	217
<i>Turpinia</i>	1.23	110	35	1390	35	2370	4.5	1432	1.70	4170
Strasburgeriaceae										
<i>Strasburgeria robusta</i>	1.04	125	13	1888	37	3115	2.0	2475	1.56	18154

Key to columns: 1 (VG), mean number of vessels per group; 2 (VD), mean diameter of vessel lumen, μm ; 3 (VM), mean number of vessels per mm^2 ; 4 (VL), mean vessel element length, μm ; 5 (BA), mean number of bars per perforation plate; 6 (TL), mean imperforate tracheary element length, μm ; 7 (MW), mean width of multiseriate rays at widest point, cell number; 8 (MH), mean height of multiseriate rays, μm ; 9 (FV), F/V Ratio, mean tracheary element length divided by mean vessel element length; 10 (ME), Mesomorphy Ratio, mean vessel diameter times mean vessel element length divided by mean number of vessels per mm^2 . For collection data and for further explanations of conventions, see Materials and Methods.

taceae and Stachyuraceae. In addition, because the various published sources are not uniform in the ways that quantitative features are measured, and may use different terminology, wood data has been collected from slides and those data are the basis for observations below. In some cases, interesting features not hitherto reported were discovered. Original quantitative data are presented in tabular form (Table 1) and observations on qualitative features are presented in the running text. Materials of all genera were available for study. The present paper thus becomes both a monograph and a summary of wood anatomy for the order Crossosomatales.

The content of the families of Crossosomatales is defined as in Matthews and Endress (2005). Ixerbaceae is considered monogeneric. *Quintinia* A.DC., formerly placed along with *Ixerba* A.Cunn. in Escalloniaceae, is currently regarded as belonging to Paracryphiaceae (Lundberg 2001). *Carpodetus* J.R.Forst. & G.Forst., also formerly of Escalloniaceae, has now been placed

in Rousseeaceae (APG II 2003). Staphyleaceae are now considered to include *Euscaphis* Sieb. & Zucc., *Staphylea* L., and *Turpinia* Vent. *Huerteia* Ruiz & Pav. and *Tapiscia* Oliv. have been removed from Staphyleaceae, and are now considered to form a family, Tapisciaceae, which along with Dipentodontaceae, form a distinct order, Huerteales (Peng et al. 2003).

MATERIALS AND METHODS

The following list of collections includes all families except for Staphyleaceae; specimens used in the study of that family are cited in Carlquist and Hoekman (1985a). Collections are cited alphabetically according to genus. *Apacheria chiricahuensis* C.T.Mason, Chiricahua National Park, Arizona, USA, *Gibson 3163* (RSA); *Aphloia myrtifolia* Galpin, Rhodesia (= Zimbabwe), *USw-21257*; *A. theiformis* (Vahl) Benn., Rhodesia, *SJRw-47359*; *Crossosoma bigelovii* S.Watson, cultivated at Rancho Santa Ana Botanic Garden,

Claremont, California, USA; *C. californicum* Nutt., cultivated at Rancho Santa Ana Botanic Garden; *Geissoloma marginatum* (L.) Juss., *Carlquist 4518*, Clock Peaks, South Africa, *Carlquist 4518* (RSA); *Glossopetalon meionandrum* Koehne, *Jones s.n.* (POM); *G. nevadense* A.Gray, *Thorne 43694* (RSA); *G. stipuliferum* H.St.John, *Duran 1930* (RSA); *Ixerba brexioides* A.Cunn., *Day 1978*, New Zealand Forest Research Institute; *Stachyurus himalaicus* Hook. f. & Thomson, Nepal, *KYOw slide 8540212*; *S. macrocarpus* Koidz., Mt. Hatsumi, Chichijima, Bonin Is., Japan, *Carlquist 15734* (RSA); *S. praecox* Sieb. & Zucc. 'gracilis,' cult. Kew, UK; *S. praecox* 'matsuzaki,' Ibaraki (*TWTw-962*); *S. praecox* subsp. *praecox*, Miyanoshita, Hakone National Park, Japan, *Carlquist 15697* (RSA); *Strasburgeria robusta* (Vieill. ex Panch. & Sebert) Guillau-min, summit of Montagne des Sources, New Caledonia, *Carlquist 725*, *Carlquist 15295* (RSA); *Velascoa recondita* Calderón & Rzed., 6 km NE of La Lagunita de San Diego, Querétaro, Mexico, *Perez & Carranza 3529* (IEB).

The sequence of the illustrations and the sequence of the data in Table 1 are alphabetical according to family.

All specimens were available in dried form. Portions were boiled in water and stored in 50% aqueous ethanol. All woods proved suitable for sectioning with a sliding microtome without softening or other special techniques. Sections for permanent slides were stained in a safranin-fast green combination. Some sections were not stained, but rather were dried between clean glass slides, mounted on aluminum stubs, sputter-coated with gold, and examined with a Hitachi S2600N scanning electron microscope (SEM; Hitachi Electronics, Inc., Tokyo, Japan). Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Terminology follows Bailey (1936), the IAWA Committee on Nomenclature (1964), and Carlquist (2001). The Kribs (1935) ray types are followed, with modifications (Carlquist 2001). For mean number of vessels per group, great care was taken because overlapping vessel element parts of a single vessel can easily be regarded as a pair of vessels when seen in trans-section. Vessel lumen diameter rather than outside vessel diameter was measured, because lumen diameter is physiologically more significant. Lumen diameter of vessels oval in trans-section was calculated by averaging the widest and narrowest chords. For Staphyleaceae, data not obtained in accordance with the above scheme were recalculated. Other data for the family are from Carlquist and Hoekman (1985a). The familial and generic means of Table 1 are based on all collections studied. Only one row of data is reported for Geissolomataceae, Ixerbaceae, and Strasburgeriaceae in Table 1 because these families are monospecific. Data on

Geissolomataceae are for stems only, and are derived from Carlquist (1975a).

RESULTS

Quantitative Data

Quantitative data are presented in Table 1. These data are self-explanatory but not self-interpreting. Interpretations of quantitative data are presented in the Discussion and Conclusions section. The purpose of means for families and genera, based on all collections studied for those respective families, may not seem evident. However, the family mean for any given feature can serve as a standard of sorts, against which quantitative data for any given species or genus can be measured. Departures from familial means for a feature by particular genera or species indicate directions (e.g., narrower vessels connote greater xeromorphy) and degree of evolution in those directions.

Growth Rings

Subtropical species in the present study which lack growth rings include *Aphloia myrtifolia* (Fig. 1), *A. theiformis*, *Geissoloma marginatum* (Fig. 19), and *Strasburgeria robusta* (Fig. 40). An insular species of *Stachyurus*, *S. macrocarpus*, has no growth rings (Fig. 34) in either stem or root. *Turpinia* lacks growth rings (Carlquist and Hoekman 1985a), although the remainder of Staphyleaceae have growth rings.

Species other than the above possess growth rings that feature wider and (at least to some extent) more numerous vessels in the earlywood, with contrasting expressions in latewood (Fig. 6; 15, top; 27; 36). In the species with more marked growth rings, difference in vessel diameter with respect to position in the growth rings is much more marked; in addition, radial diameter of tracheids is less in latewood than in earlywood (Fig. 29). A feature that is subtle but proves to be characteristic in species with more marked growth rings is the lack of vessels in the terminal two or more cell layers of latewood. Thus, conducting tissue in the last-formed portions of a growth ring consists wholly of tracheids.

Ray cells are radially narrower in latewood than in earlywood in species with more pronounced growth rings (Fig. 6, 29). In *Crossosoma bigelovii*, latewood ray cells contain more crystals than do earlywood ray cells (Fig. 12). In *Staphylea*, bars of perforation plates are wider in earlywood than in latewood (Carlquist and Hoekman 1985a).

Vessel Elements

Vessels are remarkably solitary or nearly so throughout the families studied (Fig. 1, 6, 15, 19, 22, 27, 34, 36, 40; Table 1, column 1). Macerations show

Fig. 1–5. Wood sections of *Aphloia myrtifolia* (1–2, 4–5) and *A. theiformis* (3).—1. Transection; vessels are mostly solitary.—2. Tangential section; rays are of two distinct widths.—3. Most of a perforation plate from an SEM photograph of a radial section; bars are bordered.—4. Bordered pits of a fiber-tracheid, seen from the outside surface, SEM photograph.—5. Portion of a tracheid, right, and of two strands of axial parenchyma, left, from radial section; transverse wall of a strand indicated by horizontal arrow; vertical arrow points to vertical wall bearing bordered pits between the two strands. Fig. 1–2, scale above Fig. 1 (divisions = 10 μ m); Fig. 3, bar = 20 μ m; Fig. 4, bar = 10 μ m; Fig. 5, scale above photograph (divisions = 10 μ m).

Fig. 6–11. Wood sections of *Crossosoma bigelovii*.—6. Transection, showing growth rings; vessels are few and narrow in latewood.—7. Tangential section; uniseriate rays plus multiseriate rays of various widths are present.—8–11. Perforation plates from radial section, representing variously modified versions of a scalariform pattern, from the transition between metaxylem and secondary xylem. Fig. 6–7, scale above Fig. 1; Fig. 8–11, scale above Fig. 5.

Fig. 12–16. Wood sections of Crossosomataceae.—12. *Crossosoma bigelovii*, rhomboidal crystals and smaller crystals (arrow) in ray cells of radial section.—13. *C. californicum*, SEM photograph of scalariform perforation plate from early secondary xylem of radial section.—14. *Glossopetalon stipuliferum*, SEM photograph of tracheid surfaces from tangential section, showing bordered pits.—15–16. *Crossosoma californicum*.—15. Transection; growth rings are not as short or as well demarcated as those of *C. bigelovii*.—16. Tangential section; rays are uniseriate plus narrow multiseriate. Fig. 12, scale above Fig. 5 (divisions = 10 μm); Fig. 13, scale bar = 10 μm ; Fig. 14, bar = 5 μm ; Fig. 15–16, scale above Fig. 1.

Fig. 17–21. Wood sections of Crossosomataceae and Geissolomataceae.—17–18. *Velascoa recondita*, SEM photographs from tangential section.—17. Inside of vessel, showing helical thickenings.—18. Inside surface (left) and outside surface (right) of tracheids; inside surface shows helical thickenings.—19–21. *Geissoloma marginatum*.—19. Transection; dark-staining compounds occur in some ray cells.—20. Tangential section; some multiseriate rays are notably wide.—21. SEM photograph of vessel wall from radial section, showing pit membrane remnants in lateral ends of perforations. Fig. 17–18, scale = 10 μm ; Fig. 19–20, scale above Fig. 1; Fig. 21, scale = 2 μm .

Fig. 22–26. Wood sections of *Ixerba brexioides*.—22. Transection; vessels are solitary.—23. Tangential section; only uniseriate and biseriate rays are present.—24–26. SEM photographs from radial section.—24. Perforation plate from radial section to show large number of bars (left); and outer surface of fiber-tracheid with small sparse bordered pits (right).—25. Vessel-ray pitting on inside of vessel.—26. Pit membrane remnants in lateral ends of perforations of perforation plates. Fig. 22–23, scale above Fig. 1; Fig. 24–25, scale bar = 25 μm ; Fig. 26, bar = 2 μm .

Fig. 27–30. Wood sections of *Stachyurus himalaicus*.—27. Transection, showing terminus of growth ring (above center).—28. Tangential section; many ray parenchyma cells contain a dark-staining compound.—29. Transection portion to illustrate scarcity of axial parenchyma cells (arrows).—30. Portion of radial section to show helical thickenings in a vessel (left) and in a tracheid (far right). Fig. 27–28, scale above Fig. 1; Fig. 29, scale above photograph (divisions = 10 μm); Fig. 30, scale bar = 20 μm .

Fig. 31–35. Wood sections of *Stachyurus himalaicus* (31–33) and *S. macrocarpus* (34–35).—31–33. SEM photographs of scalariform perforation plate or plate portions from radial section.—31. Bars of perforation plate show few anomalies.—32. Pit membrane remnants in lateral ends of perforations, seen from inside a vessel.—33. Pit membrane remnants in lateral ends of perforation plates, seen from outer surface of a vessel.—34. Transection; growth ring activity is absent.—35. Tangential section; uniseriate and narrow multiseriate rays are present. Fig. 31, scale bar = 25 μm ; Fig. 32, bar = 10 μm ; Fig. 33, bar = 5 μm ; Fig. 34–35, scale above Fig. 1.

Fig. 36–39. Wood sections of *Stachyurus praecox* subsp. *praecox*.—36. Transection; two growth rings are shown.—37. Tangential section; many ray cells are filled with a dark-staining material.—38. Portion of a radial section to show nature of pitting in a vessel (left) and helical thickening in a tracheid (far right).—39. Portion of a radial section to show helical thickenings in a vessel (most of photograph) and a tracheid (far right). Fig. 36–37, scale above Fig. 1; Fig. 38, scale = 10 μ m; Fig. 39, scale = 10 μ m.

Fig. 40–44. Wood of *Strasburgeria robusta*.—40. Transection; cell size notably large.—41. Tangential section; rays mostly uniseriate.—42–43. SEM photographs of inside of vessel from radial section.—42. End of perforation plate (above), showing presence of pit membranes (smaller pits) or membrane remnants; vessel-ray pitting below.—43. Pit membrane remnants (cracks are artifacts) in lateral ends of perforations.—44. Pits on tracheids from tangential section; bordered nature shown by dark-staining material in pit cavities. Fig. 40–41, scale above Fig. 1; Fig. 42–43, scale = 25 μm ; Fig. 44, scale above Fig. 5.

that vessel elements are commonly prominently tailed, even in Crossosomataceae, which have relatively short vessel elements.

Because vessels are predominantly solitary, vessel-to-vessel pitting can reliably be observed only on the tails of vessel elements, but these areas are too narrow to show scalariform pitting. Vessel-to-ray pitting in the species under consideration is most commonly opposite (Fig. 42). Some scalariform and transitional vessel-to-ray pitting was recorded in *Geissoloma marginatum*, *Ixerba brexioides* (Fig. 25), *Stachyurus macrocarpus*, and many Staphyleaceae (Carlquist and Hoekman 1985a). Scalariform vessel-to-ray pitting is shown in Fig. 38 (adjacent to that, a file of vessel-to-tracheid pitting). Vessel-to-tracheid pitting is often sparse, but only scalariform pitting facing tracheids was observed in *Geissoloma* (Carlquist 1975a). Lateral wall pitting on vessels of Crossosomataceae is alternate regardless of the cell type interface.

Perforation plates are scalariform on all vessels observed (Fig. 3, 24, 31) except for Crossosomataceae (see also Table 1, column 5). Crossosomataceae were reported to have only simple perforation plates by DeBuhr (1978). However, careful examination of woods of *Crossosoma bigelovii* (Fig. 8–11), *C. californicum* (Fig. 13), *Glossopetalon stipuliferum*, and *Velascoa recondita* reveals that scalariform perforation plates are present in the transition between metaxylem and secondary xylem. Some perforation plates in *C. bigelovii* represent slightly altered expressions of the scalariform pattern (Fig. 8, 9, 11). A few perforation plates with a single bar were observed in various places in secondary xylem of *Velascoa recondita*, but perforation plates are predominantly simple in that species. The number of bars per perforation plate in Stachyuraceae is greater than that reported by Metcalfe and Chalk (1950) or Matthews and Endress (2005).

Borders were observed on bars of perforation plates throughout the order, and are illustrated here for *Aphloia theiformis* (Fig. 3), *Crossosoma californicum* (Fig. 13), *Geissoloma marginatum* (Fig. 21), *Ixerba brexioides* (Fig. 26), and *Stachyurus himalaicus* (Fig. 32). In some species of Staphyleaceae that have slender (ca. 1 μm wide) bars, bars are minimally bordered except at the lateral ends of the perforations. Forked bars are common in many perforation plates, and are illustrated here for *Aphloia theiformis* (Fig. 3) and *Stachyurus himalaicus* (Fig. 31).

Pit membrane remnants were observed in perforation plates of Geissolomataceae, Ixerbaceae, Stachyuraceae, and Strasburgeriaceae. In *Geissoloma*, threadlike pit membrane remnants are present at lateral ends of some perforations (Fig. 21). In *Ixerba* (Fig. 26), smaller reticulate portions were observed consistently. In *Stachyurus himalaicus*, the remnants are rather vestigial and threadlike (Fig. 32) or else are perforated

portions of a laminar pit membrane (Fig. 33). Perforations of *Strasburgeria* (Fig. 43) show crescent-shaped laminar pit membranes at lateral ends of perforation plates; transitions between these and membranes covering pits entirely can be seen at the upper and lower termini of perforation plates (Fig. 42, top).

Helical sculpturing on walls of vessel elements was reported for all species of *Euscaphis* and *Staphylea*, and figured for *Staphylea*, by Carlquist and Hoekman (1985a). In Stachyuraceae, for which original data are offered in the present paper, helical thickenings on vessel walls were observed consistently in *Stachyurus himalaicus* (Fig. 30, left), and *S. praecox* subsp. *praecox* (Fig. 39). Helical thickenings tend to occur on vessel surfaces that are less densely pitted. Helical thickenings are more prominent in latewood vessels, and are not present in some earlywood vessels in the species in which they occur. The bands of helical thickenings shown for a vessel of *S. himalaicus* (Fig. 30) are curious in that they correspond in extent to the position of ray cells adjacent to the vessel. No helical thickenings were observed on vessel walls of Crossosomataceae except in *Velascoa recondita*, in which they are present on virtually all vessels. The thickenings in *Velascoa* vessels take the form of pairs of ridges accompanying and parallel to pit apertures; they extend well beyond the pit apertures, and relationship of some of the thickenings to pit apertures may not be evident (Fig. 17). The thickenings in vessels of *Velascoa* (Fig. 17) are similar to those figured for *Stachyurus praecox* subsp. *praecox* (Fig. 39).

Imperforate Tracheary Elements

Tracheids are the imperforate tracheary element type in most genera of Crossosomatales. The imperforate tracheary elements of *Ixerba* have moderately small (pit cavities about 3 μm in diameter) bordered pits (Fig. 24, right), sparsely distributed on walls of these cells. Thus, the elements are best designated transitional between fiber-tracheids and tracheids. The imperforate tracheary elements of *Euscaphis* should be considered tracheids because their pits are relatively densely placed and are about 5 μm in diameter. In *Strasburgeria*, the funnelliform pit apertures facing the lumina of imperforate tracheary elements (Fig. 44, gray) suggest those of fiber-tracheids; dark-staining compounds outline the pit cavities, which are relatively large and thus in proportion to large cell size in *Strasburgeria*. The density of the pits on radial walls (seen as dark dots running along the gray walls of the fiberlike cells, Fig. 41) and the fact that pit cavities are large relative to the narrow lumina of *Strasburgeria* imperforate tracheary elements suggest that functionally, one can regard these cells as tracheids because pit membrane area of the outers surface of the

tracheids is rather great compared to the volume of the slender lumina.

Both species of *Aphloia* exhibit tracheid dimorphism: intermixed with slender, densely pitted nonseptate tracheids are wider, more sparsely pitted, septate fiber-tracheids. Pits of the former are illustrated by light microscopy in Fig. 5 (at right); pits of the latter are shown by means of SEM photography (Fig. 4). In *A. theiformis*, one can find septate fibers in which some septa are thin-walled, while others are thicker, like those separating cells in strands of axial parenchyma. Such septate fibers can readily be distinguished from axial parenchyma strands in this species, however. The distribution of tracheids and septate fibers with respect to each other could not be discerned clearly in all cases, so I am uncertain as to whether the tracheids are vasicentric or more randomly distributed.

Pits on imperforate tracheary elements of Crossosomatales mostly range from 4–6 μm in pit cavity diameter. In *Strasburgeria*, pit cavities are about 10–12 μm in diameter; in this species, all histological features have a greater quantitative value than in the other species of the order. In Crossosomataceae, the reverse is true (Table 1), and pits on tracheids are relatively small, about 4 μm in diameter (Fig. 14).

Helical (or transverse) thickenings occur on the walls of tracheids in all species of *Stachyurus* (Fig. 30, right; Fig. 38, right; Fig. 39, far right). Helical thickenings were reported in tracheids of *Euscaphis* and *Staphylea* by Carlquist and Hoekman (1985a). Helical thickenings are characteristic of the inner surfaces of tracheids of *Velascoa* (Fig. 18, left); they resemble the helical thickenings of the vessels in that genus.

Axial Parenchyma

Diffuse axial parenchyma was observed in all genera of Crossosomatales. Departures from random diffuse parenchyma distribution have been noted in some species of *Euscaphis*, *Staphylea*, and *Turpinia*; in these genera, abaxial and vasicentric parenchyma were reported, in addition to some diffuse parenchyma (Carlquist and Hoekman 1985a). These departures from a strictly diffuse condition are not very pronounced. For example, in *Staphylea bumalda* DC., axial parenchyma is apparently exclusively abaxial, but in the form of a single parenchyma cell abaxial to only a portion of the vessels as seen in transection. In all of the genera under consideration, axial parenchyma is relatively scarce. The sparseness of parenchyma is illustrated in Fig. 29. The upper arrow indicates an axial parenchyma cell with dark-staining contents. The lower arrow in Fig. 29 indicates an axial parenchyma cell with paler contents; another axial parenchyma cell with pale contents is located a little lower down in the same vertical row of cells. Diffuse-in-aggregates axial parenchyma was not observed in Crossosomatales.

Axial parenchyma strands range from two or three cells in length (Crossosomataceae) to as many as 11 (Strasburgeriaceae). This is paralleled by length of fusiform wood cells such as vessel elements in those respective genera. Axial parenchyma cells have secondary walls in the species studied. Both bordered (Fig. 5) and simple pits, as seen in sectional view, occur on axial and transverse walls of the axial parenchyma strand.

Rays

Both multiseriate and uniseriate rays are present in all species. The term “multiseriate” is intended to include biseriate rays here. Virtually no rays wider than three cells in thickness at widest point were observed in a number of species (Fig. 23; Table 1, column 7), and in some genera (*Apacheria*, *Velascoa*, *Ixerba*) rays are biseriate or nearly so. In *Strasburgeria*, most rays are uniseriate (Fig. 41). The presentation of ray width in terms of cell number rather than microns has the merit of demonstrating a phyletic within the order toward what Metcalfe and Chalk (1950) call “rays of two distinct widths.” This condition features abundance of uniseriate, biseriate, and triseriate rays, co-occurring with rays more than 6 cells wide, but with few rays four, five, or six cells wide at the widest point in the ray. This condition is shown by both species of *Aphloia* (Fig. 2) and by *Geissoloma* (Fig. 20). Notably wide multiseriate rays occur in *Crossosoma bigelovii* (Fig. 7) but not in *C. californicum* (Fig. 15) or other species of Crossosomataceae. Stachyuraceae appear to have normal rather than bimodal distribution of ray widths. In Staphyleaceae, rays of two distinct widths occur in most species of *Euscaphis*, *Staphylea*, and *Turpinia*. Perhaps all species of these genera would show this feature if wood samples from old trees could be examined. Barghoorn (1941) has shown that width of multiseriate rays increases with stem diameter in dicotyledons at large.

Rays of Crossosomatales as a whole can be referred to Heterogeneous Type I with transitions to Heterogeneous Type II. Two of the criteria for Heterogeneous Type I (presence of upright sheathing cells on the multiseriate portion of multiseriate rays, and presence of uniseriate tips more than one cell long on multiseriate rays) are little represented in rays of *Apacheria*, *Crossosoma* (Fig. 7), *Glossopetalon*, and *Staphylea*. The rays of the *Velascoa* material studied can be referred to Paedomorphic Type I; the stem studied was about 3 mm in diameter. Very likely, procumbent cells would be present in larger stems of *Velascoa*.

Presence of uniseriate tips and presence of sheathing cells are features of multiseriate rays common in *Aphloia* (Fig. 2), *Euscaphis*, *Geissoloma* (Fig. 20), *Ixerba* (Fig. 23), *Stachyurus* (Fig. 28, 35, 37), and

Strasburgeria. Rays in *Ixerba* and *Strasburgeria* (Fig. 41) are mostly uniseriate. And the few rays with biseriate or triseriate central portions are composed mostly of uniseriate tips. Thus, rays of Geissolomataceae, Ixerbaceae, Stachyuraceae, Staphyleaceae more clearly exemplify Heterogeneous Type I, whereas rays of Crossosomataceae, and Staphyleaceae (*Staphylea* and *Tapiscia*) are closer to Heterogeneous Type II. Care must be taken in such assignments, because for any given species, rays from stems small in diameter tend to have more numerous upright cells than those from wood of stems larger in diameter (Barghoorn 1941), and thus ray types can change as a stem increases in diameter.

Ray cell walls are lignified in all species of Crossosomatales studied. Bordered pits (as seen in sectional view) are frequent on tangential ray cell walls in all of the species studied. Bordered pits are relatively uncommon on horizontally oriented walls of ray cells.

Crystals and Other Cell Inclusions

Crystals are abundant in the rays of *Crossosoma bigelovii*, as reported by DeBuhr (1978). These crystals are more abundant in latewood than in earlywood. Although most crystal presence in this species is in the form of solitary rhomboidal crystals per ray cell, a few cells contain numerous minute rhomboidal crystals (Fig. 12, arrow). Solitary crystals were observed in a few latewood ray cells in *Crossosoma californicum* and *Glossopetalon nevadense* (new reports). In *Geissoloma*, solitary crystals, often together with smaller rhomboidal crystals, occur in some ray cells (Carlquist 1975a).

Yellowish to brownish amorphous inclusions which stain deeply occur in axial parenchyma and ray cells of Aphloiaceae (Fig. 2), Geissolomataceae (Fig. 19, 20), Ixerbaceae (Fig. 22, 23), Stachyuraceae (Fig. 27, 28, 35, 37), most Staphyleaceae (Carlquist and Hoekman 1985a), and Strasburgeriaceae (Fig. 41). In these families, some axial parenchyma or ray cells may have such contents, while other parenchyma cells lack them. Deposits of this nature are not characteristic of Crossosomataceae (Fig. 7, 16).

Starch was recorded for ray cells and axial parenchyma of *Glossopetalon meionandrum*, *Stachyurus himalaicus*, *S. macrocarpus* (both roots and stems), and *Velascoa recondita*. Methods used in preservation of wood samples and preparation of sections often modify or destroy starch deposits; consequently, starch probably occurs widely in woods of the order.

DISCUSSION AND CONCLUSIONS

Evolutionary Unity within Crossosomatales

Crossosomatales contain a remarkable assemblage of primitive character states as judged by widely ac-

cepted criteria (see Carlquist 2001). Scalariform perforation plates with bordered bars are now known to be characteristic of all families, now that this feature is newly reported for in Crossosomataceae. Pit membrane remnants in scalariform perforation plates, considered a primitive feature in dicotyledons (Carlquist 1992), occur in Ixerbaceae, Stachyuraceae, and Strasburgeriaceae. Vessel elements are commonly tailed and are angular in transectional view. Scalariform, transitional, and opposite types of lateral wall pitting of vessels are characteristic of all families except Crossosomataceae. Vessel elements are notably long. The F/V values of all genera considered are low (Crossosomataceae and some Staphyleaceae excepted). All species have tracheids (arguably fiber-tracheids in some cases) as the imperforate tracheary element type. Diffuse axial parenchyma characterizes the order. Heterogeneous Type I is basic to the families, with various degrees of transition to Heterogeneous Type II. Wood is nonstoried. The preceding list contains all of the characters for which phyletic status has been established by statistical methods (see Carlquist 2001).

Cladistic theory dictates that shared primitive character states—symplesiomorphies—are not evidence of relationship. Taking that into account, one can observe that the families of Crossosomatales show differentiation from each other by only a few wood characters, and, as the data of Sosa and Chase (2003) suggest, the order probably departed from an ancestral stock rather early compared to other rosoid families. The presence of numerous primitive wood character states gives no evidence that would counter the concept of Sosa and Chase (2003) that Crossosomatales form a natural order.

The presence of mostly primitive wood character states (e.g., scalariform perforation plates) suggests an unbroken occupancy of mesic habitats by ancestral Crossosomatales. Specialized character states do not disadvantage a phylad from entering a mesic habitat, but primitive character states (bars on a perforation plate, and characters associated with that character state) do mitigate against success in a xeric habitat (Carlquist 1975b). Thus, scalariform perforation plates in secondary xylem are virtually non-existent in plants of dry habitats (Carlquist and Hoekman 1985b). Probably numerous phylads within Asteraceae (all of which characteristically have simple perforations plates) have shifted from xeric habitats into mesic ones (e.g., Madiinae, Carlquist et al. 2003). The retention of primitive character states functionally linked to each other has conceivably limited the evolutionary scope of some of the Crossosomatales, a phenomenon that conveys one meaning of the word “relictual.” Persistence of relictual phylads does involve, however, evolution of compensatory character states.

The phyletic status of some features of woods in Crossosomatales is difficult to establish. One of these

features is the presence of wide, tall rays—especially in those species that have a bimodal distribution of ray widths (“rays of two distinct widths”) and heights. Another is the presence of crystals, which have a scattered distribution within Crossosomatales. The presence of dark-staining material in parenchyma cells of wood might prove a phyletic indicator if a pathway for evolution of secondary compounds in Crossosomatales could be established. *Strasburgeria* is distinctive among Crossosomatales (and also most dicotyledons) in the unusually large size (and wall thickness) of wood cells.

Departures from Primitive Character States

Within Crossosomatales, some families have few departures from the assemblage of primitive character states mentioned above, while other families contain departures in several wood features. Those seeking character states for the purpose of cladistic construction will not find the probable apomorphies in wood anatomy useful. Instead, the apomorphies represent adaptations in wood anatomy to ecological conditions. The wood features of Crossosomataceae, all species of which inhabit seasonally arid habitats, show this principle clearly. The fewest probable apomorphies occur in Geissolomataceae, Ixerbaceae, and Strasburgeriaceae. The rays of Strasburgeriaceae, along with those of Ixerbaceae, might represent an apomorphy by rarely exceeding two cells in width. Because Ixerbaceae and Strasburgeriaceae seem closely related (Matthews and Endress 2005), such rays might represent a synapomorphy, but this feature is not a clearly definable one. The occurrence of unusually wide rays (“rays of two distinct widths”) in Aphloiaceae and Geissolomataceae might also represent apomorphies. In the case of *Geissoloma*, a fire-adapted shrub, wide rays probably represent sites for initiation of new shoots after fire; such rays are characteristic of both aboveground and belowground stems (Carlquist 1975a). The rays of Crossosomataceae represent a departure from the primitive Heterogeneous Type I condition by having short uniseriate tips—an apomorphy for the family.

The relatively low number of bars per perforation plate in Geissolomataceae may be related to shortness of vessel elements, a shortness in turn probably related to the shrubby habit of *Geissoloma*. In Asteraceae (353 collections studied), shrubs have appreciably shorter vessel elements than trees (Carlquist 1966); this is also true in a floristic survey (Carlquist and Hoekman 1985b). Presence of pit membrane remnants in scalariform perforation plates (Geissolomataceae, Ixerbaceae, Stachyuraceae, and Strasburgeriaceae) is considered a primitive feature (Carlquist 1992). Helical thickenings in vessels of *Euscaphis*, *Stachyurus*, *Staphylea*, and *Velascoa* probably represent autapomor-

phies; these thickenings are more frequent in colder climates, as well as in drier ones (Carlquist 2001). The presence of such thickenings in tracheids of *Stachyurus* and *Velascoa* is interesting, and is consistent with the probable conductive nature of tracheids in these two genera. Occurrence of helical thickenings in tracheids of the two families is probably homoplasious. The presence of fiber dimorphism is an autapomorphy in Aphloiaceae.

Crossosomataceae show marked adaptations to aridity in wood anatomy. The simple perforation plates of Crossosomataceae (which have scalariform perforation plates only in earliest secondary xylem) are such an adaptation. Simple perforation plates are advantageous not during the dry season, but during short periods during the wet season when peak conductive rates occur. High vessel density and narrow vessel lumen diameter in Crossosomataceae contribute to conductive safety because these conditions lower the probability of embolism occurrence (see Carlquist 2001). Pronounced growth rings in Crossosomataceae are probably not primarily an adaptation to cold, but rather to drought. Latewood exhibits progressively fewer vessels, terminating in two or three cell layers in which vessels are entirely absent—a xeromorphic feature (see below). The presence of scalariform perforation plates in late metaxylem and early secondary xylem is interesting. This feature is consistent with derivation of Crossosomataceae from a group with highly primitive wood features, rather than a phylad that ancestrally had simple perforation plates. In turn, this suggests that ancestors of Crossosomataceae occupied more mesic habitats. Retention of scalariform perforation plates in the metaxylem–secondary xylem boundary confirms Bailey’s (1944) idea that this region is a “refugium” of primitive characters. In turn, it also suggests a functional reason for that apparent relictualism: the relatively few vessels with scalariform perforation plates in stems of Crossosomataceae would not hinder rapid conduction during brief moist periods. The wood of *Crossosoma californicum* is a little more mesomorphic in quantitative vessel features than wood of the other species, reflecting the less severe insular habitats of *C. californicum*. The Mesomorphy Ratio (Table 1, column 10), although an arbitrary construct, reflects this. According to this ratio, the farthest advance into xeromorphy in the family is registered by *Apacheria*.

The Role of Tracheid Presence

Retention of tracheids (as opposed to abandonment of tracheids in favor of fiber-tracheids) in Crossosomataceae is consistent with entry of the family into xeric habitats. The tracheid is a conductive cell type that offers maximal conductive safety. Vessel elements offer good conductive efficiency but less conductive

safety; fiber-tracheids and libriform fibers offer mechanical strength but little or no conductive capability, as shown by the dye uptake experiments of Braun (1970). Tracheids promote conductive safety to such a great extent that other histological conditions that enhance conductive safety are often minimally represented when tracheids are present. Mean number of vessels per group is below 1.20 in Crossosomatales. Tracheids, present in all Crossosomatales, deter vessel grouping (Carlquist 1984). Figures for mean number of vessels per group are more markedly elevated in fiber-tracheid- or libriform fiber-bearing species in more arid habitats (Carlquist 1984; Carlquist and Hoekman 1985b). There is a slightly elevated figure for vessels per group in Crossosomataceae (Table 1, column 1). This is attributable not to any advantage of vessel grouping, but to the random contacts of vessels in the very narrow growth rings, which feature high density of vessels.

Growth rings form a class of wood adaptations for promoting conductive safety. In woods that have fiber-tracheids or libriform fibers rather than tracheids, presence of numerous vessels in latewood and grouping of those vessels provide conductive safety: this is illustrated in Type 4 and Type 13 ("ulmiform" latewood) by Carlquist (1980, 2001). In these two types, the background is not composed of tracheids, but rather, fiber-tracheids or libriform fibers. On the contrary, vessels become fewer and narrower—finally absent—in growth rings of Crossosomatales. These growth rings (Type 5 of Carlquist 1980, 2001) provide the net effect of greater tracheid density in latewood (both because of less space occupied by vessels in latewood and because of smaller radial diameter of tracheids in latewood). Thus, numbers of the cell type with the greatest safety actually increase during production of latewood.

In most dicotyledons, vessel element length is markedly less in species of arid habitats than in species of mesic habitats (Carlquist 1966; Carlquist and Hoekman 1985b). However, in Crossosomataceae, vessel elements are longer than they are in species of dicotyledons of arid habitats. Shortening of vessel elements is seen as an adaptation for improvement of conductive safety (Carlquist 2001). However, apparently this adaptation contributes less to conductive safety than tracheid presence does. Thus, in phylads with tracheid presence in wood, vessel element shortening with progressive entry into xeric sites is diminished.

Retention of tracheids is very likely an advantage in several families well represented in arid or highly seasonal (with respect to moisture availability) habitats: Elaeagnaceae, Krameriaceae, Rosaceae, and Zygophyllaceae for example (families with vasicentric tracheids would make the list much longer). In addition, the many dicotyledons with vasicentric tracheids in secondary xylem occupy such habitats; vasicentric tra-

cheids potentially provide much of the safety that pervasive tracheid presence assures (Carlquist 1985). Tracheid presence is only one mechanism permitting a woody plant to cope with drier environments. Others shown by Crossosomataceae include smaller plant size, smaller leaf area, drought deciduousness, heteroblasty (short shoot formation), and probably some features that would require devices to measure (e.g., diffusive resistance of leaves). Ultimately, a synthesis between secondary xylem features and those of habit and foliage will provide a much more satisfying understanding of how woody plants adapt to aridity and cold.

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