Wood and Stem Anatomy of Phytolaccoid and Rivinoid Phytolaccaceae (Caryophyllales): Ecology, Systematics, Nature of Successive Cambia

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WOOD AND STEM ANATOMY OF PHYTOLACC OID 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 Phytolacoideae. All species have nonbordered perforations plates, as elsewhere in suborder Phylocaccineae. 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 multisierate, 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, Centrosperrnae, 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 (*Hilleria*) (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 Phytolacoideae of various authors. Phytolacoideae 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 removed *Sarcobatus* from Chenopodiaceae as Sarcobataceae and placed it close to Phytolaccaceae (= within suborder Phytolaccinae). 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 Phytolaccaceae, 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, Phytolaccinae, 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). Bata­
tea, Schindleria, Trichostigma, Rivina, Seguieria, spp.,

**DISCUSSION AND CONCLUSIONS.**

Information from wood anatomy is potentially use­
fur 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
Phytolaccaceae or even the families of Caryophyll­
lales. The present paper constitutes one in a series of
studies presenting new information about wood anat­
omy of Caryophyllales. Earlier papers in the series in­
clude studies of Caryophyllaceae (Carlquist 1995),
Portulacaceae and Hectorellaceae (Carlquist 1998a),
Petiveria and Rivina (Carlquist 1998b), Basellaceae
(Carlquist 1999a), Agdestis (Carlquist 1999b), Steg­
nosperma (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
anatomy of Caryophyllales is useful, but as he indi­
cates, 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: Plumbagina­
ceae and Polygonaceae. Wood of the former was sur­
veyed recently (Carlquist and Boggs 1996), and a
study of wood anatomy of Polygonaceae is in pro­
gress. A detailed comparison of the component fami­
lies of Caryophyllales, including tabular comparisons,
will conclude this series of papers, and that paper will
be based on newly expanded definitions of Caryophyl­
lales (e.g., Williams et al. 1994).

Wood anatomy of Phytolaccaceae is especially in­
teresting with respect to ecology and habit. Some gen­
era are lianas (Gallesia, Seguieria), whereas others are
shrubs (Anisomeria), trees (Phytolacca dioica, Trich­
ostigma 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 DIS­
CUSSION AND CONCLUSIONS.

The following phytolaccoid genera have been re­
ported to have successive cambia: Agdestis, Anisomer­
ia, Barbeuia, Ercilla, Gallesia, Petiveria, Phytolacca,
Rivina, Seguieria, and Stegnosperma (Pfeiffer 1926;
Heimerl 1934). Successive cambia have not been re­
ported in Hilleria, Ledenbergia, Lophiocarpus, Micro­
tea, Schindleria, Trichostigma, or in the family now
commonly removed from Phytolaccaceae, Achatocar­
p paceae (Pfeiffer 1926; Heimerl 1934). The phyloge­
etic question posed by this distribution is whether
presence of successive cambia is a plesiomorphy or an
apomorphy in phytolaccoids. In a few cases, the ap­
pearance 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 succes­
sive 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 succes­
sive cambia in Phytolaccaceae s.l. is now known with
reasonable accuracy. The three families now included
along with phytolaccoids in Phytolaccaceae (Aizo­
ageae, 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 is­
sue. However, the anatomical nature of successive
 cambia needs clarification, and each pertinent genus
that is studied in detail yields information on this ques­
tion. 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 pa­
pers on this meristematic activity in Phytolacca
(Wheat 1997; Mikesell 1979) are not entirely in agree­
ment, and the disagreements in terminology and inter­
pretation widen if we include studies on lateral meri­
stem origins and action in Nyctaginaceae (Studholme
and Philipson 1966, Esau and Cheadle 1969, Steven­
son and Popham 1973). I have attempted to clarify the
nature of lateral meristem activity in several genera of
Phytolaccaceae s.l.: Agdestis (Carlquist 1999b), Bar­
beuia (Carlquist 1999d), Petiveria (Carlquist 1998b),
and Stegnosperma (Carlquist 1999c). In a single phy­
logenetic unit such as Caryophyllales, the mechanism
of lateral meristem origin and action leading to pro­
duction 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,
than 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; Hilleria latifolia (Lam.) H. Walt., Bundibugyo, Uganda, MADw-43651; Petiveria alliacea L., cultivated at the Heidelberg Botanical Garden (231787); 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, Rillaub R56207 (RSA); Rivina humilis L., adventive on the University of Hawaii campus, Honolulu, Hawaii, Carlquist 8162 (SBG); Seguieria 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 Rivinioideae. Vessel diameter in Table 1 is presented as lumen diameter. No vessel density or vessel grouping data could be presented for Seguieria americana because narrow vessels cannot be differentiated from vasicentric tracheids as seen in transsection. 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 transsectional area of conjunctive tissue can range from relatively little to about 50% of stem transsectional 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 obseerved in Gallesia integrifolia (Fig. 1, 3) and in Seguieria 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 Seguieria, 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 Stegnosperma (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 Hilleria 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
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 66 \( \mu \text{m} \) for *Phytolacca dodecandra* and the figure for the remainder of the species studied is below 50 \( \mu \text{m} \). This figure can be appreciated when one reads that the mean vessel diameter (outside diameter) for dicotyledons as a whole (649 \( \mu \text{m} \)) ranges widely. Wider vessels tend to be thicker walled, most conspicuously in *Gallalesia integrifolia* and *Trichostigma octandrum* (Fig. 3). Diameter of lateral wall pits ranges between 5 \( \mu \text{m} \) and 10 \( \mu \text{m} \) 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 \( \mu \text{m} \). 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 *Gallesia 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 μm]; Fig. 3, 4, scale above Fig. 3 [divisions = 10 μm].)
Fig. 5–8. Wood sections of *Gallesia 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 S. 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 \(\mu m\)].)
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 Seguieria 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 (Hilleria latifolia, Seguieria 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 vasicentric axial parenchyma was recorded for all but two of the species studied, but in Seguieria americana, axial parenchyma is very scarce. In Gallesia integrifolia and Trichostigma octandrum, scanty vasicentric axial parenchyma is present, but there is also apotracheal parenchyma in the form of patches and radially wide but tangentially short bands. In Seguieria 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 Phytolaccoideae, 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 Seguieria americana (Fig. 10). Multiseriate rays of Phytolaccoideae are illustrated by Anisomeria chilensis (Fig. 23), Hilleria 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, Seguieria 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 Hilleria 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 storied pattern of the axial parenchyma in this species conforms to similar storing 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 Seguieria americana, rhomboidal crystals occur
Fig. 13–16. Wood sections of *Trichostigma octandrum*—13. Transsection; 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 fibroform cells. As in *Gallesia*, these fibroform 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 fibroform secondary xylem cells of *Hilleria 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 *Seguieria 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), *Seguieria 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 1999b). 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 styleid, to right of center, broken into pieces by the sectioning process. (Scales in each = 5 μm.)
Fig. 22–25. Wood sections of *Anisomeria chilensis* (Fig. 22–24) and *Hiliera latifolia* (Fig. 25).—22. Transection; vessels in clusters and radial multiples, rarely in contact with rays.—23. Tangential section; rays are mostly multiserate.—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. Transections 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 vasicentric tracheids are present in Seguiera americana; Trichostigma octandrum has some very narrow vessels and a few vasicentric tracheids. Narrow vessels have much the same effect as vasicentric tracheids where conductive safety is concerned (Carlquist 1985).

Systematic Conclusions

All of the genera in the present study have libriform fibers and vasicentric 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, Phytolaccodoideae and Rivinoidae, of Phytolaccaceae. In contrast, tracheids plus diffuse axial parenchyma characterize Stegnosperma (Carlquist 1999c) and Barbevia (Carlquist 1999d); Agdestis Carlquist 1999b) has vasicentric tracheids plus libriform fibers and vasicentric parenchyma only. Brown and Varadarajan (1985) group these three genera closely; the anatomical data tend to support that these three genera, whether recognized as monogenic 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.

Rivinoidae differ from Phytolaccoideae on the basis of crystal types. All of the genera of Rivinoidae studied have elongate crystals, ranging from large (scleroids) to small rhomboids. Raphides characterize stems of Phytolaccoideae. Species of Rivinoidae 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 Rivinoidae are studied.

One question concerning phylogeny of Caryophyllales that has not been addressed frequently is the likely phylogeny of woodiness within the order. Within...
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 Phytolaccaceae). The rays of the family thus qualify as paedomorphic (Carlquist 1988) and thus may indicate an herbaceous ancestry either for the entire subfamily Phytolaccaceae.

**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 pleisiomorphic 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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