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WOOD ANATOMY OF *AGDESTIS* (CARYOPHYLLALES): SYSTEMATIC POSITION AND NATURE OF THE SUCCESSIVE CAMBIA

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ABSTRACT

Features in which *Agdestis* differs from Phytolaccaceae s. s. include presence of both libriform fibers and vasicentric tracheids (rather than one or the other); bands and strands of thin-walled apotracheal parenchyma (in addition to paratracheal scanty parenchyma), and raylessness (also reported for *Bougainvillea* of Nyctaginaceae, a family close to Phytolaccaceae). Dimorphism in vessel diameter in *Agdestis* (narrow vessels like libriform fibers in diameter) is attributable to the lianoid habit. Packets of crystals coarser than typical for raphides occur idioblastically in *Agdestis*, as do raphides in *Phytolacca*. In *Phytolacca* and in other Phytolaccaceae, one finds an unusual feature that occurs in *Agdestis*: nonbordered simple perforation plates. Anatomical data support *Agdestis* as forming a monogeneric subfamily within Phytolaccaceae s. l. The nature of successive cambia in *Agdestis* is compared with those in other Phytolaccaceae and in Nyctaginaceae. A common pattern is probably present, although differences in terminology and observations obscure the pattern. The term “interxylary phloem” is a misnomer because conjunctive tissue is not secondary xylem as generally understood. After cessation of the cambium in the first cylinder, radial rows of cells form outside the phloem and inside the cortex; this activity may constitute a lateral meristem. Apparently within the radial rows of cells, successive cambia form; each of these cambia produce secondary phloem externally and secondary xylem internally. There is little or no cambial activity in interfascicular areas.

Key words: cambial variants, Caryophyllales, Centrospermae, interxylary phloem, lianas, Phytolaccaceae, raylessness, successive cambia, tracheids.

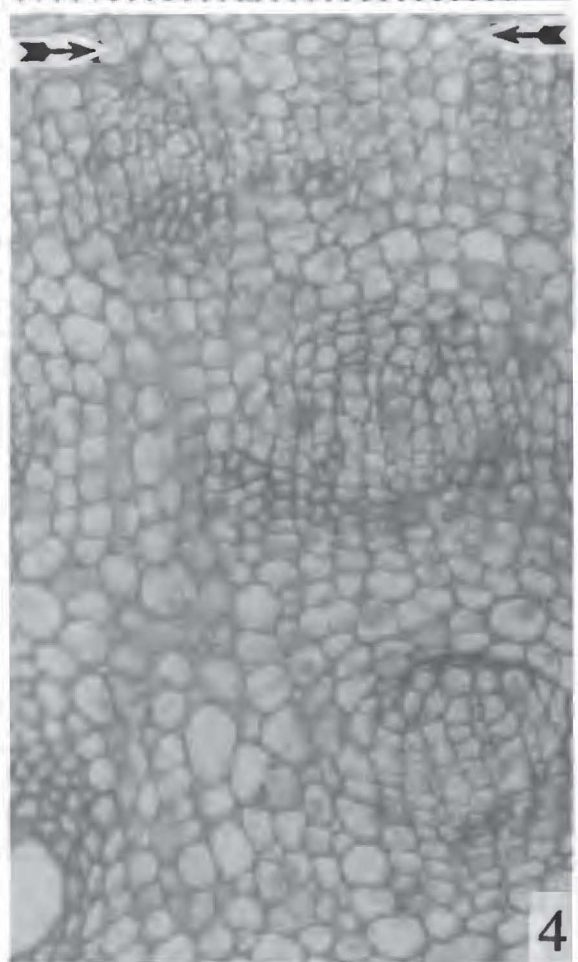
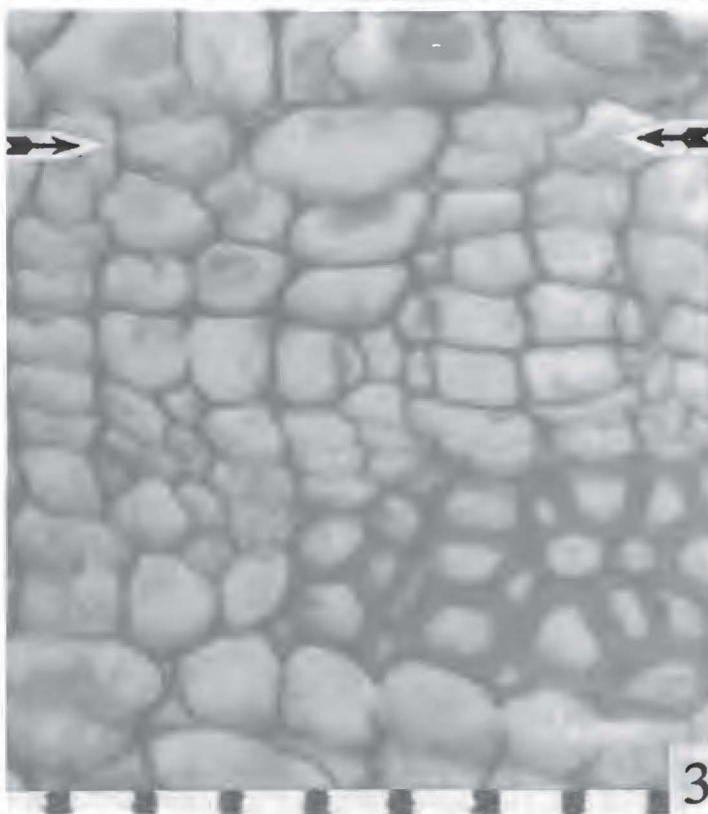
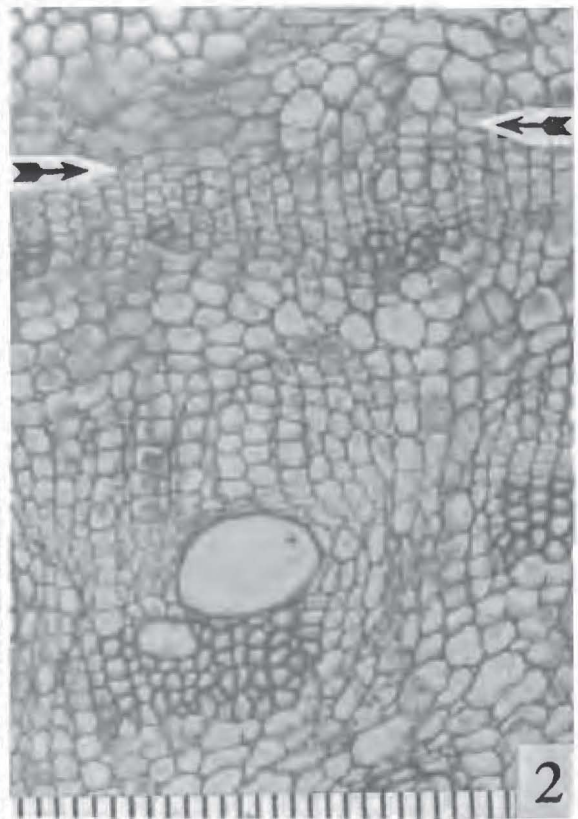
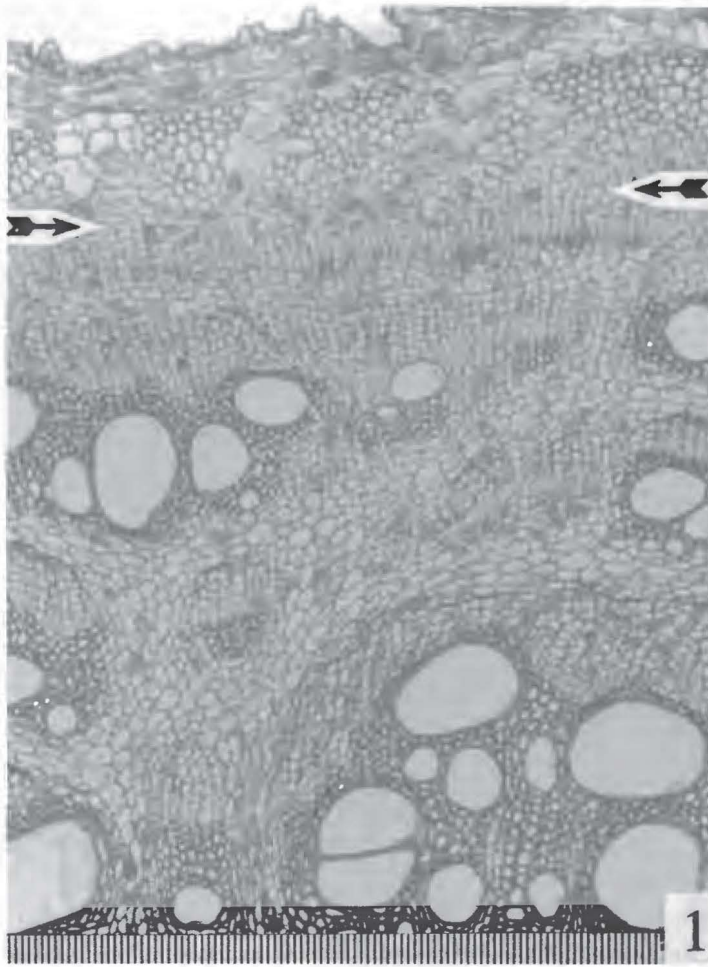
INTRODUCTION

Although all authors have recognized a single species of *Agdestis*, *A. clematidea* Moc. & Sessé (Walter 1909, Heimerl 1934), the genus has been included with uncertainty in Phytolaccaceae (Walter 1909). Some authors remove from Phytolaccaceae s. l. a number of segregate families, such as Achatocarpaceae, Agdestidaceae, Barbeuiaceae, Gisekiaceae, Petiveriaceae, Rivinaceae, and Stegnospermaceae (e.g., Behnke 1997, who added Sarcobataceae as a family in this alliance). A compromise position was offered by Thorne (in Cronquist and Thorne 1994), who recognized those proposed families as subfamilies within a Phytolaccaceae that excludes, among groups traditionally included in the family, only Achatocarpaceae and Stegnospermataceae; this treatment was earlier offered by Dahlgren (1980). Some support for segregation of families from the traditional Phytolaccaceae has been offered by cladistic and phenetic studies. These show trees in which the traditional Phytolaccaceae are separated into several groups, with such nonphytolaccaceous genera as *Bougainvillea*, *Mirabilis*, and *Mollugo* intervening between the groups (Brown and Varadarajan 1985; Rettig et al. 1992; Manhart and Rettig 1994; Rodman 1994; Downie and Palmer 1994; Downie et al. 1997). Authors of a more inclusive Phy-

tolaccaceae emphasize the diversity within Phytolaccaceae s. l. (e.g., Heimerl 1934).

Behnke (1997), while endorsing the segregate families, groups them with Aizoaceae and Nyctaginaceae into a suborder which he names Phytolaccineae. This treatment corresponds to the “phytolaccaceous alliance” of Hershkovitz (1991), although Hershkovitz did not include Aizoaceae. Within the “phytolaccaceous alliance,” Hershkovitz (1991) hypothesizes that “*Agdestis* links Phytolaccaceae s. s. with Rivinaceae.” Brown and Varadarajan (1985) in their phenetic studies produced trees that show *Agdestis* close to *Barbeuia* and *Stegnosperma*. The molecular studies cited above do not support such a grouping. Obviously, there is no unanimity in treatment of the “phytolaccaceous alliance” or Phytolaccineae at this point, but the diversity of taxonomic treatments serves to underline the problems inherent in classification of a diversified group.

Data on wood anatomy of *Agdestis* have not been available hitherto (Gibson 1994; Gregory 1994). Although Gibson (e.g., 1973, 1978) has contributed much to our knowledge of comparative wood anatomy of Cactaceae, knowledge of wood in other families of Caryophyllales has lagged behind. The order is not notably woody, and the core of studies on wood anatomy has traditionally been provided by tree species.



In order to develop more comprehensive data for the order, I have contributed studies on Caryophyllaceae (Carlquist 1995); Portulacaceae and Hectorellaceae (Carlquist 1998); and Basellaceae (Carlquist 1999). Two families are commonly cited as outgroups of Caryophyllales; wood of one of these, Plumbaginaceae, has been surveyed (Carlquist and Boggs 1996), and a survey of the other, Polygonaceae, is in progress.

Agdestis is a scandent subshrub (Walter 1909), and thus invites comparison to wood of scandent Caryophyllales, such as *Bougainvillea* (Esau and Cheadle 1969; Stevenson and Popham 1973) as well as to wood of lianas at large (Carlquist 1985). *Agdestis* tends to be a climber within savannah areas, such as the post oak woodland of eastern Texas, and is distributed from Nicaragua, Guatemala, southern Mexico, eastern Texas, and Florida to Cuba, Hispaniola, and Puerto Rico; it is probably naturalized in Brazil (Walter 1907; Heimerl 1934).

In comparing wood of *Agdestis* with that of other Phytolaccaceae s. l. or with that of the suborder Phytolaccineae as a whole, one must take into account the successive cambia of *Agdestis* and other Phytolaccaceae. Even in Phytolaccaceae s. s., some genera have successive cambia (*Anisomeria*, *Gallesia*, *Phytolacca*, *Seguieria*) whereas others have been reported to have only a single cambium (*Hillieria*, *Ledenbergia*, *Monococcus*, *Trichostigma*) according to Pfeiffer (1926), who was uncertain about presence of successive cambia in *Agdestis*. This situation provides a challenge in comparative wood anatomy because wood formed from successive cambia may differ from that produced by a single cambium. More significantly, genera with successive cambia have been subject to varied interpretations with respect to ontogeny and action of a thickening meristem and of the cambia that produce secondary xylem and phloem (see CONCLUSIONS). With varied interpretations of these ontogenetic events, diverse terminology has also arisen (see Artschwager 1920, 1926; Balfour, 1965; Esau and Cheadle, 1969; Stevenson and Popham 1973; Wheat 1977; Mikesell 1979; Baird and Blackwell 1980; Gibson, 1994). The material of *Agdestis* was suitable for analysis of the successive cambia and their origin, although not definitively so. A preliminary discussion of these phenomena is undertaken here. Although the successive cambia of Caryophyllales may not be identical to those in

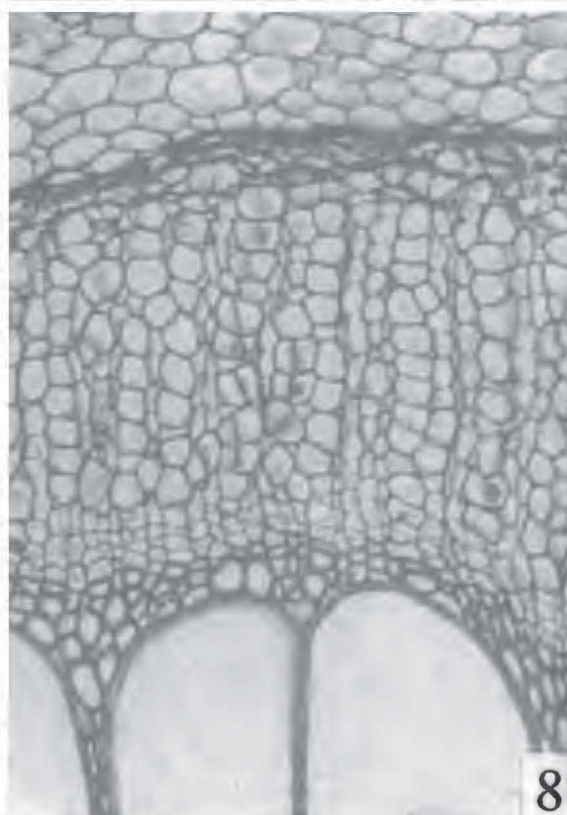
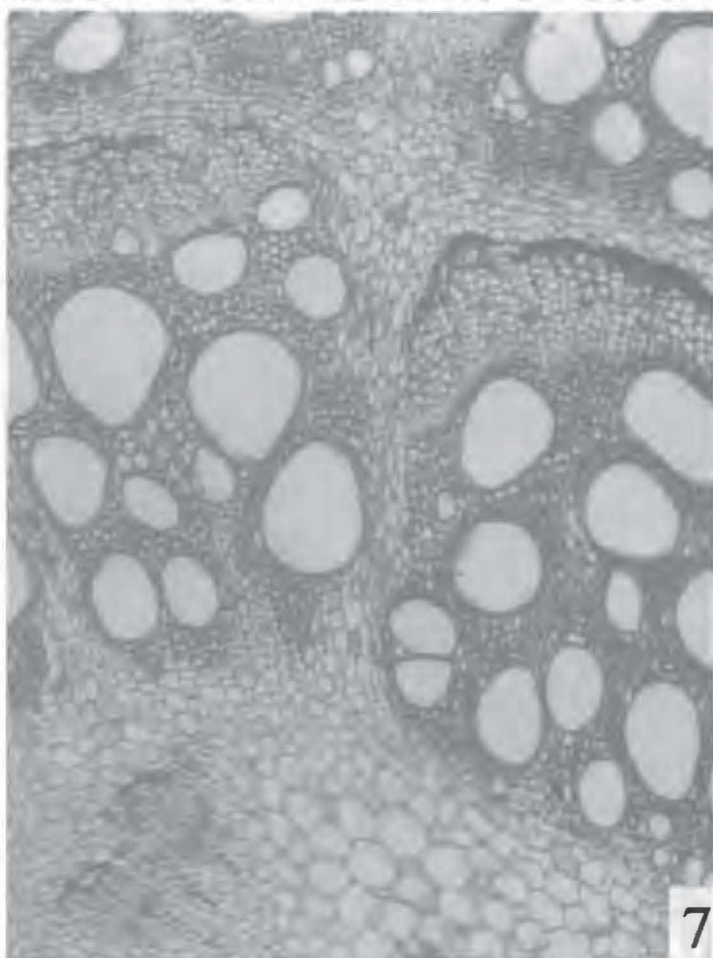
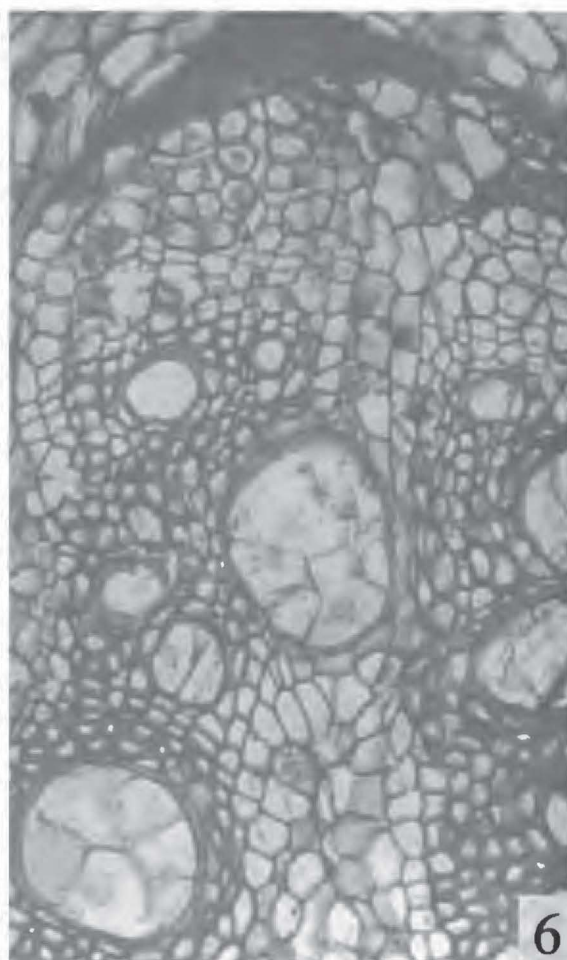
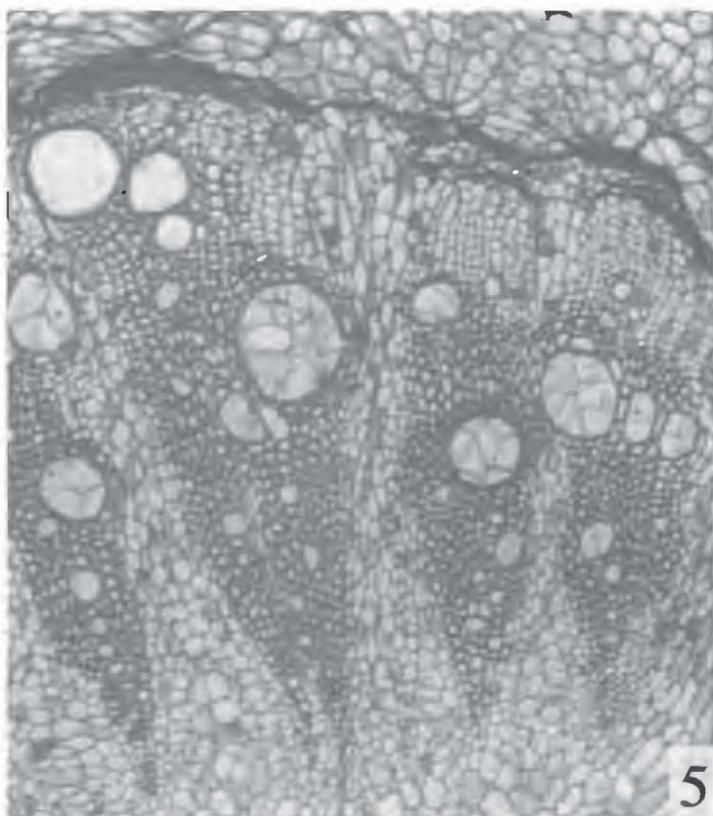
other dicotyledons, the studies cited above indicate that the ontogeny and histology involved in this form of cambial activity is less diverse than the literature might lead one to believe. Therefore, careful descriptions of each genus that shows successive cambia will lead to better understanding of this phenomenon in angiosperms and in Gnetales.

MATERIALS AND METHODS

Fresh material of the basal decimeter of a living stem of *A. clematidea* was provided by the San Antonio Botanical Garden. Upon receipt, this stem was subdivided and fixed in 50% aqueous ethanol. Pieces from near the base (Fig. 5–8) and from about 5 cm above the base (Figs. 1–4, 9–13) were softened and sectioned according to the schedule of Carlquist (1982). Sections were stained with a safranin-fast green combination according to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen 1940). Macerations were prepared by means of Jeffrey's Fluid (Johansen 1940) and stained with safranin.

Terms are according to the IAWA Committee on Nomenclature (1964), except for the terms vasicentric tracheid and successive cambia, which follow Carlquist (1988). Terms and concepts relative to successive cambia have not been applied uniformly and are discussed in the CONCLUSION section. Vessel diameter and vessel grouping cannot be determined accurately for *Agdestis*, because narrow vessels grade into vasicentric tracheids. Both of these latter cell types appear much the same as libriform fibers in transection, and therefore data relative to each of these cell types cannot be obtained accurately from transections. Macerations, where the cell types could be identified, were used as a basis for the quantitative data given for cell types other than the wider vessels. For these, transections were used. Mean lumen diameter was used for vessels, because this measurement reflects physiological capabilities of vessels better than measurements of external dimensions. For reasons cited above, vessel grouping could not be determined accurately. However, because of the many narrow vessels, vessel groups obviously contain many cells.

←
Fig. 1–4. Transections of stem of *Agdestis clematidea*.—1. Portion from outer surface (top) to near pith; in this and other figures, pairs of arrows indicate outer limit of radial rows of cells located internal to cortical cells; these radial rows are composed of presumptive parenchyma cells (or meristematic cells) external to secondary phloem.—2. Portion to show that in maturation of secondary xylem from the successive cambia, formation of fibriform cells precedes formation of wide vessels.—3. Radial rows of cells adjacent to cortical cells (top) and the products of a cambium: sieve tube elements and companion cells above, and thick-walled secondary xylem cells below.—4. Portion to show little or no cambial activity in interfascicular regions; maturation of secondary phloem is somewhat earlier than that of secondary xylem. (Fig. 1, scale below Fig. 1 [divisions = 10 μ m]; Fig. 2, 4, scale below Fig. 2 [divisions = 10 μ m]; Fig. 3, scale below Fig. 3 [divisions = 10 μ m].)



RESULTS

Cambial Action and Products

In Fig. 1, a representative portion of a stem transection is shown. There is a cylinder of bundles that experience secondary growth in the center of the stem, but cambial action within these bundles is not extensive (Fig. 7). Diversely shaped strands and arcs of vascular tissue external to the first cylinder of bundles are the result of the action of successive cambia, and these cambia originate within the tissue produced by a thickening meristem. In Fig. 1, one can see both large and small vascular strands of approximately the same age, so that sizes of vascular strands are not indicators of comparative age—in some, the cambium ceases function sooner than in others. In Fig. 5, there is a tangentially wide arc of vascular tissue that begins as several distinct xylem strands or points that are joined as cambial action between them produces secondary xylem. At the bottom of Fig. 7 is a pair of small vascular strands that have originated in the pith of the stem later than bundles of the main cylinder above them.

The cortex of the stem contains strands of thin-walled fibers separated from each other by large parenchyma cells (Fig. 1, top). Internal to the cortex one can locate a thickening meristem (paired horizontal arrows in Fig. 1–4). This meristem produces radial files of cells to the interior of the stem; few or no cells are produced to the exterior of the meristem. Thus, the outermost cells in the radial files are the meristem cells and may be identified where these radial files contact the cortex cells that do not align with the radial files (especially evident in Fig. 3). Within the radial files, cambia originate. Each of these successive cambia tends to produce phloem earlier than secondary xylem; at least, larger quantities of secondary phloem accompany smaller quantities of secondary xylem in recently-active cambia (e.g., Fig. 4, extreme lower right). The vascular strand, Fig. 4, center, shows extensive secondary phloem but only two or three layers of xylem fibers (or other narrow tracheary elements) and no wider vessels. Formation of the wide vessels tends to follow the formation of the fibriform secondary xylem cells.

In Fig. 1–4, phloem accumulations are relatively moderate. The vascular strands shown in Fig. 5–8 are older and external to the radial files of sieve tubes and companion cells is a band of crushed secondary phlo-

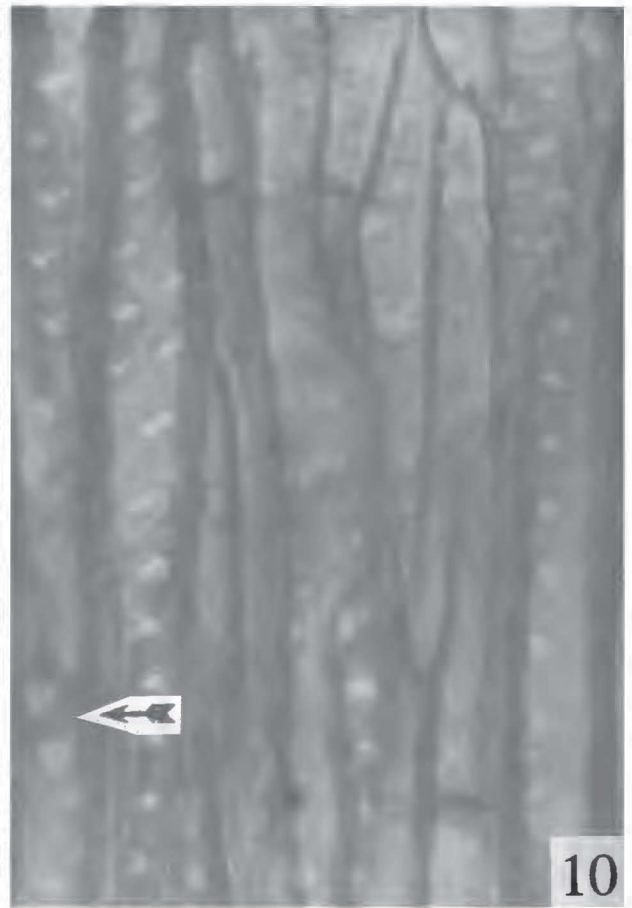
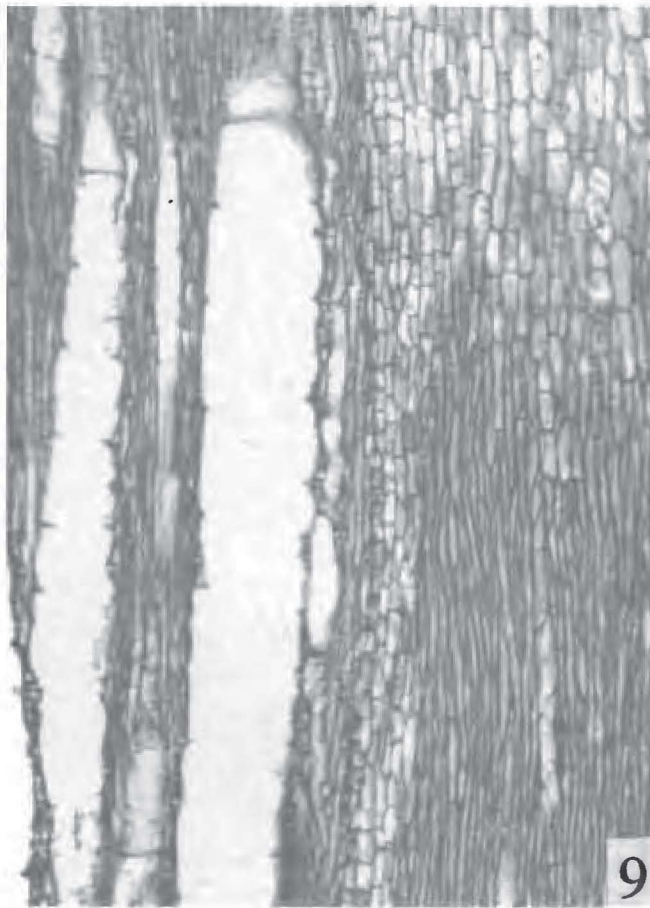
em, especially conspicuous in Fig. 5 and Fig. 6, top. Radial files of secondary phloem are shown well in Fig. 8. In Fig. 6 are two strands of secondary xylem that have fused as the cambium has made additions to the xylem; this fusion occurs at the point where a large vessel is present (Fig. 6), center.

No rays in the ordinary sense are formed by the successive cambia. Tangential sections (Fig. 9) show no rays within fascicular xylem. One could term the conjunctive tissue between the vascular strands as rays, however. In *Agdestis*, some interfascicular areas show no perceptible cambial activity (Fig. 4, bottom, center) or relatively few divisions in interfascicular zones (Fig. 2, lower right).

Wood Histology

Poorly defined growth rings are present; as in other groups of angiosperms with successive cambia, the margin of a growth ring is within the secondary xylem (narrower vessels are followed by tangential bands of wider vessels). One might think that a season's growth would end with cessation of activity in a cambium, so that a growth ring terminus would correspond to conjunctive tissue between successive vascular arcs, but I have not observed that either in *Agdestis* or in other angiosperms with successive cambia. Vessels tend to be dimorphic in diameter; either vessels are mostly wide or else they mostly are as narrow as imperforate tracheary elements. About half of the cells that appear to be libriform fibers (e.g., Fig. 1–3, 5–7) are actually fibriform vessels (e.g., perforation plates were observed in several of the narrow vessels shown in Fig. 10). About a third of the fibriform elements, as seen in transection, are vasicentric tracheids. The narrow vessels and vasicentric tracheids have intervascular pits 4–5 μm in diameter (Fig. 10), much like the (slightly larger) intervascular pits of the wider vessels (Fig. 12). About one-sixth of the fibriform cells are actually libriform fibers with small simple pits. The libriform fibers of the secondary xylem are nonseptate; the fibers of the cortex are much wider and are characteristically septate, in contrast. Mean lumen diameter of the wider vessels is 56 μm (range = 17–149 μm), and the mean length of wider vessel elements is 150 μm . Mean lumen diameter of the narrow vessels is 8 μm ; mean length of the narrow vessel elements is 334 μm . Mean length of vasicentric tracheids is 322 μm .

Fig. 5–8. Transections from base of stem of *Agdestis clematidea*.—5. Adjacent xylem areas that fuse, above, as a cambium changes so as to produce one broad arc of secondary xylem rather than several strands.—6. Two strands of secondary xylem that fuse where a large vessel (center) occurs; tyloses present in vessels; crushed secondary phloem at top.—7. Pith (below) and vascular strands; a pair of recently-formed vascular strands in the pith are at lower left.—8. Radial files of sieve-tube elements and companion cells, above, and portions of three large vessels and adjacent fibriform secondary xylem cells, below. (Fig. 5, 7, scale below Fig. 1; Fig. 6, 8, scale below Fig. 2.)



Mean length of libriform fibers is 452 μm . Vessel density cannot be determined, but is certainly above 10 vessels per group, on account of the many narrow vessels that occur in the apparently fibriform axial xylem.

Perforation plates are simple in the wider vessels, mostly simple in the narrower vessels, but occasionally a pair of circular perforation plates may be seen (Fig. 10, arrow). The perforation plates have a feature relatively unusual in dicotyledons: perforation plates are nonbordered (Fig. 13, right top and right bottom).

Axial parenchyma is present as paratracheal strands of three to four cells. Adjacent to wide vessels, vessel enlargement results in lateral (horizontal) elongation of the cells (Fig. 13), rather than the usual vertically elongate axial parenchyma cells one might expect (several such are seen in Fig. 10 and 11). Large minimally bordered pits are present on walls of axial parenchyma cells that face vessels (Fig. 11, upper left). Although not shown in any of the figures of this paper, some of the secondary xylem in *Agdestis* contains strands and tangential bands of thin-walled axial parenchyma. The paratracheal axial parenchyma has rather thick lignified walls, in comparison (Fig. 10, 11, 13).

Secondary xylem and secondary phloem are entirely rayless (Fig. 9). Wood is nonstoried with respect to all cell types. Tyloses are present in some of the wider vessels in older stems (Fig. 5, 6). The tyloses are thin-walled and do not have discernible contents.

Conjunctive tissue is composed of thin-walled parenchyma. Idioblasts containing packets of elongate crystals, like coarse raphides, occur in cortex, pith, and conjunctive tissue. No mucilage enveloping the packets of crystals was observed.

CONCLUSIONS

The origin and products of successive cambia are topics in need of a thorough review. Such a review is made difficult by virtue of the occurrence of successive cambia in a wide range of families (for a listing, see Carlquist 1988). However, the material of *Agdestis* shows some of these phenomena and comments may therefore be appropriate here. After the cambium of the first cylinder of stem bundles begins to slow in its production of secondary xylem and secondary phloem, radial rows of cells which may constitute a lateral meristem (perhaps the "primary thickening meristem" cited in *Bougainvillea* by Stevenson and Popham 1973) originate in the cortex. Cells produced by these rows

appear to mature into "conjunctive tissue" (of various authors; also termed "secondary parenchyma" by Gibson 1994).

Before maturation into conjunctive tissue, cambia may form within the immature products of the radial rows of cells or "thickening meristem" ("prodesmogen strands" maturing into "desmogen" after activity of such cambia according to the terms of Stevenson and Popham 1973). The observations of Wheat (1977) for *Phytolacca* show that the cambium forms first and then produces secondary xylem and secondary phloem, whereas the terminology of Stevenson and Popham (1973) implies procambium-like strands in which phloem, xylem, and a "desmogenic" cambium differentiate simultaneously. Distinguishing between these two concepts is not easy when studying cell lineages, however. Wheat (1977) believed that each cambium produces xylem internally and phloem externally, but that it also forms, "... parenchyma cells on both sides before it forms derivatives which mature into lignified xylem elements or conductive elements of the phloem. The parenchyma thus formed toward the outside later becomes the site of the origin of the succeeding cambium." I was unable to find this ontogenetic sequence in my material of *Agdestis*.

The interpretation of Esau and Cheadle (1969) in *Bougainvillea* claims, "... successive cambia each of which functions bidirectionally in producing xylem and conjunctive tissue to the inside and phloem and conjunctive tissue to the outside." The interpretation of Esau and Cheadle (1969) suggests that conjunctive tissue is a product not of each of the successive cambia, but of the thickening meristem. If I interpret the Esau and Cheadle concept correctly, they find that a cambium produces first conjunctive tissue and then secondary xylem to the inside, and first conjunctive tissue and then secondary phloem to the outside and thus changes from production of rectangular conjunctive cells to production of prosenchymatous xylary cells or phloic cells, on respective sides of each of the cambium—and this change would have to occur simultaneously and uniformly along the tangential surface of the phloem side and the xylem side of the cambium.

The analysis of Mikesell (1979) in *Phytolacca* shows that the role of terminology in studies of successive cambia is critical. Mikesell uses "primary thickening meristems" as a synonym for "successive

Fig. 9–13. Tangential sections of stem of *Agdestis clematidea*.—9. Secondary xylem containing vessels (left half of photograph); secondary xylem containing mostly fibriform cells (right, lower two-thirds) and conjunctive tissue (right, upper one-third).—10. Fibriform vessels and (just to right of center) several axial parenchyma cells from near a wider vessel; arrow indicates a pair of circular perforation plates.—11. Axial parenchyma from near a wider vessel; large circular axial parenchyma-to-wider vessel pits at upper left.—12. Intervascular pitting from wider vessel.—13. Wider vessels (right and left) with intervening axial parenchyma cells; the rims of two perforation plates (upper right, lower left) lack borders. (Fig. 9, scale below Fig. 1; Fig. 10–13, scale below Fig. 3.)

cambia" as used above, and envisions origin of these "primary thickening meristems" from "diffuse lateral meristems" (the latter = "lateral meristem" as used above), which Mikesell does not detail. Mikesell (1979) says that *Rivina* has "no primary thickening meristem," perhaps a way of saying that only a single cambium is present in stems and roots. Mikesell (1979) has the concept that the "primary thickening meristem" in interfascicular areas can give rise to "external conjunctive tissue" and "internal conjunctive tissue," concepts that could also be considered ray tissue produced by the successive cambia. However, Mikesell states that, "At isolated locations along the primary thickening meristem in pokeberry, patches of xylem and phloem differentiate from newly produced internal and external conjunctive tissue, respectively." If a cambium produces phloem externally and xylem internally, then the "internal and external conjunctive tissue" in that sentence refer to immature products of a vascular cambium, on their way to becoming phloem and xylem, respectively. Should the term "conjunctive tissue" apply to tissue ("secondary parenchyma") produced by a thickening meristem, and not tissue derived from one of the successive cambia? The central question is not so much terminology, which can be clarified or replaced by better terms, but the interpretation of ontogenetic sequences and development of criteria for those interpretations.

One must agree with Stevenson and Popham (1973) and Mikesell (1979) that the term "interxylary phloem" is a misnomer in instances as in Phytolaccaceae where successive cambia occur, because the phloem is not encased within secondary xylem, but between secondary xylem to the inside (produced by one of the successive cambia) and conjunctive tissue to the outside. Conjunctive tissue is not wood, but "secondary parenchyma" in Gibson's (1994) usage (conjunctive tissue can also be sclerenchyma, however), and thus the phloem cannot be truly interxylary. This issue has been discussed before (Carlquist 1988). Reluctance to accept this treatment may stem from the thought that ontogenetic studies are required in order to apply terms correctly, but woods with a single cambium producing strands of phloem internally are easily distinguished from instances of successive cambium formation without recourse to developmental studies. The term "intraxylary phloem" refers to phloem strands adjacent to pith and is not relevant here.

The occurrence of a multiplicity of types of origin and activity in successive cambia is unlikely. The same basic type probably characterizes other dicotyledons with successive cambia, such as Menispermaceae (Carlquist 1996a), as well as Gnetales (Carlquist 1996b, Carlquist and Robinson 1995).

The successive cambia in *Bougainvillea* produce no rays in fascicular areas (Esau and Cheadle 1969; Ste-

venson and Popham 1977), and *Agdestis* conforms to this pattern also. Interfascicular tissue in *Agdestis* develops sluggish cambial activity or none at all. In these respects, *Agdestis* is unlike *Phytolacca* (Wheat 1997) or other Phytolaccaceae s. l. in which rays are formed actively (Metcalf and Chalk 1950; Gibson 1994; Carlquist, unpubl.). As noted by Gibson (1994), one must take care in citing Metcalfe and Chalk's (1950) account of Phytolaccaceae because data on Gyrostemonaceae have been commingled in their summary of Phytolaccaceae.

Raylessness in *Bougainvillea* and in *Agdestis* might represent either a synapomorphy or a homoplasy; resolution of this will likely come with study of more Nyctaginaceae and more Phytolaccaceae s. l. Another feature by which *Agdestis* differs from Phytolaccaceae s. s. is presence of vasicentric tracheids. *Trichostigma* (Phytolaccaceae) has true tracheids—no libriform fibers are present. Further studies will likely elucidate whether the libriform fibers in *Agdestis* are derived from tracheids, or whether occurrence of libriform fibers in wood of *Agdestis* represents retention of a primitive condition, with the tracheids developed as modifications of narrow vessels.

One of the bases for familial segregation of *Stegnosperma* from Phytolaccaceae is the presence of tracheids in *Stegnosperma* (Bedell 1980). The presence of fibriform vessels, as in *Agdestis*, is seen in some lianas (Carlquist 1985). The presence of vasicentric tracheids is also common in lianas (Carlquist 1985). However, libriform fibers, not tracheids, are present in *Bougainvillea*, which qualifies as a liana. Thus, nature of imperforate tracheary elements is a feature that distinguishes *Agdestis* from Phytolaccaceae s. s. as well as from Nyctaginaceae.

Agdestis has paratracheal scanty axial parenchyma with lignified walls, as do other Caryophyllales (Metcalf and Chalk, 1950; Gibson 1994). However, the presence of strands and tangential bands of thin-walled axial parenchyma with nonlignified walls is a distinctive feature of secondary xylem of *Agdestis*.

Lack of borders on perforation plates occurs in *Agdestis* but also elsewhere in Phytolaccaceae (Carlquist, unpubl.). This feature is quite unusual in dicotyledons, and is most easily interpreted as a synapomorphy, a feature indicating relationship between *Agdestis* and Phytolaccaceae s. s. Another such feature is formed by the idioblastic occurrence of coarse raphides in *Agdestis*, an expression close to the typical raphides of *Phytolacca* and not far from the elongate crystals in wood or stems of several genera of Phytolaccaceae s. s.

In sum, the anatomy and histology of stems of *Agdestis* support the idea that it is a distinctive genus within Phytolaccaceae s. l., but not radically different from the balance of the family. Treatment of *Agdestis* as a monogeneric subfamily of Phytolaccaceae (e.g.,

Thorne, in Cronquist and Thorne 1994) seems a logical treatment at present. Thorne's treatment suggests the diversity of Phytolaccaceae s. l. as stressed by various workers, such as those who contributed to the book edited by Behnke and Mabry (1994).

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