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WOOD AND STEM ANATOMY OF STEGNOSPERMA (CARYOPHYLLALES); PHYLOGENETIC RELATIONSHIPS; NATURE OF LATERAL MERISTEMS AND SUCCESSIVE CAMBIAL ACTIVITY

by

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SUMMARY

Wood and bark histology data on stems of two species of *Stegnosperma* (Stegnospermataceae, or Phytolaccaceae s.l.) is presented, complementing previous accounts. Wood of *Stegnosperma* is relatively primitive within Caryophyllales because of presence of tracheids, diffuse parenchyma, and both multiseriate and uniseriate rays. The solitary nature of vessels is held to be correlated with tracheid presence, as in other groups of dicotyledons with vessels solitary or nearly so. Bark anatomy is newly reported for the genus. The method of section used permits analysis of divisions in cells with primary walls. Radial rows of parenchyma ('secondary cortex') develop in the inner cortex and are perpetuated by tangential divisions collectively termed a diffuse lateral meristem here. Successive cambia form within the radial rows of parenchyma. Despite diverse terminology and interpretations in literature on plants with successive cambia, the successive cambia and their origin in *Stegnosperma* are believed to represent the same anatomical phenomena as in other Phytolaccaceae s.l.

Key words: Bark anatomy, cambial variants, Caryophyllales, ecological wood anatomy, Phytolaccaceae, Stegnospermataceae, successive cambia, tracheids, vessel elements.

INTRODUCTION

Stegnosperma Benth., placed in Phytolaccaceae by most earlier workers, has in recent years been treated as the basis of a monogeneric family, Stegnospermataceae, with three species (Bedell 1980). Other families formerly included in Phytolaccaceae but now often recognized as segregates include Achatocarpaceae, Agdestidaceae, Barbeuiaceae, and Rivinaceae (= Petiveriaceae) (Brown & Varadarajan 1985; Takhtajan 1987; Cronquist & Thorne 1994). Behnke (1997), who has removed *Sarcobatus* from Chenopodiaceae as Sarcobataceae, believes that *Sarcobatus* may be closer to Phytolaccaceae than to other families of Caryophyllales. The cladistic studies of Rodman (1994) show *Stegnosperma* to be basal to the remainder of the Caryophyllales (least homoplastic tree). Molecular studies diverge: they place *Stegnosperma*

as basal to suborder Portulacineae (Rettig et al. 1992); or basal to suborders Phytolaccineae and Portulacineae, and thus basal to most families of Caryophyllales (Manhart & Rettig 1994), on a clade that includes Caryophyllaceae and Molluginaceae (Downie & Palmer 1994). These various placements are mentioned because they have implications for the phylogenetic status of successive cambia and tracheids in *Stegnosperma*.

Bedell (1980) offered data on wood anatomy of two species of *Stegnosperma*, based on material of *S. cubense* and *S. halimifolium* similar to that studied here. Horak (1981a) presented comparative wood data on the three species of *Stegnosperma*, together with a discussion of successive cambia ('anomalous secondary thickening' of some authors) in Caryophyllales. Horak (1981b) has also provided a perspective on origin of successive cambia in time and space in *Stegnosperma*. The present paper supplements these papers and offers new data.

The nature of successive cambia in Caryophyllales has been subject to varied interpretations and terminology (Studholme & Philipson 1966; Esau & Cheadle 1969; Stevenson & Popham 1973; Wheat 1977; Mikesell 1979; Bailey 1980; Baird & Blackwell 1980; Carlquist 1998b, 1999, in press). All of these references include genera of Caryophyllales; most of the studies deal with Phytolaccaceae or Nyctaginaceae, which are placed close to each other in suborder Phytolaccineae. Although the present study does not offer the basis for discovering and describing the probable unity (but with significant variations) in the mechanisms for successive cambial activity and origin, the present paper is one of a series of studies that will hopefully lead to a review of these topics. Successive cambia are widespread in vascular plants (Pfeiffer 1926; Horak 1981a). Successive cambia in such diverse families as Gnetaceae (Carlquist & Robinson 1995; Carlquist 1996a, 1996b), Convolvulaceae (Carlquist & Hanson 1991), Menispermaceae (Carlquist 1996c), and Simmondsiaceae (Bailey 1980), to mention a few, provide cell sequences that appear similar to those of Caryophyllales and should be included in a synthesis of the phenomenon of successive cambium formation and origin.

As the book edited by Behnke and Mabry (1994) and the literature cited above indicates, there has been intense interest in recent years in the familial composition of Caryophyllales and phylogeny of the order. A group that has been studied so actively provides a framework for incorporation of new data, such as offered here, in such a way that phyletic information is enhanced. We do not yet know whether successive cambium presence is a plesiomorphy or an apomorphy in cladistics of Caryophyllales. In addition, data from wood and stem anatomy offer potential lines of evidence as to whether *Stegnosperma* should be included within Phytolaccaceae or not, and if not, how close to Phytolaccaceae s.s. it lies.

Although many studies have been undertaken on Caryophyllales, we have few detailed studies on wood anatomy of the order (Gibson 1994) except for Cactaceae (e.g., Gibson 1973) and Didiereaceae (Rauh & Dittmar 1970). Lack of wood and bark studies very probably are related to the non-arboreal habits of Caryophyllales: wood anatomy is best known for arboreal species of dicotyledons. To improve the level of

information on wood anatomy of Caryophyllales, I am engaged on a series of papers on the order, mostly on families and genera for which few data on wood and bark are available. Families covered in this new series include Caryophyllaceae (Carlquist 1995); Portulacaceae and Hectorellaceae (Carlquist 1998a); Basellaceae (Carlquist 1999), Agdestis (Carlquist in press); and Petiveria and Rivina (Carlquist 1998b), genera placed either in Phytolaccaceae or Rivinaceae (= Petiveriaceae). The data of Bedell (1980) and Horak (1981b) on wood of *Stegnosperma* are taken into account in the present paper and not repeated. However, additional data and interpretations on wood are included here. The thin sections of liquid-preserved stems of S. halimifolium studied here provide unusually clear examples of the nature and origin of successive cambia, and so these topics are described in detail.

MATERIALS AND METHODS

Bedell (1980) recognizes three species of *Stegnosperma*: *S. cubense* A. Rich. (Cuba, Dominican Republic, Jamaica, Pacific coast of central Mexico); *S. halimifolium* Benth. (coastal Baja California, Mexico); and *S. watsonii* D. J. Rogers (coastal Sonora and northern Sinaloa, Mexico). The specimen of *S. cubense* studied here is the same as that studied by Bedell (Iltis 670, SJR-MADw 369). The specimen of *S. halimifolium* studied here was collected in the field (flats of open scrub, 10 km N of La Paz, Mexico, Carlquist s.n., 1969) and preserved in 50% aqueous ethanol.

Vascular plants with successive cambia have alternating bands of hard (secondary xylem) and soft (conjunctive tissue; secondary phloem) tissue, a condition that provides great difficulty when one attempts to section with a sliding microtome. Therefore, an alternative method (Carlquist 1982) was employed. This method yielded thin sections, free of tearing, in which divisions within successive cambia and in tissues leading to initiation of successive cambia could be analyzed more accurately. Horak (1981a) used a sliding microtome for most of his work; Bedell (1980) used 'standard techniques'. In my experience, acceptable sliding microtome sections of species with successive cambia must be cut at relatively great thicknesses (to minimize tearing and cell collapse) so that analysis of divisions within meristematic areas is not readily undertaken.

Terms are in accordance with the IAWA Committee on Nomenclature (1964). Notable in this regard is the term 'tracheid' (= 'fiber-tracheid' as used by Bedell 1980 and Horak 1981a). The term 'successive cambia' is used for series of vascular cambia that lead to concentric vascular rings, following the usage of Pfeiffer (1926) and Carlquist (1996a, 1996b, 1996c). The term 'anomalous secondary thickening' covers a wide range of cambial phenomena, and is misleading ('anomalous' means 'without order').

RESULTS

The findings reported below are supplementary to those of Bedell (1980) and Horak (1981a) and are either new reports or new interpretations.

Secondary xylem

Vessel elements are circular in outline in *S. halimifolium* (Fig. 1, 8), but oval in outline (radially widened) in *S. cubense* (Fig. 7). Pits on lateral walls of vessels have grooves that interconnect two or three pit apertures ('coalesced pit apertures') (Fig. 6). These grooves are especially well shown in longisections of vessels in which portions of the wall are shaved away. Only nonbordered perforation plates were observed; the fused edges of adjacent perforation plates form points as seen in longisections of vessels (Fig. 5, 6). Bedell (1980) claimed frequent bordered perforation plates.

Imperforate tracheary elements are densely covered with alternate circular bordered pits. The pit cavities of these pits vary in axial diameter, as do those of vessels, but in both cell types, axial pit diameter of about 4 μm is common in both species (compare Fig. 3 and 4). The similar size of pits in both cell types is one reason to use the term tracheid for the imperforate tracheary elements. The tracheids of *Stegnosperma* are indistinguishable in morphology from the vasicentric tracheids of *Quercus* and other angiosperms with vasicentric tracheids (Carlquist 1985), providing another reason to term the imperforate tracheary elements tracheids.

Vessels in both species of *Stegnosperma* qualify as solitary. The incidence of two or three vessels in contact is very small, and is attributable to diameter and density characteristic of the species of *Stegnosperma*. Thus, the vessel grouping is probably statistically as minimal as could be expected.

Axial parenchyma is primarily diffuse in both species. Diffuse axial parenchyma is common in *S. halimifolium* (Fig. 8), although as reported by Horak (1981a), axial parenchyma in radial chains may be found (Fig. 8); paratracheal axial parenchyma in this species is so scanty as to be explained merely as diffuse parenchyma cells in contact with vessels by virtue of random parenchyma distribution. In *S. cubense*, axial parenchyma is commonly diffuse (Fig. 7, upper arrow), but also paratracheal (Fig. 7). One can also find short tangential bands of axial parenchyma in *S. cubense* (Fig. 7, parenchyma between the wide arrows). In both species, axial parenchyma is formed in strands of two cells (the division between the two cells of a strand indicated by an arrow in Fig. 2). Bedell (1980) reports that axial parenchyma is absent in *Stegnosperma*.

Rays are claimed to be multiseriate only in *Stegnosperma* by Horak (1981a), but Bedell (1980) cites uniseriate as well as multiseriate rays for both species, and gives quantitative data for both ray types in both species. Both multiseriate and uniseriate rays may be seen in the tangential section of secondary xylem of *S. halimifolium* in Figure 2. Some multiseriate rays are relatively wide (four to five cells). Two such rays run vertically through both vascular bands of Figure 1; they consist wholly of parenchyma and are produced by each successive cambium. In the 'fascicular' zones (i.e., those vascular band portions bearing secondary phloem, Fig. 1), rays are narrower. Starch presence in rays of *Stegnosperma* has not been mentioned hitherto, but starch is abundant in ray cells of liquid-preserved material (Fig. 3, right).

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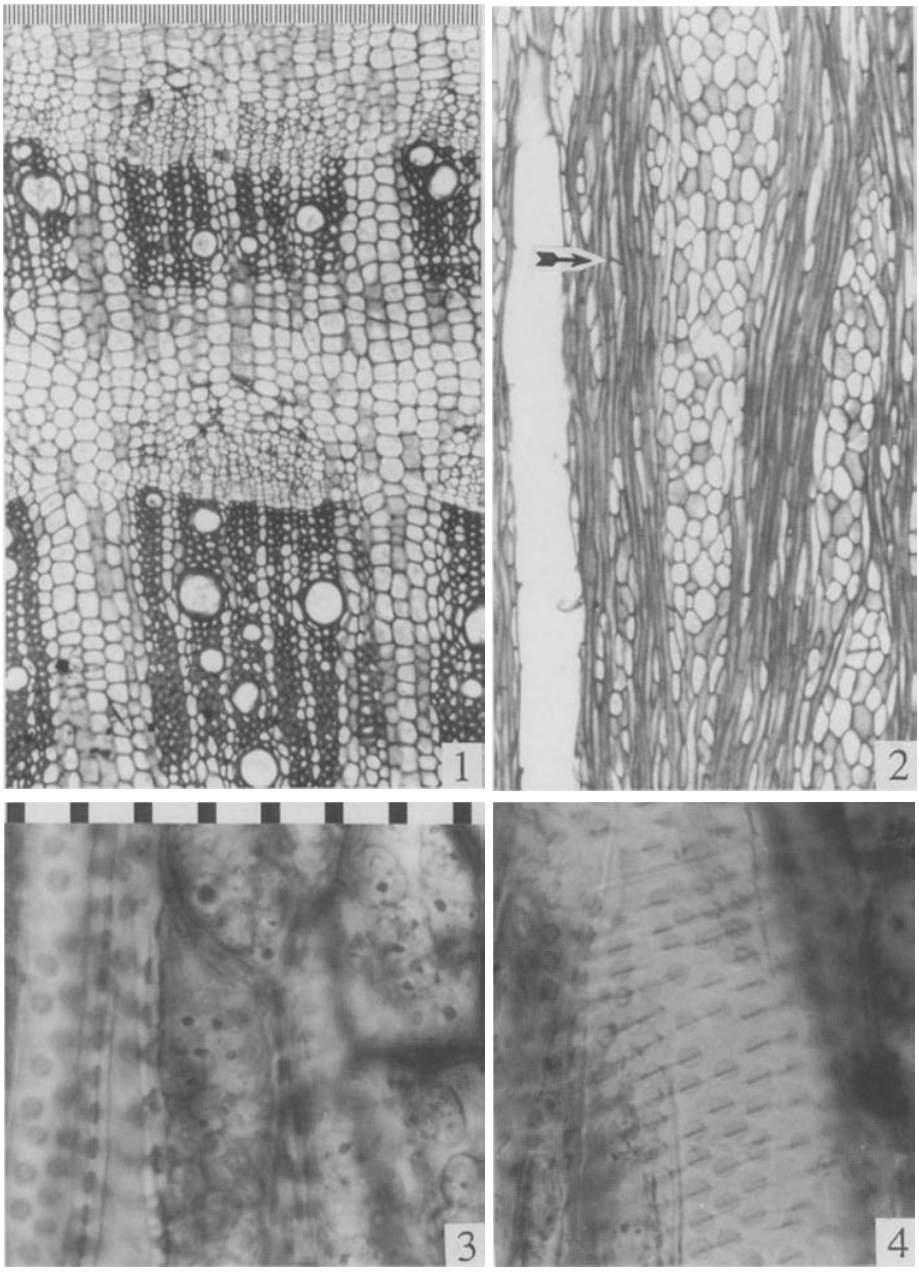
Fig. 1–4. Wood sections of *Stegnosperma halimifolium*. – 1: Transection, showing two vascular bands; two wide rays run vertically in the photograph and are intercontinuous through the two vascular bands. – 2: Tangential section, showing wide rays and also uniseriate to narrow



multiseriate rays; the arrow indicates the division in a two-celled strand of axial parenchyma. – 3: Tangential section portion to show tracheids with conspicuous circular pits, left, and ray cells containing starch (hila appear as dark dots), right. – 4: Vessel from tangential section to show alternate circular pits, some of which are interconnected by grooves. — Fig. 1 & 2, magnification scale above Fig. 1 (divisions = 10 μm); Fig. 3 & 4, scale above Fig. 3 (divisions = 10 μm).

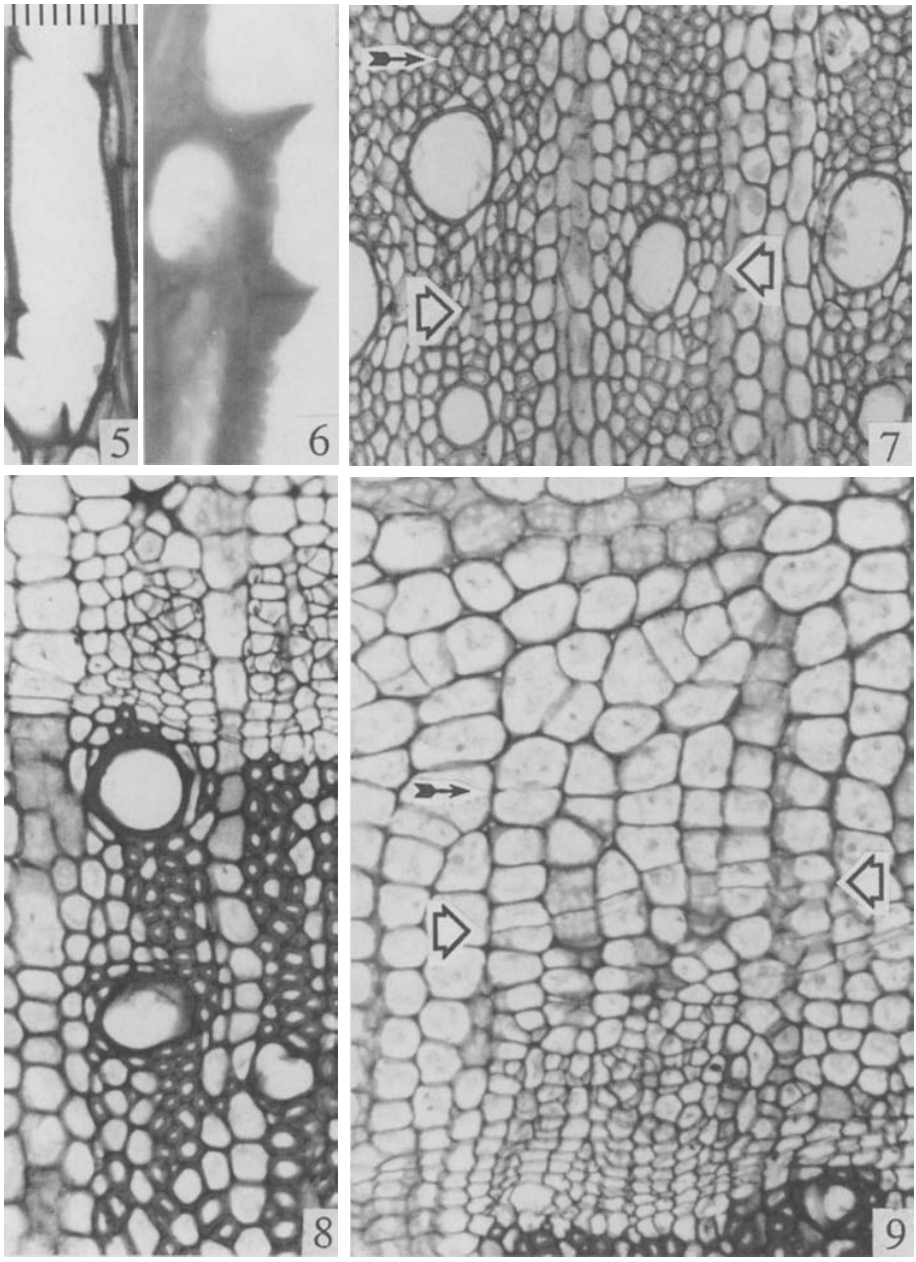


Fig. 5–9. Wood sections of *S. halimifolium* (5, 6, 8, 9) and *S. cubense* (7). – 5: Median longisection of a vessel from a tangential section to show three perforation plates in sectional view. – 6: Two perforation plate longisections from edge of vessel from tangential section; as in Fig. 5, the perforation plates are nonbordered. – 7: Transection of secondary xylem to show parenchyma types in *S. cubense*: a tangential band of parenchyma is present between the tips of the two wide, short arrows, below; a diffuse axial parenchyma cell is indicated by the

Successive cambia, their products and their origin

In mature stems of *Stegnosperma*, there is a periderm (Fig. 12, top, cells in radial rows) inside of which, from outside to inside, are outer parenchymatous cortex, a band of cortical sclerenchyma (Fig. 12, near bottom), and parenchymatous inner cortex (Fig. 12, bottom). In the older stem studied, there are radial rows of parenchyma between the inner cortex and the youngest vascular cambium. In Figures 9, 10, and 11, the most recent vascular cambium, which has not as yet yielded mature xylem or phloem, is denoted by pairs of wide, short arrows in each of these photographs. I am applying the simple descriptive term 'secondary cortex' for the radial rows of parenchyma cells in which the cambia originate.

Within the radial rows of secondary cortex, one can see recent periclinal (tangential) divisions (narrow arrows in Fig. 9, 10, 11) that maintain the radial rows and potentially increase their radial length. The radial length of the rows is, in fact, not increased because new vascular cambia form at a distance of about four or five cell layers (or secondary cortex) external to the phloem produced by the preceding vascular cambium (Fig. 1, 9, 10, 11). Those four or five layers of parenchyma mature into what are termed conjunctive tissue by most workers because they are bands of parenchyma between the products of the vascular cambia. The conjunctive tissue lies between the earliest secondary xylem formed by one vascular cambium and the secondary phloem produced by the preceding vascular cambium (Fig. 1).

The meristematic action (tangential or periclinal divisions) within the radial rows of the secondary cortex is termed 'diffuse lateral meristem' here ('diffuse' because the periclinal divisions do not take place in a single layer, as in a vascular cambium, but at various points in the radial rows of secondary cortex). Some recent periclinal divisions of this sort are indicated by the long narrow arrows in Figures 9, 10, and 11. The divisions within one radial file of secondary cortex are only loosely synchronized in time and space with divisions in adjacent radial files. A vascular cambium is, by contrast, functionally a single layer of cells that usually produces secondary phloem externally and secondary xylem internally (the vascular cambia in *Stegnosperma* correspond to this description).

The radial rows of parenchyma (secondary cortex) are not interpreted here as derived from phloem parenchyma; that mode of origin was suggested by Horak (1981a). The outermost phloem parenchyma cells of each vascular band are narrow, less than half the tangential width of the secondary cortex cells, and much more numerous than

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narrow arrow, above. – 8: Secondary phloem (above) and secondary xylem to show axial parenchyma types in *S. halimifolium*; extending downward from left side of each of the two larger vessels are radial strips of axial parenchyma; a few paratracheal and diffuse parenchyma cells are also present. – 9: A small portion of secondary xylem (bottom) above which is secondary phloem; between the secondary phloem and two or three cell layers at the top of the photograph are radial rows of parenchyma cells ('secondary cortex'); below in the radial rows short wide arrows indicate the origin of a vascular cambium; the narrow arrow, above, indicates one of several periclinal divisions in the radial rows of parenchyma. — Magnification scale for Fig. 5, 7–9 above Fig. 5 (divisions = 10 μm). Scale for Fig. 6 above Fig. 3.

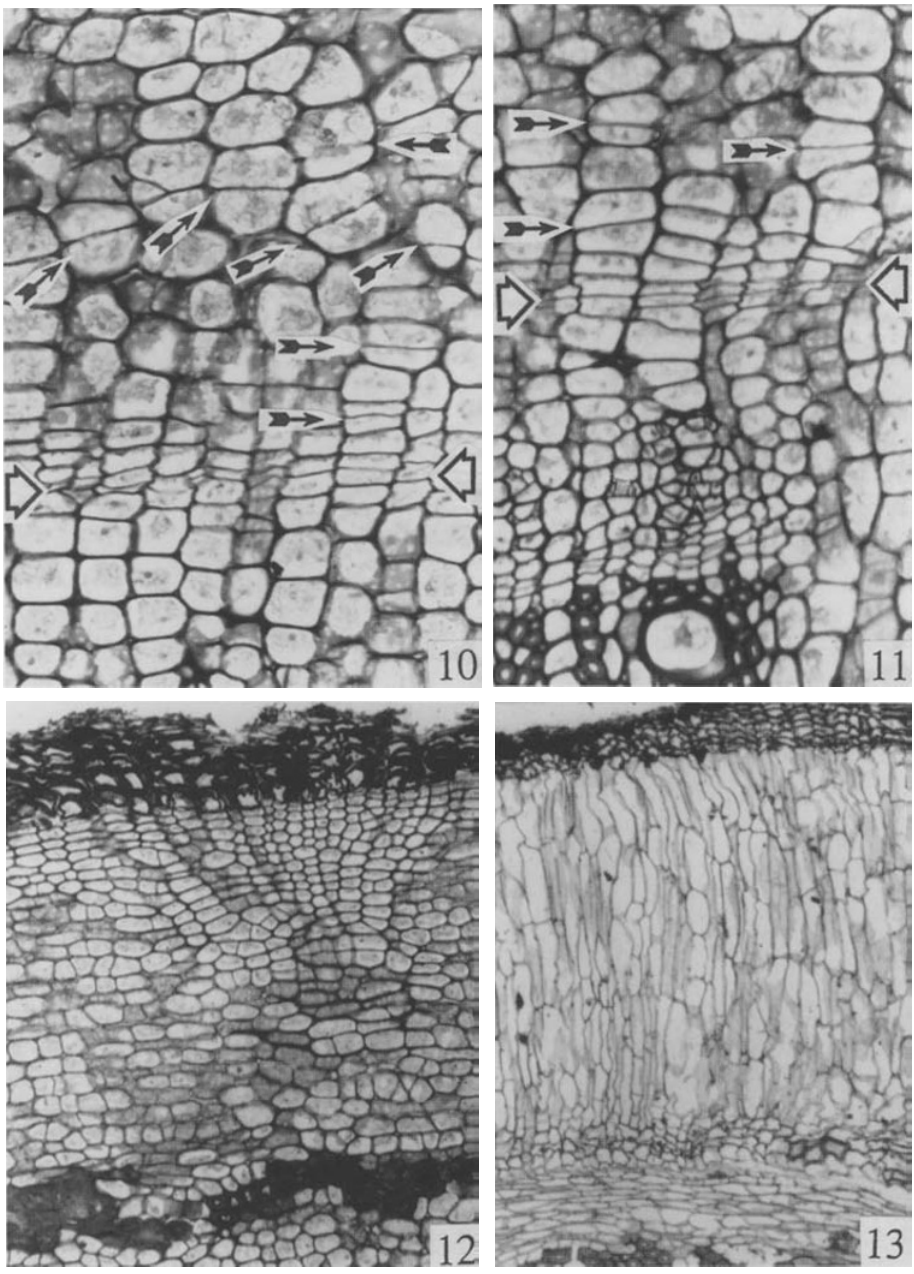

Fig. 10–13. Transections of secondary cortex (10 & 11) and bark (12 & 13); 10–12: *S. hamilifolium*; 13: *S. cubense*. – 10: Photograph shows area between secondary phloem (just below bottom of photograph) and inner cortex (about two layers at top of photograph); within the radial rows of the secondary cortex, a vascular cambium (wide, short arrows) is originating; numerous periclinal divisions in the radial rows of secondary cortex cells are indicated by narrow arrows. – 11: Photograph shows some secondary xylem (bottom), secondary phloem

the radial files and there is no evidence that they widen. The outermost phloem parenchyma cells are readily apparent because sieve tube elements and companion cells are crushed, and therefore the outermost secondary phloem is composed mostly of phloem parenchyma (Fig. 9, 11). If one views longisections of vascular cambia and their products in *Stegnosperma*, one finds that the conjunctive tissue cells are much shorter than sieve tube elements or tracheary elements, but they are about the same axial length as the secondary cortex cells. Moreover, the wide rays (which can be termed interfascicular tissue) are not in radial alignment with any phloem parenchyma derived from axial secondary phloem (Fig. 1).

Bark

Bark of *Stegnosperma* has not been described hitherto, although one of Horak's (1981a) figures includes a transection of young bark. Bark of *S. halimifolium* (Fig. 12) is composed of phellem cells, the outermost of which have dark contents; internal to these radial rows and aligned with them are thin-walled phelloderm cells, a thicker accumulation than in the bark of most dicotyledons. The juncture between these two tissues is comprised of the radially narrow phellogen cells usually present in periderm. Internal to the periderm are thin-walled cortical parenchyma cells not aligned with the radial rows of the periderm, then a band one to several cells in width of brachysclereids, and, internal to the brachysclereids, several layers of thin-walled cortical parenchyma cells. The bands of thin-walled cortical parenchyma and the sclerenchyma band are present in the primary stem, and persist by radial elongation (and conversion of some parenchyma cells to sclerenchyma as gaps develop in the sclerenchyma band by increase in circumference of the stem). The secondary cortex is derived from the innermost thin-walled cortical cells and is described in the 'successive cambia' section above. There has been no widely-accepted statement concerning whether secondary cortex should be included under the concept of bark, although the juncture between the innermost cortical parenchyma and the secondary cortex forms a boundary that can be identified readily in most species with successive cambia.

The bark of *S. cubense* has dark-staining phellem (Fig. 13, top). Unlike *S. halimifolium*, *S. cubense* bark has thin-walled radially elongate phellem cells internal to the dark-staining outer phellem. A band of phelloderm three to four cells thick is present internal to the phellogen; the phelloderm cells have moderately thick walls. Internal to the phelloderm are thin-walled cortical parenchyma cells, then a few layers of brachysclereids, and then more thin-walled cortical parenchyma, as in *S. halimifolium.*

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above that, and secondary cortex (radial rows of parenchyma); origin of a vascular cambium indicated by wide, short arrows; periclinal divisions in the radial rows indicated by the narrow arrows; note that the phloem parenchyma cells are much narrower than the parenchyma cells of the radial rows. – 12: From top to bottom, phellem (dark); phelloderm (radial rows of thin-walled cells); outer cortical parenchyma; sclerenchyma band (dark); inner cortical parenchyma band. – 13: From top to bottom, outer phellem (dark); inner phellem (radially elongate cells); phelloderm (circular cells, some with thicker walls); outer cortex; sclerenchyma band. — Fig. 10 & 11, magnification scale above Fig. 5; Fig. 12 & 13, scale above Fig. 1.

DISCUSSION AND CONCLUSIONS

Ecological conclusions

Horak (1981b) reports mean vessel diameter in *S. cubense* of 91.8 μm (external diameter rather than lumen diameter, presumably), compared with much narrower mean diameters in the other species: 53.6 μm in *S. halimifolium* and 53.4 μm in *S. watsonii*. He reports mean vessel element length in *S. cubense* as 320 μm, a little longer than the mean length in *S. halimifolium* (278 μm) and *S. watsonii* (291 μm). These data mark *S. cubense* as having markedly more mesomorphic wood than *S. halimifolium* according to widely accepted criteria (Carlquist 1975). Although detailed ecological observations are not available for the three species, wood data are very reliable indicators of ecology unless factors such as succulence or lianoid habit are present. *Stegnosperma* is not succulent in the ordinarily understood sense of the word, but it is drought deciduous, an effective method of dealing with lowered water availability. A sample of dicotyledonous species with successive cambia (Carlquist 1975: 206) gives mean vessel diameter of 68 μm and mean vessel element length as 146 μm. Vessel diameter in *Stegnosperma* approaches the figure for that sample, but vessel elements in *Stegnosperma* are appreciably longer.

The vessels of *Stegnosperma* are characteristically solitary. The wood of *Stegnosperma* is an excellent example of the phenomenon of deterrence of vessel grouping in species that possess tracheids (rather than fiber tracheids or libriform fibers) in wood (Carlquist 1984). The reason for this correlation is that tracheids form an excellent subsidiary conductive system which can suffice when vessels embolize in case of drought and freezing. *Stegnosperma* has imperforate tracheary elements that qualify as tracheids because of the diameter and density of pits. These tracheids are probably just as capable of conduction as the tracheids of gymnosperms or the vasicentric tracheids of numerous families of dicotyledons (Carlquist 1985). The conductive status of tracheids such as those in *Stegnosperma* wood is affirmed by the work of Braun (1970), in which tracheids and vasicentric tracheids of dicotyledonous woods are shown to be conductively active by means of photographs of fluorescent dyes in water-conducting cells. In dicotyledon species with tracheids or with large quantities of vasicentric tracheids, a mechanism for preserving the conductive pathways of wood despite embolizing of vessels is present. This mechanism is much more effective than grouping of vessels, and accounts for the lack of vessel grouping in dicotyledon species with tracheids or abundant vasicentric tracheids. Evidence from conductive physiology thereby enhances the definitions of tracheids offered by the IAWA Committee on Nomenclature (1964). The presence of tracheids plus vessels with simple perforation plates, as in *Stegnosperma*, is a combination found in numerous xeromorphic woods (Carlquist & Hoekman 1985). The abundant vasicentric tracheids of *Agdestis* (Phytolaccaceae s.l, or Agdestidaceae) are likely related to the lianoid habit of that genus (Carlquist in press).

Habital conclusions

Horak (1981a) recorded mean vessel element length for each of seven successive secondary xylem increments of a *Stegnosperma* stem. His data show that there is very

little change; at most, there is a small decrease in vessel element length in the later-formed xylem increments. This is only slightly suggestive of an age-on-length curve for vessel element length in dicotyledons with paedomorphic wood (Carlquist 1962). However, it is more like the paedomorphic curve than the age-on-length curve for woody dicotyledons that have a single cambium, in which a marked increase in vessel element length occurs with the onset of secondary growth (Bailey & Tupper 1918). There is a plausible reason for this. If each of the cambia in a species with successive cambia originates in the secondary cortex, as claimed for *Stegnosperma* in this paper, its products should be similar in length. Each of the cambia produces a limited amount of secondary xylem, so that a marked change in vessel element length over time is unlikely. In contrast, in woody dicotyledons with a single cambium, the cambium can persist for many years and thus changes in length of fusiform tracheary elements within the cambial layer can occur over time.

The ray cells of *Stegnosperma* are mostly upright. Only a few of the radial files of ray cells are composed of procumbent cells (Fig. 2; see also Bedell 1980). Horak (1981a) describes the rays of *Stegnosperma* as 'predominantly heterocellular'. The high proportion of upright ray cells in the genus agrees with Paedomorphic Type I rays (Carlquist 1988).

One can view each of the vascular increments of *Stegnosperma* stems as juvenile secondary xylem and secondary phloem, with little or no attainment of a mature ray structure (in which procumbent cells predominate). The lack of change in vessel element length over time in *Stegnosperma* (Horak 1981a) can likewise be interpreted as permanent juvenilism. One cannot conclude, because of the complication offered by the successive cambia, whether the ancestors of *Stegnosperma* were woody or herbaceous. If one looks at cladograms such as those of Rodman (1994) in terms of shifts between woody and herbaceous habits, one finds no clear pattern, although in several of the families more conspicuous woodiness occurs (Cactaceae, Didiereaceae, Nyctaginaceae). Phytolaccaceae s.l. contains both woody and herbaceous genera, and genera with a single cambium as well as those with successive cambia. Consequently, Phytolaccaceae s.l. is an important group for analysis of changes in habit and presence or absence of successive cambia. Molecular data from a large number of genera and species are needed to offer evidence on these points.

Phylogenetic conclusions

In contrast to Phytolaccaceae s.s., *Stegnosperma* has tracheids instead of libriform fibers. *Agdestis*, which comprises a monospecific family very likely a satellite of Phytolaccaceae s.s. (Rodman 1994) has abundant vasicentric tracheids (Carlquist in press). Some genera of Caryophyllaceae have tracheids, while other genera have fiber tracheids and yet others have libriform fibers (Carlquist 1995). Presence of tracheids in *Stegnosperma* would qualify as a symplesiomorphy, since that family is often regarded as basal in Caryophyllales (Rodman 1994). Caryophyllaceae occupies a basal or near-basal position in most cladograms (see Rodman 1994), so that one could interpret presence of tracheids in some genera of the family as a remnant of a primitive condition.

Diffuse axial parenchyma is common in *Stegnosperma*, but has not been reported in other Caryophyllales, in which scanty vasicentric (paratracheal) parenchyma has been reported (Metcalfe & Chalk 1950; Gibson 1994; Carlquist 1995). Diffuse axial parenchyma is regarded as a primitive condition (Kribs 1937; Carlquist 1988).

The presence of both multiseriate and uniseriate rays also in *Stegnosperma* is also commonly regarded as more primitive than presence of multiseriate rays exclusively (Kribs 1935), the latter condition found in most Phytolaccaceae s.l. (Carlquist 1998b, in press, and unpublished data).

Thus, wood data support the concept that *Stegnosperma* is basal in Caryophyllales (Rodman 1994). Wood data when more completely known may show that Phytolaccaceae s.l., if diverse in some respects, is composed of groups closer to each other than to non-phytolaccaceous Caryophyllales. For example, nonbordered perforation plates in vessels is an unusual condition in dicotyledons at large, but it occurs in Phytolaccaceae s.l. (Carlquist 1998b, in press, unpublished data) as well as in *Stegnosperma*.

Conclusions on successive cambial action and origin

1) In dicotyledons at large, the first cambium in a species that produces successive cambia as in other woody dicotyledons; the second cambium is formed by periclinal divisions in the primary cortex. There is general agreement in the literature on these points. However, prior to origin of the second cambium, periclinal divisions in the inner cortex may form radial rows of what is termed secondary cortex here, as in *Rivina* (Carlquist 1988b). The radial rows of secondary cortex parenchyma are conspicuous in *Stegnosperma*.

2) The second cambium in a species with successive cambia is formed not immediately outside the secondary phloem formed by the first cambium, but is separated from that phloem by several cell layers of secondary cortical parenchyma. This is true of subsequently formed vascular cambia also. The layers of secondary cortex between the vascular bands mature into what is termed conjunctive tissue. Because the conjunctive tissue is not formed from a vascular cambium, by definition it does not belong to secondary xylem; it is not wood. Therefore, the term 'included phloem' should not be applied to phloem of species with successive cambia. 'Included phloem' applies properly to species with a single cambium in which strands of phloem are formed internally by the vascular cambium (e.g., Onagraceae, Strychnaceae).

3) The radial rows of parenchyma derived from periclinal divisions of inner cortex, and therefore termed secondary cortex here, are potentially decreased in radial extent by formation of a new vascular cambium, which is formed several cells (of secondary cortex) external to the phloem of the preceding vascular band. The secondary cortex cells between the preceding vascular band and the new vascular cambium mature into conjunctive tissue and thus potentially decrease the radial extent of the secondary cortex. However, the radial extent of the radial parenchyma rows is maintained by periclinal divisions in parenchyma cells outside the

youngest cambium and its products in *Stegnosperma*. These divisions are not localized in a single layer as are those of the vascular cambium, but occur at various points within the radial files of secondary cortex cells. Therefore, the divisions are collectively called a diffuse lateral meristem. This interpretation conflicts with that of Horak (1981a), who believes that the radial rows of parenchyma are lengthened by addition of increments of parenchyma derived from phloem parenchyma of each of the vascular bands. The reasons why that interpretation is not confirmed here are cited above.

4) Each of the vascular bands in *Stegnosperma* are continuous around the stem and they form concentric rings as seen in transections of the stem in gross aspect. However, radial strips of parenchyma about five cells wide are present within each of these bands (two such strips are seen in each of the two vascular bands, Fig. 1, and are continuous between the two bands). Divisions occur in the cambium of these bands prior to cessation of function of the cambium of each vascular band, and the cambium of these bands is continuous tangentially with the vascular cambium in 'fascicular zones' that produce sieve elements and tracheary elements. Therefore, these radial strips of parenchyma must be considered wide xylem and phloem rays. Narrower rays are formed in the fascicular portions of the vascular bands.

5) Ontogenetic sequences are not always easy to demonstrate, and descriptive terms and phrases are not always easily applied to preparations or photomicrographs of preparations. However, diverse terminology and interpretations have been applied to stem (and root) ontogeny of Phytolaccaceae s.l. Nevertheless, the data so far reported suggest a single basic phenomenon, albeit with variations. *Stegnosperma* represents one of these variations, and others will be described as studies are added to this series of papers. The diversity of descriptions in papers on anatomy of stems and roots in Phytolaccaceae s.l. should not lead a reader to conclude that a series of ontogenetically unlike mechanisms are present. In part, the interpretative difficulty has arisen from the fact that some workers have concentrated on a single species or a few closely related species and not compared with what has been found in other groups. The present series on wood and stems of Caryophyllales will carefully examine the stem ontogeny of all available species of the order in which successive cambia are present. The results obtained from study of those species, when combined with comparisons from other families of dicotyledons and Gnetales with successive cambia, will hopefully lead to clarification of phenomena related to successive cambia.

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