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WOOD AND STEM ANATOMY OF PHYTOLACCOID AND RIVINOID PHYTOLACCACEAE (CARYOPHYLLALES): ECOLOGY, SYSTEMATICS, NATURE OF SUCCESSIVE CAMBIA

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ABSTRACT

Quantitative and qualitative wood features are presented and analyzed for seven species of subfamily Rivinoideae and four of subfamily Phytolacchoideae. All species have nonbordered perforations plates, as elsewhere in suborder Phylolaccineae. Libriform fibers characterize both subfamilies, but vasicentric tracheids occur in two rivinoid species. Axial parenchyma is vasicentric scanty (apotracheal bands and patches in one species). Rays are mostly multiseriate, with procumbent cells infrequent in most species. Rivinoids and phytolaccoids differ from each other in ray height and width and in crystal types. The xeromorphic wood of *Petiveria* and *Rivina* is related to their short duration (woody herbs) in disturbed soil that dries readily. Woods of other genera are moderately mesomorphic, correlating with seasonally tropic habitats. Genera of Phytolaccaceae studied here have the same ontogenetic features leading to successive cambia as *Stegnosperma*. *Phytolacca dioica* has amphivasal pith bundles in which secondary growth occurs. Vessel restriction patterns are newly reported for the family.

Key words: cambial variants, Caryophyllales, Centrospermae, ecological wood anatomy, pith bundles, successive cambia, vasicentric tracheids, vessel restriction patterns.

INTRODUCTION

Phytolaccaceae are a curious assemblage because the component groups are diverse with respect to ovary and fruit characters that in other angiosperm alliances are often accepted as familial criteria. Differences in carpel number, stigma number, and fruit texture define subfamilies and genera of Phytolaccaceae (Heimerl 1934). The genera of Rivinoideae (segregated by some as Rivinaceae) have a single carpel but may have samaras (*Gallesia*, *Seguieria*); diverse hooked and bristly dry fruits (*Monococcus*, *Petiveria*), dry fruits without appendages (*Ledenbergia*, *Schindleria*); fleshy spherical fruits (*Rivina*, *Trichostigma*); and reticulate semifleshy fruits (*Hillieria*) (Heimerl 1934). Such diverse fruits often are prime features used to separate otherwise close angiosperm families (e.g., Myrsinaceae from Primulaceae).

If the abovementioned genera are removed from Phytolaccaceae as Rivinaceae, and other genera (e.g., *Achatocarpus*, *Agdestis*, *Barbeuia*, *Gisekia*, *Stegnosperma*) commonly segregated from the family are also removed, Phytolaccaceae then are equivalent to the subfamily Phytolacchoideae of various authors. Phytolacchoideae comprise polycarpic (3–16 carpels) ovaries that mature into colorful and fleshy (*Phytolacca*) or leathery to dry (e.g., *Anisomeria*, *Ercilla*) fruits.

Various authors have endorsed removal from Phytolaccaceae of Achatocarpaceae, Agdestidaceae, Barbeuiaceae, Gisekiaceae, Rivinaceae (= Petiveriaceae), and Stegnospermataceae (Cronquist and Thorne 1994, Behnke 1997). In addition, Behnke (1997) has re-

moved *Sarcobatus* from Chenopodiaceae as Sarcobataceae and placed it close to Phytolaccaceae (= within suborder Phytolaccineae). The families mentioned above, whether or not one treats them as segregate families of Phytolaccaceae (e.g., Behnke 1997) or subfamilies within a more inclusive Phytolaccaceae (Thorne in Cronquist and Thorne 1994), seem satellites of Phytolacchoideae, as shown by Rodman et al. (1984) and Rodman (1994). However, there is not a consensus at present on the contents of Phytolaccaceae, and therefore I am citing genera (the definitions of which are not so controversial) and subfamilies (by implication, subfamilies of a more inclusive Phytolaccaceae) rather than attempting to use either a Phytolaccaceae s.l. or a Phytolaccaceae s.s. Our concepts of the contents of Caryophyllales and the clades (and therefore family and suborder definitions) within the order are currently in flux, as the study by Williams et al. (1994) shows. Phytolaccaceae as traditionally conceived may not be a monophyletic group, based on cladistic analysis of DNA sequence data (James Rodman, pers. comm.).

Thorne (in Cronquist and Thorne 1994) and Behnke (1997) placed the families (or genera) listed above within a suborder, Phytolaccineae, that also includes Aizoaceae, Nyctaginaceae, and possibly Halophytaceae. Gyrostemonaceae can be found included in Phytolaccaceae by earlier authors (e.g., Walter 1909), but Gyrostemonaceae are one of the glucosinolate families that group with other Capparales; and the exclusion of Gyrostemonaceae from Caryophyllales as a whole and

therefore also Phytolaccaceae in particular is entirely justified (Goldblatt et al. 1976; Behnke 1977). Bataceae have been similarly repositioned from Caryophyllales to Capparales (Behnke and Turner 1971).

Information from wood anatomy is potentially useful either for segregation of the families listed above from Phytolaccaceae or for recognition of a more inclusive Phytolaccaceae. Likewise, some wood features, such as the occurrence of nonbordered perforation plates, may prove to unite the families of the suborder Phytolaccineae or even the families of Caryophyllales. The present paper constitutes one in a series of studies presenting new information about wood anatomy of Caryophyllales. Earlier papers in the series include studies of Caryophyllaceae (Carlquist 1995), Portulacaceae and Hectorellaceae (Carlquist 1998a), *Petiveria* and *Rivina* (Carlquist 1998b), Basellaceae (Carlquist 1999a), *Agdestis* (Carlquist 1999b), *Stegnosperma* (Carlquist 1999c), and *Barbeuia* (Carlquist 1999d). In pursuing this series, some families will not be included because other authors have covered them thoroughly, e.g., Cactaceae (Gibson 1973 and other papers by him) and Didiereaceae (Rauh and Dittmar 1970). The compilation of Gibson (1994) on wood anatomy of Caryophyllales is useful, but as he indicates, the citation of wood features for Phytolaccaceae by Metcalfe and Chalk (1950) unfortunately includes Gyrostemonaceae without citing them separately and thus must be read with care. For citations prior to 1994 on wood anatomy of Phytolaccaceae, see Gibson (1994) and Gregory (1994). Two families consistently appear as outgroups to Caryophyllales: Plumbaginaceae and Polygonaceae. Wood of the former was surveyed recently (Carlquist and Boggs 1996), and a study of wood anatomy of Polygonaceae is in progress. A detailed comparison of the component families of Caryophyllales, including tabular comparisons, will conclude this series of papers, and that paper will be based on newly expanded definitions of Caryophyllales (e.g., Williams et al. 1994).

Wood anatomy of Phytolaccaceae is especially interesting with respect to ecology and habit. Some genera are lianas (*Gallesia*, *SeQUIERIA*), whereas others are shrubs (*Anisomeria*), trees (*Phytolacca dioica*, *Trichostigma octandrum*) or woody herbs that are annual or of short duration (*Petiveria alliacea*, *Phytolacca* spp., *Rivina humilis*). Wood features in relation to growth forms and habitats are analyzed in the DISCUSSION AND CONCLUSIONS.

The following phytolaccoid genera have been reported to have successive cambia: *Agdestis*, *Anisomeria*, *Barbeuia*, *Ercilla*, *Gallesia*, *Petiveria*, *Phytolacca*, *Rivina*, *SeQUIERIA*, and *Stegnosperma* (Pfeiffer 1926; Heimerl 1934). Successive cambia have not been reported in *Hillieria*, *Ledenbergia*, *Lophiocarpus*, *Microtea*, *Schindleria*, *Trichostigma*, or in the family now

commonly removed from Phytolaccaceae, Achatocarpaceae (Pfeiffer 1926; Heimerl 1934). The phylogenetic question posed by this distribution is whether presence of successive cambia is a plesiomorphy or an apomorphy in phytolaccoids. In a few cases, the appearance of a second cambium is delayed (Horak 1981); successive cambia were not found by Heimerl (1934) in a stem of *Stegnosperma* 5.5 mm in diameter, for example. Perhaps the genera that lack successive cambia have a genetic basis for formation of successive cambia but also a modifier or repressor gene that delays their appearance for the length of life of the plant. In any case, the generic distribution of successive cambia in Phytolaccaceae s.l. is now known with reasonable accuracy. The three families now included along with phytolaccoids in Phytolaccineae (Aizoaceae, Nyctaginaceae, and Sarcobataceae) all have successive cambia and are relevant to the phylogenetic status of successive cambia in the order. Very likely, more molecular data may clarify the phylogenetic issue. However, the anatomical nature of successive cambia needs clarification, and each pertinent genus that is studied in detail yields information on this question. Each of the successive cambia in a stem or root is a vascular cambium that produces xylem internally and phloem externally (except for cambia formed in the pith region); that concept is not in question. Rather, the nature and origin of the meristem that *leads to production* of these cambia and to conjunctive tissue (between the successive vascular bands) form a series of questions that have proved controversial. The papers on this meristematic activity in *Phytolacca* (Wheat 1997; Mikesell 1979) are not entirely in agreement, and the disagreements in terminology and interpretation widen if we include studies on lateral meristem origins and action in Nyctaginaceae (Studholme and Philipson 1966, Esau and Cheadle 1969, Stevenson and Popham 1973). I have attempted to clarify the nature of lateral meristem activity in several genera of Phytolaccaceae s.l.: *Agdestis* (Carlquist 1999b), *Barbeuia* (Carlquist 1999d), *Petiveria* (Carlquist 1998b), and *Stegnosperma* (Carlquist 1999c). In a single phylogenetic unit such as Caryophyllales, the mechanism of lateral meristem origin and action leading to production of successive cambia and conjunctive tissue seems to represent a basic pattern, although variations on that pattern are entirely conceivable on the basis of present information. If there proves to be a single basic type of meristem origin and action in Caryophyllales, then comparisons can be made with various orders of angiosperms as well as with Gnetales.

MATERIALS AND METHODS

The collections studied are as follows: *Anisomeria chilensis* (Miers) H. Walt., cultivated at the University

of California Botanical Garden, Berkeley (53.1304); *Gallesia integrifolia* (Spreng.) Harms, Jauja, Satipo Reserva Forestal, Junin, Peru, MADw-22446; *Hillieria latifolia* (Lam.) H. Walt., Bundibugyo, Uganda, MADw-43651; *Petiveria alliacea* L., cultivated at the Heidelberg Botanical Garden (2317187); *Phytolacca americana* L., adventive outside fence of Strybing Arboretum, Golden Gate Park, San Francisco, CA, Carlquist 8180 (SBG); *P. dioica*, cultivated at the Huntington Botanical Gardens, San Marino, CA; *P. dodecandra* L'Herit., Talla, Congo Republic, Ritlaub R56207 (RSA); *Rivina humilis* L., adventive on the University of Hawaii campus, Honolulu, Hawaii, Carlquist 8162 (SBG); *Sequiaria americana* L., Estado Sao Paulo, Brazil, MADw-SJR 11431; *Trichostigma octandrum* (L.) H. Walt., Liali, Dominican Republic, USw-59757; *T. peruvianum* (Moq.) H. Walt., Tocache Nuevo, Mariscal Caceres, San Martin, Peru, MADw-38857. Species nomenclature follows Heimerl (1934).

The specimens of *Petiveria alliacea*, *Phytolacca americana*, *P. dioica*, and *Rivina humilis* were preserved in 50% aqueous ethanol. The material of *Petiveria alliacea* and of the three species of *Phytolacca* were sectioned in paraffin after softening according to the technique of Carlquist (1982) because mixture of hard and very soft tissues in a stem makes this technique advantageous. Satisfactory sections of the remaining species, which have greater tissue homogeneity and only moderate cell wall hardness, were obtained with a sliding microtome. Sections were stained with a safranin-fast green combination. Some sections were left unstained, dried between clean slides, mounted on aluminum stubs, sputter coated, and observed with a Bausch and Lomb Nanolab scanning electron microscope (SEM). Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Data on *Petiveria* and *Rivina* have been published previously (Carlquist 1998b), but quantitative data on these two genera are included here to present a more coherent picture of Phytolaccaceae subfamily Rivinoideae. Vessel diameter in Table 1 is presented as lumen diameter. No vessel density or vessel grouping data could be presented for *Sequiaria americana* because narrow vessels cannot be differentiated from vasicentric tracheids as seen in transection. Vessel diameter for this species was obtained from macerations. Figures for vessel density in Table 1 are based on views of secondary xylem only, and areas of secondary phloem and conjunctive tissue were not included for purposes of computation. The transectional area of conjunctive tissue can range from relatively little to about 50% of stem transectional area in Phytolaccaceae with successive cambia. In *Phytolacca dioica*, amount of expansion of parenchymatous conjunctive tissue by radial enlargement of cells (possibly a form of succulence) varies from one vascular band to another and

from one stem to another. The conductive area per mm² of stem transection in that species thus varies so greatly that a vessel density figure based on views that include conjunctive tissue would not be meaningful. Terminology follows the IAWA Committee on Nomenclature (1964) and, for ray types and vasicentric tracheids, Carlquist (1988). The sequence of genera in the plates of the present study follows the generic sequence of Heimerl (1934).

RESULTS

Growth Rings

Growth rings were observed in *Gallesia integrifolia* (Fig. 1, 3) and in *Sequiaria americana*. Although one might expect a growth ring to begin with the initiation of a vascular cambium, the latewood:earlywood boundary in species with successive cambia occurs within a band of vascular tissue, not at the beginning (or end) of it. In *Gallesia* and *Sequiaria*, vessel elements do not narrow progressively within a growth ring; instead, narrow latewood vessels appear very shortly before the end of the growth ring (Fig. 3, lower left). Wide, thin-walled libriform fibers (which are not subdivided and therefore are not axial parenchyma) are located at growth ring margins in *Gallesia*, but may be found elsewhere within a growth ring also (Fig. 1).

Vessel Restriction Patterns

The tendency for vessels to be confined to central portions of fascicular areas in secondary xylem, and thus for vessels not to be in contact with rays, has been referred to the concept "vessel restriction patterns" (Carlquist 1988). Although a tendency toward this condition is shown in the rivinoids studied here, vessel restriction patterns are most clearly shown here in *Anisomeria chilensis* (Fig. 22) and *Trichostigma octandrum* (Fig. 13).

Vessel Elements

All perforation plates in Phytolaccaceae are simple. They are also nonbordered, a feature that appears to be characteristic for the suborder Phytolaccineae. Nonbordered perforation plates have been figured for *Agdestis* (Carlquist 1999b), *Barbeuia* (Carlquist 1999d), and *Stegnosperra* (Carlquist 1999c). A vestigially bordered perforation plates is shown for *Trichostigma octandrum* in Fig. 19, far right.

The mean number of vessels per group (Table 1, column 1) ranges widely, from 1.17 in *Hillieria latifolia* to 3.84 in *Trichostigma octandrum* (Fig. 13). Vessels are grouped in radial multiples or chains (Fig. 1, 3, 13, 26) or sometimes in either radial or tangential multiples (Fig. 22, 28).

Mean vessel lumen diameter (Table 1, column 2) is

Table 1. Wood characteristics of Phytolaccaceae.

Species	1 VG	2 VD	3 VM	4 VL	5 VW	6 PD	7 FL	8 MH	9 MW	10 UH	11 RH	12 MR
Subfamily Rivinoideae												
<i>Gallesia integrifolia</i>	1.93	39	53	247	5.8	10	965	700	4.0	—	USP	182
<i>Hillieria latifolia</i>	1.17	38	53	212	2.0	8	374	585	3.0	—	Us	152
<i>Petiveria alliacea</i>	1.84	18	157	170	2.3	5	442	288	3.2	59	USp	19
<i>Rivina humilis</i>	2.00	24	190	176	2.2	5	412	377	2.8	111	USP	22
<i>Seguieria americana</i>	?	40	?	261	2–5	5	438	472	2.8	112	USP	?
<i>Trichostigma octandrum</i>	3.84	34	85	277	3–10	5	304	436	2.4	191	Us	277
<i>T. peruvianum</i>	1.90	30	55	350	2.0	7	676	555	2.4	—	U	191
Subfamily Phytolacchoideae												
<i>Anisomeria chilensis</i>	2.80	32	71	182	3.7	5	484	1032	4.1	—	USP	82
<i>Phytolacca americana</i>	2.24	41	52	208	2.2	8	592	2523	4.0	—	Usp	164
<i>P. dioica</i>	1.68	42	88	237	3.6	10	627	2362	7.0	—	Us	113
<i>P. dodecandra</i>	1.36	56	45	189	3.5	10	617	2921	5.5	—	US	235
All species, means	2.08	36	85	228	3.3	7.1	539	1114	3.7	93		144

Key to columns: 1 (VG), mean number of vessels per group; 2 (VD), mean vessel diameter, μm ; 3 (VM), mean number of vessels per mm^2 ; 4 (VL), mean vessel element length, μm ; 5 (VW), mean vessel wall thickness, μm ; 6 (PD), mean diameter of vessel pits, μm ; 7 (FL), mean libriform fiber length, μm ; 8 (MH), mean height of multiseriate rays, μm ; 9 (MW), mean multiseriate rays width, cells; 10 (UH), mean height of uniseriate rays, μm ; 11 (RH), ray histology (U = upright, S = square, P = procumbent; upper case indicates predominant types); 12 (MR), Mesomorphy Ratio (vessel diameter times vessel element length divided by vessels per mm^2).

notably small in the two woody herbs, *Petiveria* and *Rivina*. In no species, however, is mean lumen diameter wide, considering that the widest mean figure is 56 μm for *Phytolacca dodecandra* and the figure for the remainder of the species studied is below 50 μm . This figure can be appreciated when one reads that the mean vessel diameter (outside diameter) for dicotyledons as a whole is 94 μm (Metcalf and Chalk 1950). That figure is probably biased by the tendency for studies to be based on mesic trees rather than on herbs, shrubs, or small trees; the latter range of habits characterizes the species of the present study. Vessel density in Phytolaccaceae (Table 1, column 3) is almost perfectly inverse to vessel diameter, with deviation from that relationship in *Trichostigma peruvianum*, which has comparatively low vessel density. Because of the exclusion of secondary phloem and conjunctive tissue from the computations on vessel density, the vessel density reported in *Phytolacca dioica* and *P. dodecandra* is appreciably higher than the figure that would have been obtained had conjunctive tissue been included. The stems of *P. americana* had only two vascular bands, the first of which was very wide, so conjunctive tissue does not form a large proportion of the stem in that species.

Vessel element length in Phytolaccaceae (Table 1, column 4) ranges from 170 μm to 350 μm . The mean for the species studied as a whole (228 μm) is roughly half of the vessel element length reported by Metcalfe and Chalk (1950) for dicotyledons as a whole (649 μm). The shortest vessel elements are in the woody herbs *Petiveria alliacea* (170 μm) and *Rivina humilis* (176 μm).

The figure for vessel wall thickness (Table 1, col-

umn 5) ranges widely. Wider vessels tend to be thicker walled, most conspicuously in *Gallesia integrifolia* and *Trichostigma octandrum* (Fig. 3). Diameter of lateral wall pits ranges between 5 μm and 10 μm in the species studied. Shape of pit cavities on lateral walls of vessels is uniformly circular to slightly oval. Pit apertures are elongate and slitlike in most species, but circular or nearly so in *Phytolacca dioica* and *Trichostigma peruvianum*. Pit apertures of *P. dodecandra* are widely elliptical in contrast to the narrowly elliptical shape of pit apertures on lateral vessel walls of the remaining species. Grooves of various length interconnecting pit apertures may be seen on the inner surfaces of vessels in *Trichostigma octandrum* (Fig. 17–19). There are no helical thickenings on vessel surfaces of any Phytolaccaceae studied.

Vessels are rarely in contact with rays, but rather appear confined to centers of fascicular areas in *Seguieria americana* (Fig. 9), *Trichostigma octandrum* (Fig. 13), and *Anisomeria chilensis* (Fig. 22). This condition is termed a vessel restriction pattern and has been reported in woods of a scattering of dicotyledon families (Carlquist 1988).

Macerations show that vasicentric tracheids are almost as abundant as narrow vessels in *Seguieria americana*. Mean length of vasicentric tracheids in that species is 315 μm . Vasicentric tracheids are present but not abundant in *Trichostigma octandrum* (Fig. 15, right).

Libriform Fibers

Other than the vasicentric tracheids mentioned above, all imperforate tracheary elements in the spe-

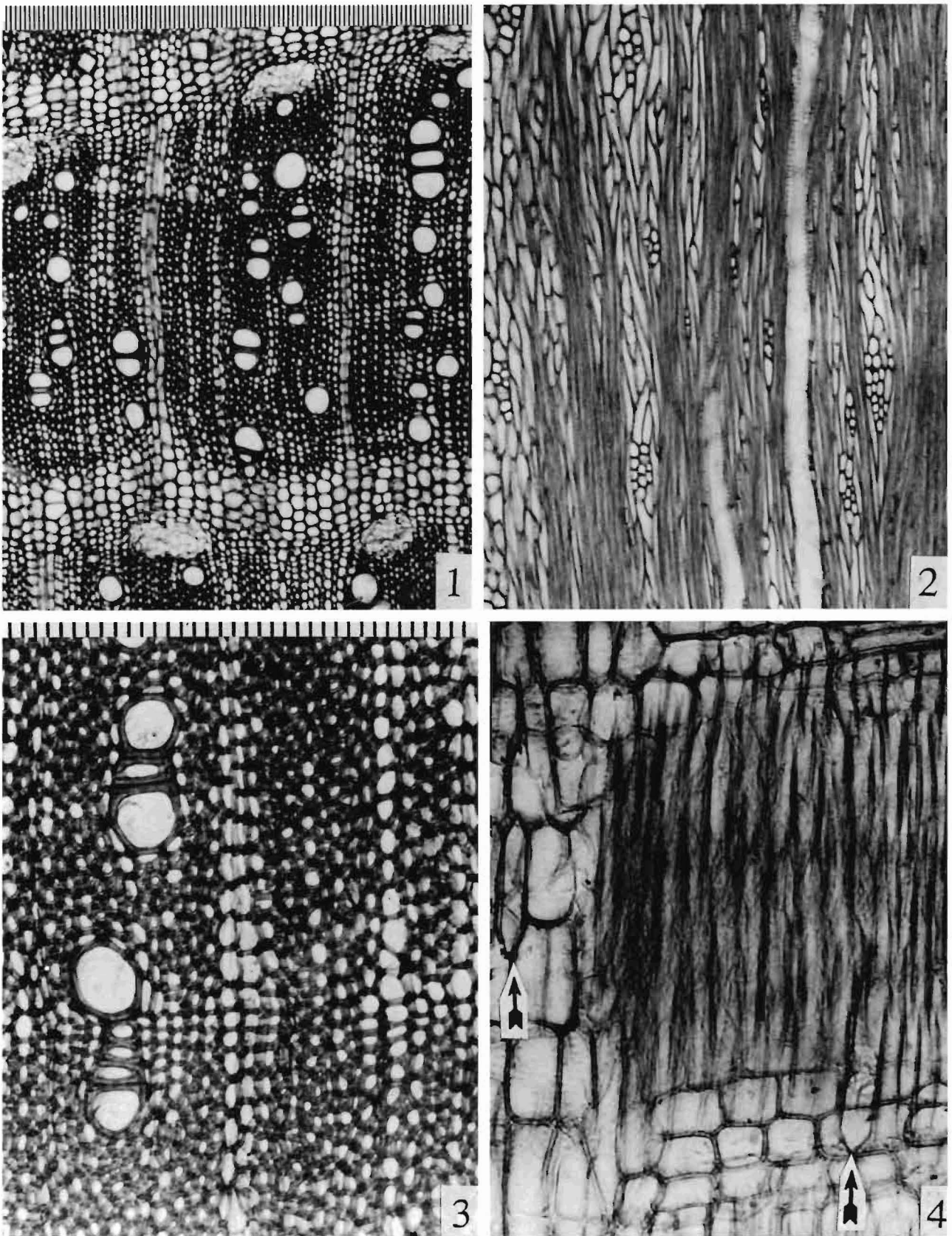


Fig. 1-4. Wood sections of *Galesia integrifolia*.—1. Transection; a band of conjunctive tissue near top and another near bottom.—2. Tangential section; rays both multiseriate and uniseriate; some cells of conjunctive tissue at extreme left.—3. Transection; growth ring is demarcated by four narrow latewood vessels in a radial multiple, below, which terminates above in a larger earlywood vessel.—4. Radial section; rays at top and bottom, right; at left, a band of conjunctive tissue; styloids indicated by arrows. (Fig. 1, 2, scale above Fig. 1 [divisions = 10 μ m]; Fig. 3, 4, scale above Fig. 3 [divisions = 10 μ m].)

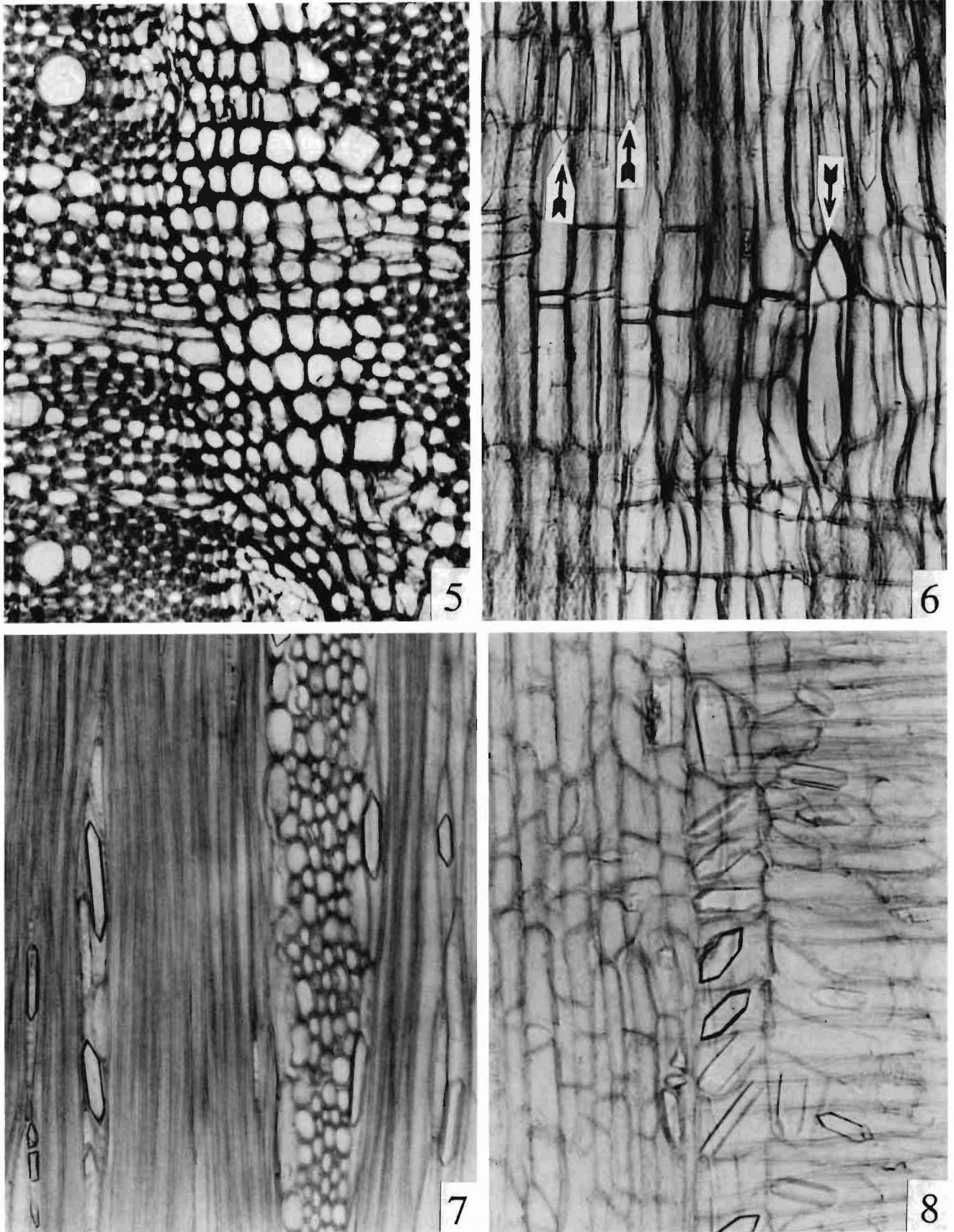


Fig. 5-8. Wood sections of *Galesia integrifolia*.—5. Transection; conjunctive tissue (top to bottom, middle of photograph) contains two styloids in sectional view (adjacent to secondary xylem at right).—6. Radial section; large styloid adjacent to ray plus smaller elongate rhomboidal crystals (arrows).—7. Tangential section; elongate rhomboidal crystals in sheathing cells of ray, right, and in axial xylem, left.—8. Radial section of ray (horizontal axis oriented vertically); numerous rhomboidal crystals present. (Fig. 5-8, scale above Fig. 3.)

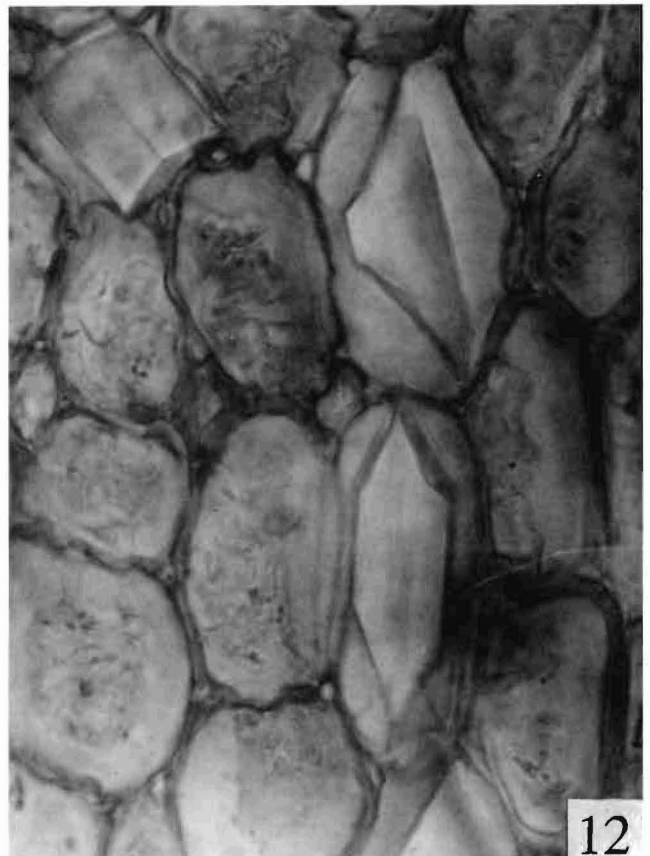
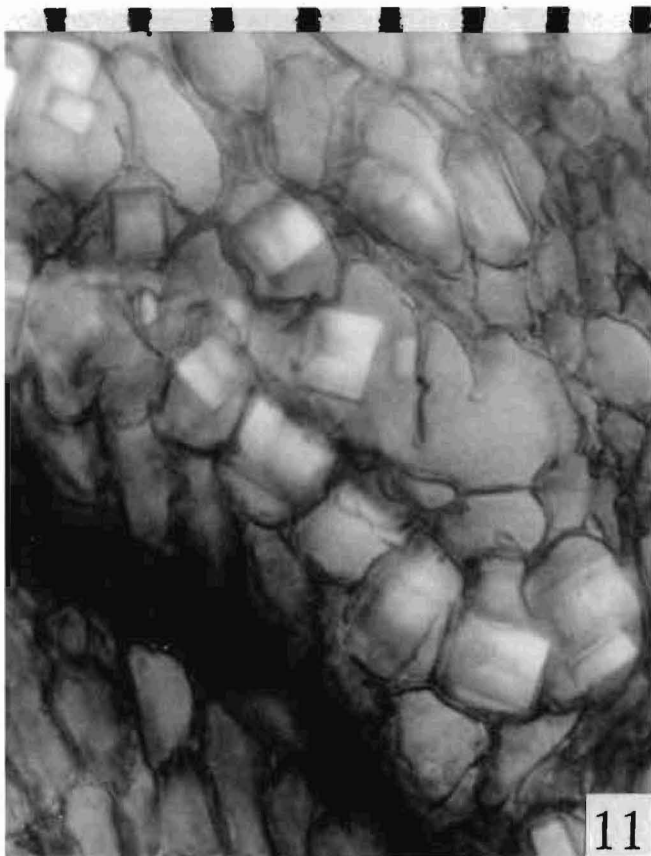
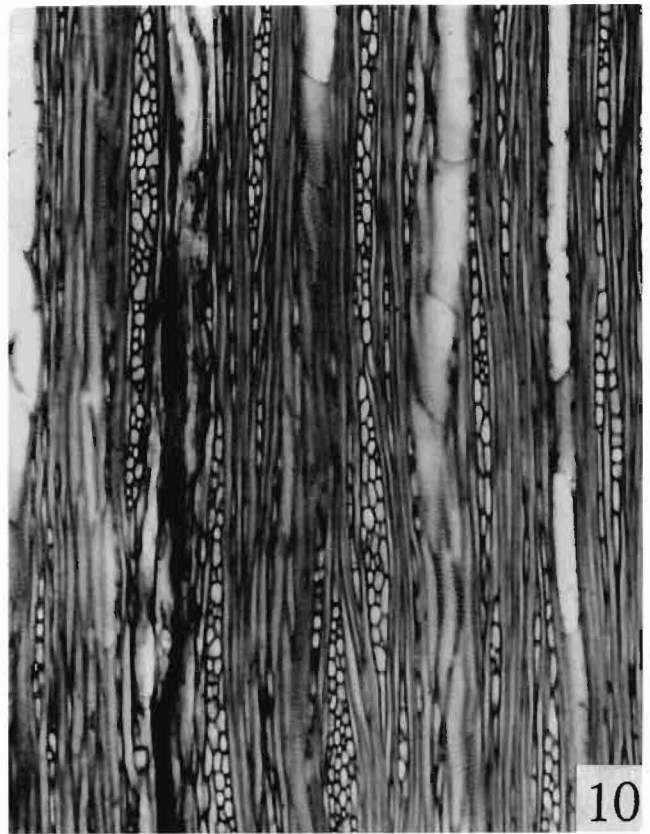
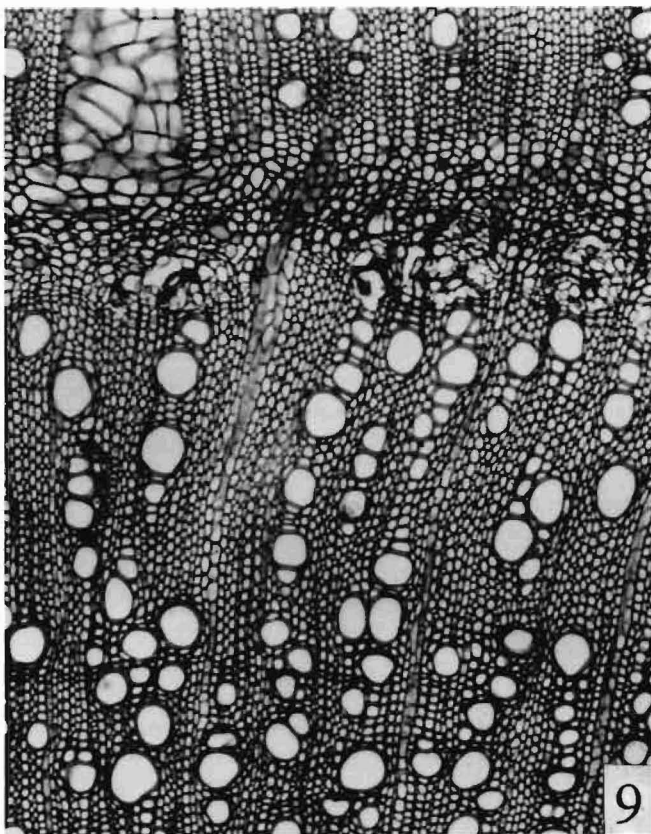


Fig. 9–12. Wood sections of *Seguiera americana*.—9. Transection; conjunctive tissue left to right near top; multiseriate ray with cell proliferation upper left.—10. Tangential section; multiseriate and uniseriate rays are present; dark gray streak at left is secondary phloem.—11. Transection of dilated phloem ray to show about 10 styloids in sectional view (pale squares, one per cell).—12. Tangential section of ray; two rhomboidal crystals in sectional view to right of center, and a mirror-image rhomboid extreme upper left. (Fig. 9, 10, magnification scale above Fig. 1; Fig. 11, 12, scale above Fig. 11 [divisions = 10 μ m].)

cies studied are libriform fibers that bear very small (ca. 1–3 μm) slitlike pits. Careful examination of the pits did not reveal any unequivocal borders. Starch was observed in libriform fibers of *Petiveria alliacea*, *Rivina humilis*, and *Seguiera americana*. Cytoplasm remnants were observed in libriform fibers of *Trichostigma peruvianum*. These four species have living fibers, therefore. No septate fibers were observed.

Mean length of libriform fibers (Table 1, column 7) varies greatly within both subfamilies. An interesting consequence of this diversity is that the F/V ratio (libriform fiber length divided by vessel element length) ranges from more than 3.0 (*Anisomeria chilensis*, *Gallesia integrifolia*, *Phytolacca dodecandra*) to less than 2.0 (*Hillieria latifolia*, *Seguiera americana*, *Trichostigma octandrum*, and *T. peruvianum*).

Most species studied have relatively thin-walled libriform fibers; the mean wall thickness for all species is 2.7 μm (e.g., Fig. 15, left). The notable exceptions are *Anisomeria chilensis* (5 μm) and *Phytolacca dodecandra* (5.5 μm).

Axial Parenchyma

Scanty vascentric axial parenchyma was recorded for all but two of the species studied, but in *Seguiera americana*, axial parenchyma is very scarce. In *Gallesia integrifolia* and *Trichostigma octandrum*, scanty vascentric axial parenchyma is present, but there is also apotracheal parenchyma in the form of patches and radially wide but tangentially short bands. In *Seguiera americana*, ray-adjacent parenchyma was recorded in addition. Axial parenchyma is in strands of two, less commonly three, cells. The exception to this is *Trichostigma octandrum*, in which axial parenchyma is dimorphic: either in strands of two cells and lacking in crystals; or not subdivided and containing a large styloid or occasionally several smaller styloid-like crystals (Fig. 16, 21).

Rays

Rays in Phytolaccaceae are mostly multiseriate; appreciable numbers of uniseriate rays occur only in four species of Rivinoideae (Table 1, column 10). The mean height of uniseriate rays is much less than that of multiseriate rays for any given species (Table 1, column 8), Rivinoideae have shorter mean multiseriate ray height than the Phytolacchoideae, with no overlap in ranges of mean ray heights between the two subfamilies. The phytolaccoids also have multiseriate rays that are appreciably wider than those of the rivinoids (Table 1, column 9). Multiseriate rays of the Rivinoideae are illustrated here by *Gallesia integrifolia* (Fig. 2; some rays associated with axial parenchyma cells and, left, conjunctive tissue cells) and *Seguiera americana* (Fig. 10). Multiseriate rays of Phytolacchoideae

are illustrated by *Anisomeria chilensis* (Fig. 23), *Hillieria latifolia* (Fig. 25), *Phytolacca americana* (Fig. 27), and *P. dioica* (Fig. 29).

With respect to ray histology, procumbent cells are common only in *Gallesia integrifolia* (Fig. 2), *Rivina humilis*, *Seguiera americana* (Fig. 10), and *Anisomeria chilensis* (Table 1, column 11). Even in the species just named, upright cells are about as common as procumbent cells and are not restricted to ray tips and sheaths. Multiseriate rays composed primarily of upright cells with few procumbent cells characterize *Petiveria alliacea*, *Trichostigma octandrum* (Fig. 14), and *Phytolacca americana* (Fig. 27). Multiseriate rays composed wholly of upright cells were observed in *Hillieria latifolia* (Fig. 25), *Trichostigma peruvianum*, *Phytolacca dioica* (Fig. 29), and *P. dodecandra*.

Ray cell walls are all lignified, but relatively thin: 1.0–1.3 μm predominantly. Pits among ray cells are simple or have inconspicuous borders.

Tyloses

Tyloses were observed in *Trichostigma octandrum* (Fig. 14, left). The tyloses have primary walls or secondary walls. Some of the tyloses contain small rhomboidal crystals.

Storied Structure

The axial parenchyma of *Trichostigma octandrum* is indistinctly storied. The storying pattern of the axial parenchyma in this species conforms to similar storying in the narrow vessel elements.

Crystals

In *Gallesia integrifolia*, styloids or similarly shaped smaller rhomboidal crystals are common in conjunctive tissue (Fig. 5) and in secondary xylem (Fig. 6–8). Crystals are very common in the axial secondary xylem in fibriform cells with thin lignified walls in this species (Fig. 6, right; Fig. 7, left). These fibriform cells are nonseptate and could conceivably be considered either a type of axial parenchyma or a type of libriform fiber. The tissue mentioned above as bands or patches of axial parenchyma are rich in styloids; these cells in *Gallesia integrifolia* and *Trichostigma octandrum* are the same length as libriform fibers in length and nonseptate, although thinner walled than libriform fibers, so they are considered crystal-containing libriform fibers here. Styloids are common in *Gallesia integrifolia* in the upright sheathing cells of multiseriate rays (Fig. 7, right; Fig. 8); they are less common in procumbent ray cells. Small rhomboidal crystals like styloids in shape occur in phloem parenchyma of *Gallesia* and the other genera.

In *Seguiera americana*, rhomboidal crystals occur

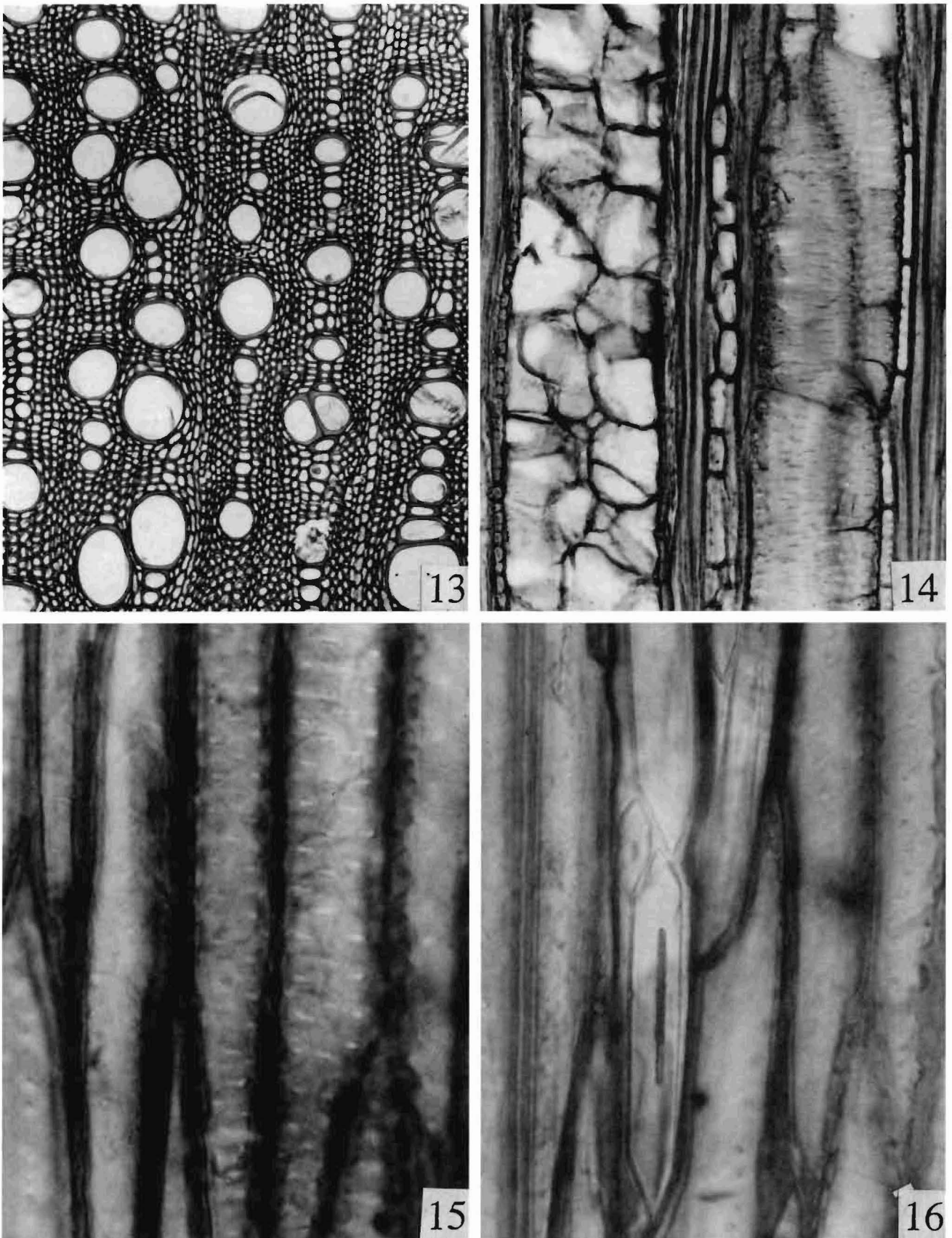


Fig. 13–16. Wood sections of *Trichostigma octandrum*.—13. Transection; vessels are in radial chains, and very few are in contact with rays.—14. Tangential section; tyloses in vessel at left.—15. Tangential section; vasicentric tracheids at right, libriform fibers at left.—16. Tangential section; to left of center, styloid and smaller rhomboidal crystals. (Fig. 13, 14, scale above Fig. 1; Fig. 15, 16, scale above Fig. 11.)

in wider rays (Fig. 11, 12). Some of the rhomboidal crystals are elongate parallel to the stem axis, hence the square crystal transections shown in Fig. 11.

In *Trichostigma octandrum*, styloids are common in fibriform cells. As in *Gallesia*, these fibriform cells are not subdivided. One large styloid plus smaller elongate crystals may occur in a single cell (Fig. 16, right), as in *Gallesia integrifolia*. When tangential sections are viewed with SEM, the large styloids are clearly evident (Fig. 21), although they usually appear broken into segments. A few parenchyma cells in *Trichostigma octandrum* contain very small rhomboidal crystals (Fig. 20). Rhomboidal crystals were also observed in some tyloses. Styloids were observed in fibriform secondary xylem cells of *Hillieria latifolia*.

In *Anisomeria chilensis*, raphides occur idioblastically in the upright and square ray cells (Fig. 24). Raphides also occur in conjunctive tissue of *Phytolacca dioica* and *P. dodecandra*.

Starch

Starch remnants (degraded starch grains) were observed in the libriform fibers of *SeQUIERIA americana* and *Trichostigma peruvianum*. These fibers are therefore living fibers. Starch was observed in ray cells and conjunctive tissue of *Phytolacca dodecandra*.

Successive Cambia

Of the species studied here, successive cambia were observed in *Gallesia integrifolia* (Fig. 1, 5), *SeQUIERIA americana* (Fig. 9), and in all of the species of *Phytolacca* (Fig. 30–33). Within Phytolaccaceae, most attention has been paid to the successive cambia of *Phytolacca* (Wheat 1977; Mikesell 1979). *Phytolacca dioica* offers particularly favorable material because it is a tree that produces an indefinite number of bands of vascular tissue, whereas the other species are mostly annuals that produce one to three bands of vascular tissue.

Three examples of the meristematic region of the stem of *P. dioica* are illustrated here (Fig. 30–32). At left in each is the secondary xylem of the most recent vascular increment. The vascular cambium is to the right of this, and the secondary phloem to the right of the vascular cambium. Fracturing of cell walls occurs easily in the cambial region, but the sections illustrated show reasonably intact cambial regions. To the right of the secondary phloem and to the left of the sclereid band in Fig. 30–32 are radial rows of secondary cortex (secondary parenchyma). These rows are derived from parenchyma of the inner cortex. The sclereid band demarcates the inner cortex (converted into secondary parenchyma by periclinal divisions in cells of the cortex at an earlier stage) from the parenchyma of the

outer cortex (far right in Fig. 30–32), which does not subdivide into radial rows.

Radial rows of secondary cortical parenchyma cells were illustrated for *Petiveria* and *Rivina* (Carlquist 1998b). The periclinal divisions in the rows are roughly synchronized in time and in number. In these two genera, the first cambium of the stem, and the second, derived from divisions of cortex, have occurred. Because only one or two bands of vascular tissue have been observed in these two genera, divisions within the radial rows of secondary cortex leading to formation of a third or fourth vascular cambium have not been reported. In *Phytolacca dioica* and the other genera with numerous bands of vascular tissue in stems (and roots), new vascular cambia develop by an abrupt cylinder of periclinal divisions in the secondary cortex. These new vascular cambia do not develop adjacent to the secondary parenchyma of the preceding vascular band. Instead, several layers of parenchyma cells intervene between secondary phloem and the site of origin of a new vascular cambium. These layers of parenchyma are therefore internal to the secondary xylem that will be produced by the new vascular cambium, and will mature into conjunctive tissue. The conjunctive tissue is a derivative of secondary cortex, not the vascular cambia, and therefore the conjunctive tissue should not be included in the concept of secondary xylem.

Vascular cambia in *Phytolacca dioica* appear abruptly at intervals, whereas periclinal divisions producing secondary cortex occur continuously during the growing season. This ontogenetic pattern is much the same as the pattern evident in *Stegnosperma* (Carlquist 1999c). The three views (Fig. 30–32) of the meristematic region of the stem of *P. dioica* are presented to show the nature of periclinal divisions (narrow arrows) in secondary cortex in different portions of a stem. The vascular cambium is illustrated with wide arrows. The numerous periclinal divisions in the secondary cortex of Fig. 31 may indicate early stages in origin of a vascular cambium. Divisions are less abundant in the secondary cortex of Fig. 32, moderately abundant in the secondary cortex of Fig. 30.

Pith Bundles and Secondary Growth in Them

In the pith of *P. dioica*, vascular bundles characteristically form. These bundles are amphivasal in construction (Fig. 33). Secondary growth occurs in the pith bundles. In accordance with the amphivasal organization of the pith bundles, the cambium of the pith bundles produces secondary xylem externally and secondary phloem internally. As secondary growth proceeds, early-formed phloem is crushed (dark gray circle, Fig. 33, center).

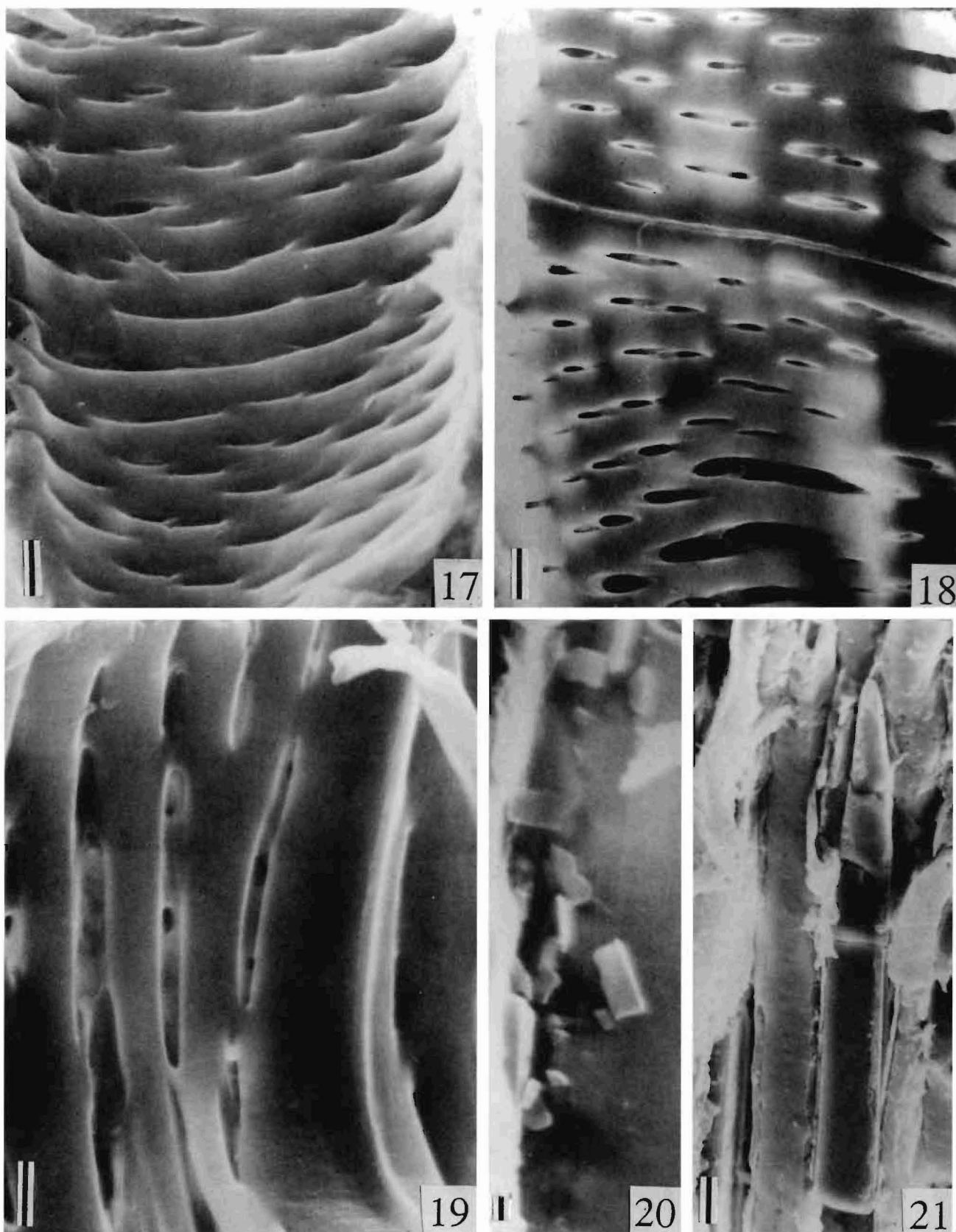
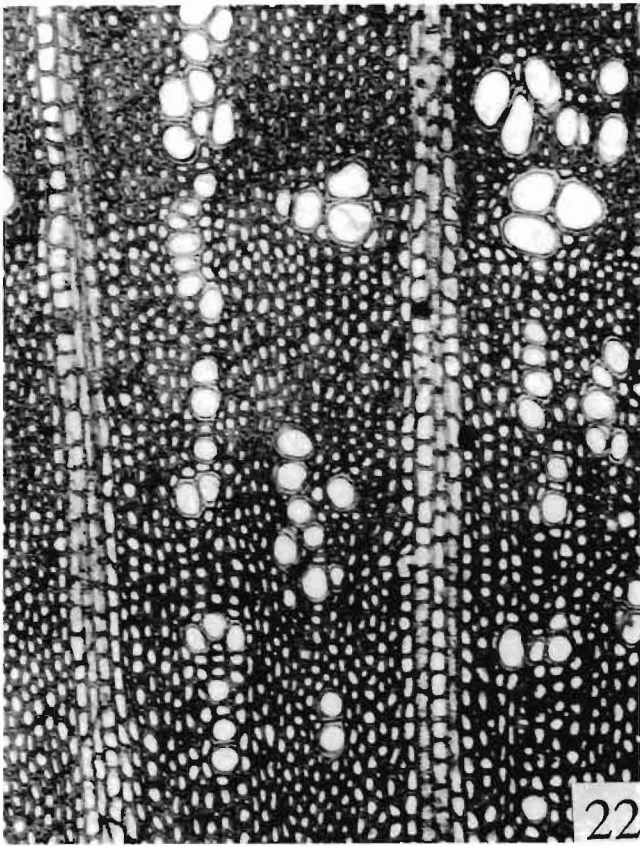
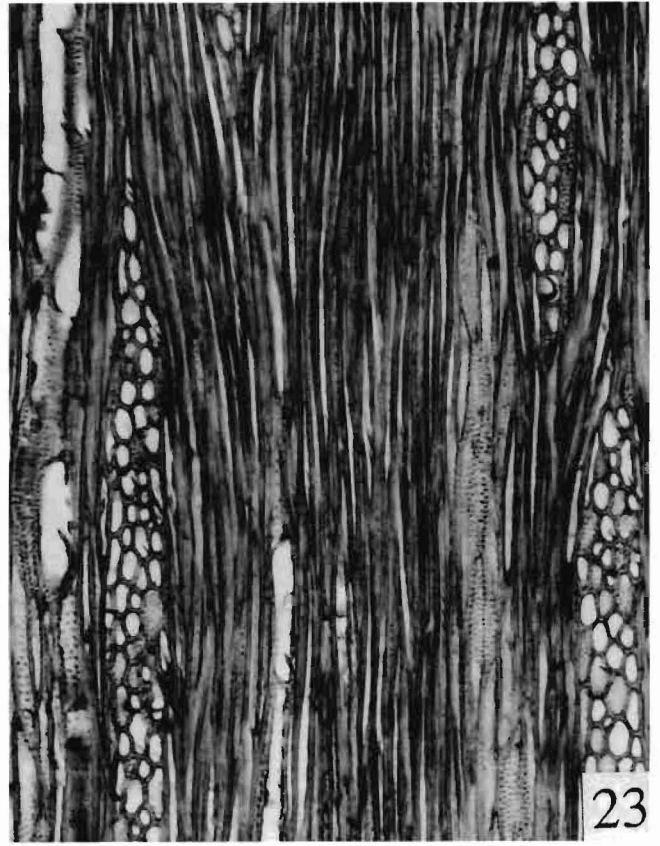


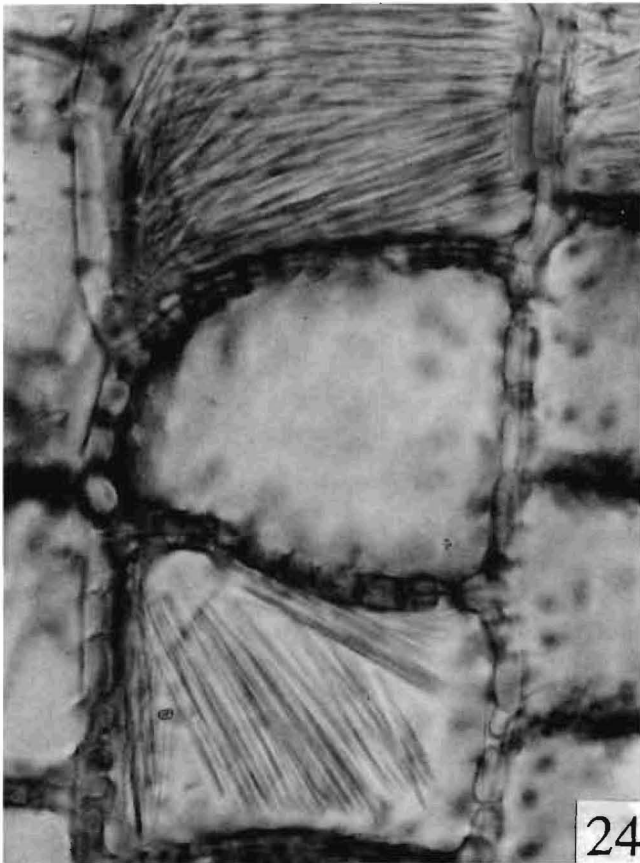
Fig. 17-21. SEM photographs of a tangential section of *Trichostigma octandrum* wood.—17-19. Inner surfaces of vessels.—17. Grooves interconnect many pit apertures.—18. Pit apertures mostly not interconnected or interconnected in pairs by grooves; slender perforation plate above center is nonbordered or nearly so.—19. Grooves interconnecting pit apertures (left, center) and a perforation plate that is vestigially bordered below and nonbordered near top of photograph.—20. Numerous small rhomboidal crystals within an axial parenchyma cell.—21. Portion of large styloid, to right of center, broken into pieces by the sectioning process. (Scales in each = 5 μm .)



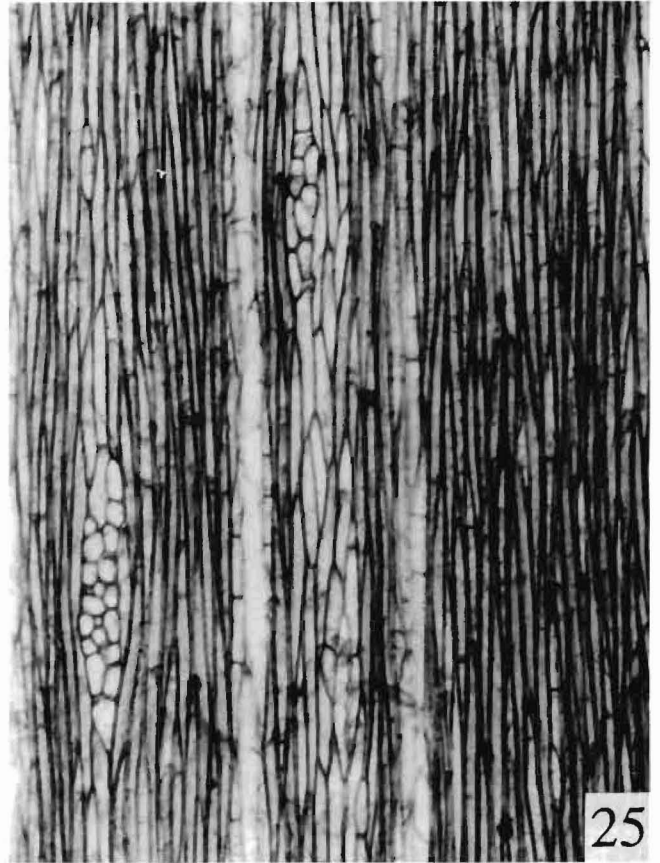
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Fig. 22–25. Wood sections of *Anisomeria chilensis* (Fig. 22–24) and *Hillieria latifolia* (Fig. 25).—22. Transection; vessels in clusters and radial multiples, rarely in contact with rays.—23. Tangential section; rays are mostly multiseriate.—24. Radial section, horizontal ray axis oriented vertically; raphides in cells at top center and bottom center of photograph.—25. Tangential section; upright ray cells (center) are long and therefore difficult to distinguish from libriform fibers. (Fig. 22, 23, 24, scale above Fig. 1; Fig. 24, scale above Fig. 11.)

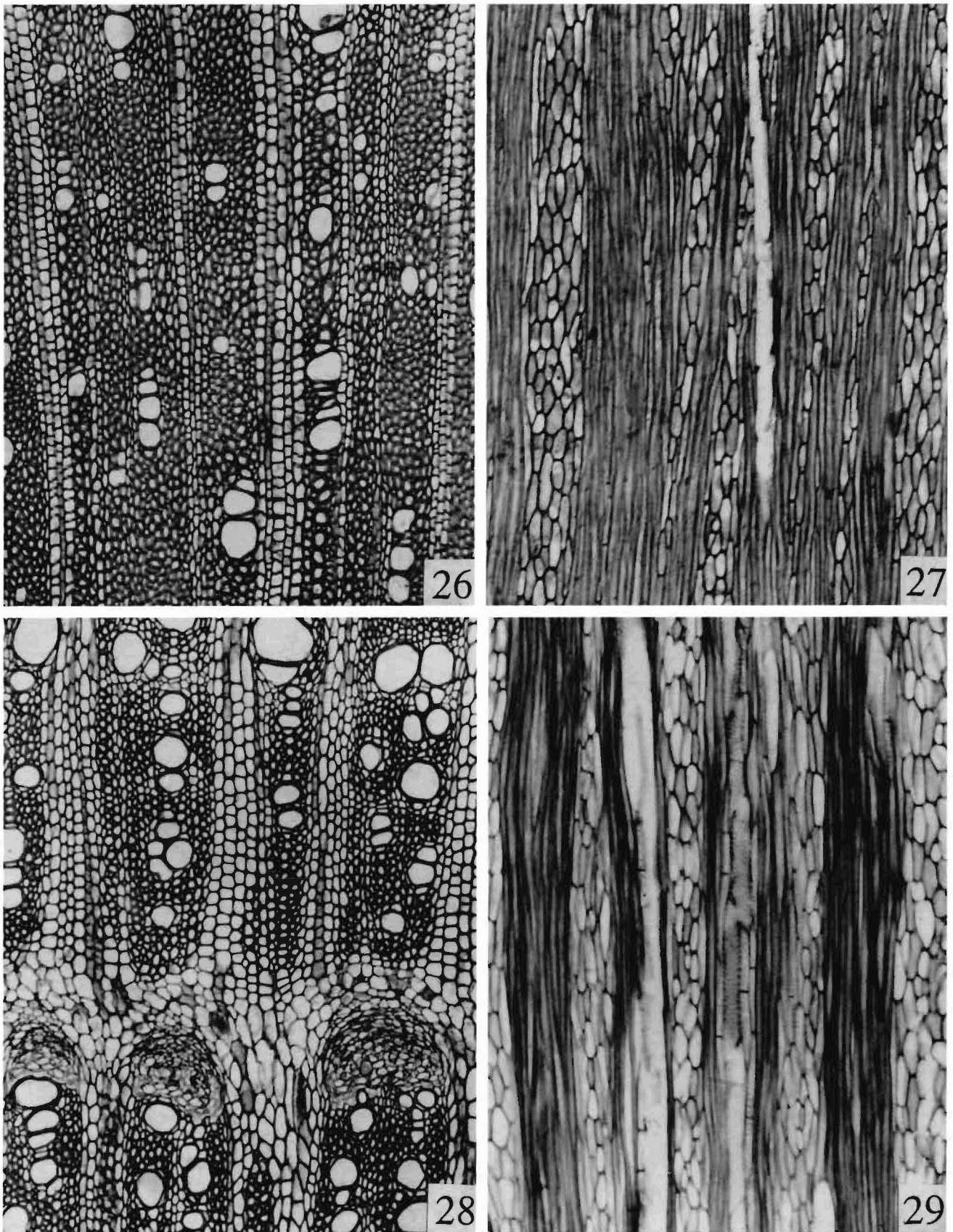


Fig. 26–29. Wood sections of *Phytolacca*.—26–27. *P. americana*.—26. Transection. Vessels in radial multiples, contact between vessels and rays frequent.—27. Tangential section; rays multiseriate, composed of upright cells.—28–29. *P. dioica*.—28. Transection; portions of two vascular bands, with conjunctive tissue (left to right, below center) separating them.—29. Tangential section; multiseriate rays very tall, composed mostly of upright cells. (Fig. 26–29, scale above Fig. 1).

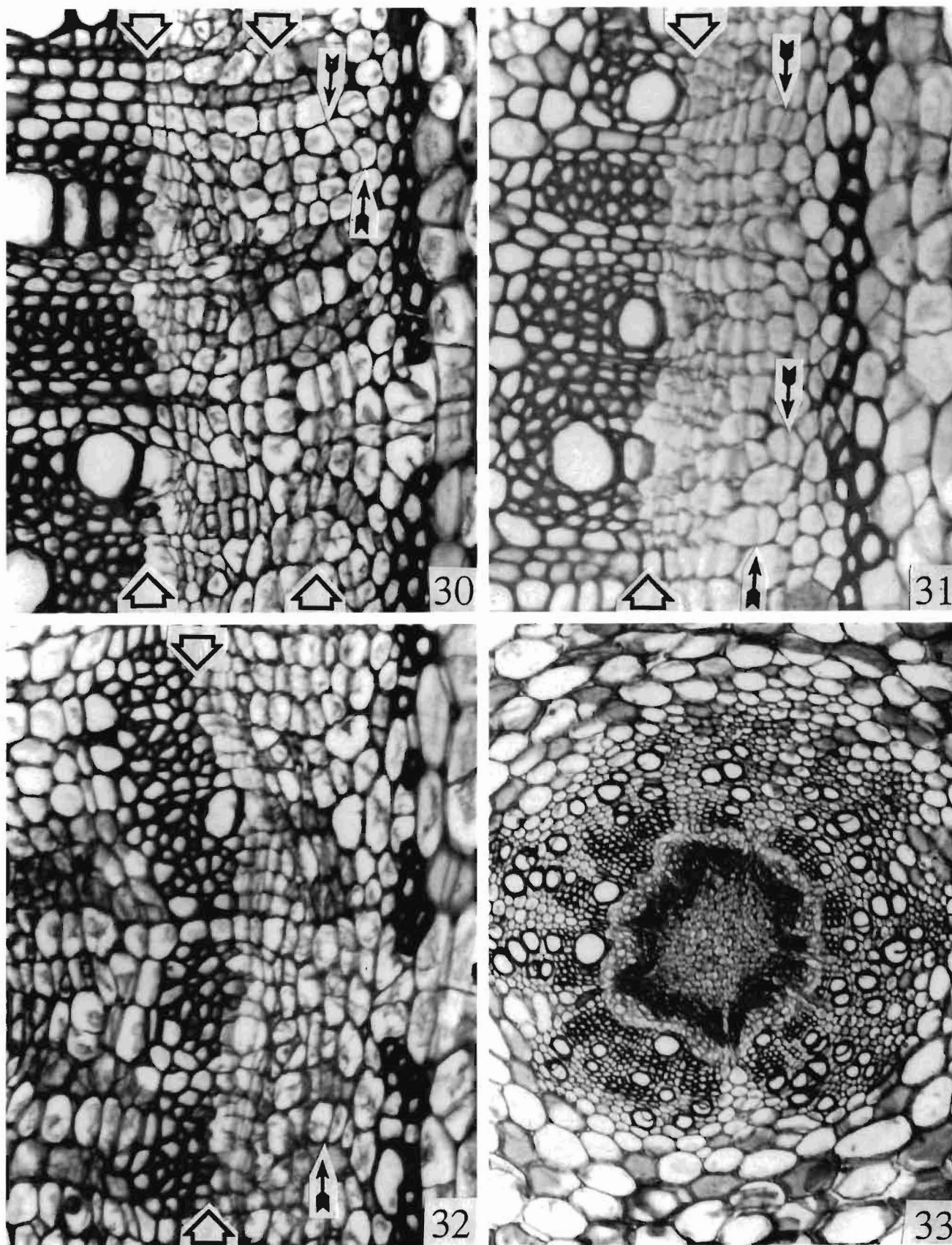


Fig. 30–33. *Phytolacca dioica* stem.—30–32. Transsections of the meristematic region of the outer stem, outer stem at right; the pairs of wide arrows indicate vascular cambia, narrow arrows denote periclinal divisions in secondary cortex.—30. Vascular cambium that has produced secondary xylem and secondary phloem (wide arrows at left) and probable origin of a new vascular cambium (wide arrows at

CONCLUSIONS

Ecological Conclusions

Table 1, column 12 gives values for a ratio termed Mesomorphy (for definition of this ratio, see Table 1). This ratio is not an index of conductive efficiency, but takes into account both conductive safety and conductive efficiency: narrower vessels have been shown to embolize less readily (Carlquist 1975, Hargrave et al. 1994). The lowest figures for the Mesomorphy Ratio in Phytolaccaceae are in *Petiveria alliacea* and *Rivina humilis*. These species are short-lived rather weedy woody herbs; as such, their roots are in relatively shallow soil likely to dry readily, so that a xeromorphic wood formulation would be of selective value. The remainder of the species of Phytolaccaceae have relatively moderate Mesomorphy values, but not as high as those in tropical rain forest trees, in which the Mesomorphy value often lies in the range of 2000–5000. The woods of Phytolaccaceae are typical in vessel features of species from seasonally dry tropical areas. The Mesomorphy values for *Phytolacca* are deceptively low because conjunctive tissue, often rather succulent in this genus, has not been included in computations of vessel density (number of vessels per mm²). The Mesomorphy Ratio for the wood of *Anisomeria chilensis* indicates a wood more xeromorphic than that of *Phytolacca*. The higher number of vessels per group in *Anisomeria*, an indication of xeromorphy (Carlquist 1975, 1984), is also higher.

Among the genera of Rivinoideae, there are several structural features suggesting xeromorphy other than those that involve vessel dimensions. In *Trichostigma octandrum*, the number of vessels per group is elevated, and more numerous vessels per group is likely a mechanism that safeguards conductive pathways despite embolisms in some of these vessels (Carlquist 1984). Appreciable numbers of vascentric tracheids are present in *Seguieria americana*; *Trichostigma octandrum* has some very narrow vessels and a few vascentric tracheids. Narrow vessels have much the same effect as vascentric tracheids where conductive safety is concerned (Carlquist 1985).

Systematic Conclusions

All of the genera in the present study have libriform fibers and vascentric parenchyma (*Gallesia integrifolia* and *Trichostigma octandrum* have bands or patches of apotracheal parenchyma, in addition). In

these respects, the phytolaccoids and rivinoids are close, and support the suggestion by Brown and Varadarajan (1985) that they constitute the two subfamilies, Phytolaccoideae and Rivinoideae, of Phytolaccaceae. In contrast, tracheids plus diffuse axial parenchyma characterize *Stegnosperma* (Carlquist 1999c) and *Barbeuia* (Carlquist 1999d); *Agdestis* (Carlquist 1999b) has vascentric tracheids plus libriform fibers and vascentric parenchyma only. Brown and Varadarajan (1985) group these three genera closely; the anatomical data tend to support that these three genera, whether recognized as monogeneric families or not, perhaps as basal elements within the suborder Phytolaccineae, and perhaps a near-basal position in Caryophyllales as a whole, as suggested by Brown and Varadarajan (1985). This arrangement is shared to various extents by the analyses of Downie and Palmer (1994), Manhart and Rettig (1994), and Rodman (1994), although the disparity among the results of these studies is more impressive than the similarities. Very likely, a sampling of more genera and analyses of more DNA sites will clarify the classification. Thus far, all of the genera of Phytolaccaceae s.l., have been shown to possess nonbordered perforation plates, an unusual feature in dicotyledons as a whole. This feature may prove to be common to all Phytolaccineae, although studies of Aizoaceae and Nyctaginaceae, currently in progress, are needed. Because of their rarity in dicotyledons, nonbordered perforation plates have likely been overlooked by some workers.

Traditionally, *Anisomeria* has been placed close to *Phytolacca* (e.g., Heimerl 1934). Evidence for this treatment is to be found in anatomy: the occurrence of idioblasts containing raphides in ray cells and conjunctive tissues of both *Anisomeria* and *Phytolacca* supports placement of the two genera close to each other.

Rivinoideae differ from Phytolaccoideae on the basis of crystal types. All of the genera of Rivinoideae studied have elongate crystals, ranging from large (styloids) to small rhomboids. Raphides characterize stems of Phytolaccoideae. Species of Rivinoideae differ in size, abundance, and distribution of the elongate crystals (see *Crystals* above), and this suggests that generic and specific criteria may well be evident when all of the species of Rivinoideae are studied.

One question concerning phylogeny of Caryophyllales that has not been addressed frequently is the likely phylogeny of woodiness within the order. Within

←
right.—31. Vascular cambium that has produced a relatively small amount of secondary xylem and secondary phloem; some of the periclinal divisions in the secondary cortex indicated.—32. Vascular cambium that has produced only a little secondary xylem and phloem; only a few periclinal divisions are evident in the secondary cortex.—33. Transection of a pith bundle from a stem about two years old, to show secondary growth in an amphivasal pith bundle; protoxylem at periphery. (Fig. 30–32, scale above Fig. 3; Fig. 33, scale above Fig. 1.)

the Phytolaccaceae studied here, upright cells compose at least half of the cells in multiseriate rays (and nearly all of cells in the uniseriate rays; upright ray cells predominate in *Phytolacca*). The rays of the family thus qualify as pedomorphic (Carlquist 1988) and thus may indicate an herbaceous ancestry either for the entire subfamily Phytolacchoideae.

Successive Cambial Activity

An analysis of all aspects relative to origin and action of successive cambia will be attempted when the current series of papers on Caryophyllales is completed. However, my observations at present indicate that radial rows of secondary cortex, formed in the inner cortex, result from periclinal divisions that may be designated a lateral meristem. In Phytolaccaceae s.s., new vascular cambia originate in the secondary cortex, several cell layers away from the phloem of the preceding vascular band. Those several cell layers mature into conjunctive tissue. Periclinal divisions may increase the radial width of the conjunctive tissue to a minor extent. Each vascular cambium produces secondary phloem to the outside and secondary xylem to the inside, like the vascular cambium of a dicotyledon with only a single cambium.

The above description is very much like those offered for *Stegnosperma* (Carlquist 1999c) and *Simmondsia* (Bailey 1980). For the present, an attempt has been made to use a simple descriptive terminology with which to record observations. A number of different terms for the phenomena related to successive cambial activity have been offered by authors who have dealt with successive cambia. Comparisons of the terminology and of the interpretive schemes of these authors must await a more thorough review, in which successive cambia in diverse dicotyledons and in Gnetales can be considered.

Whether occurrence of successive cambia is a plesiomorphic or an apomorphic feature in Caryophyllales is an interesting question that is better addressed when more extensive data are available. For the present, one can say that the families placed basally in cladograms of Phytolaccaceae s.l., including those based on molecular data (e.g., Manhart and Rettig 1994), Caryophyllaceae and Stegnospermataceae, have successive cambia (in at least some genera in the case of Caryophyllaceae). One can find tracheids in at least some genera in these two families (Carlquist 1995, 1999c); tracheids are considered a primitive type of tracheary element according to traditional criteria (e.g., Metcalfe and Chalk 1950, p. xlv). Families thought to be outgroups of Caryophyllales also possess successive cambia in a few genera: Polygonaceae (e.g., *Rumex*; Pfeiffer 1926) and Plumbaginaceae (e.g., *Aegilites*; Pfeiffer 1926; Carlquist and Boggs 1996); these

families, as well as Simmondsiaceae, can be included within a more inclusive Caryophyllales (Williams et al. 1994). The presence of successive cambia in so many families and genera of Caryophyllales, despite the absence of the phenomenon in others (e.g., Cactaceae and Didieriaceae lack successive cambia), leads to another possibility. The basal groups, as well as derived clades and the outgroups of Caryophyllales might have the genetic basis for formation of successive cambia, but one or more genes that delay or suppress formation of successive cambia may have been developed within several clades of Caryophyllales.

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