Wood anatomy of selected Cucurbitaceae and its relationship to habit and systematics

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Introduction

Cucurbitaceae are a family often thought to be non-woody. Indeed, Metcalfe & Chalk (1950), who for most families of dicotyledons devote a section to "wood" omit such a section for Cucurbitaceae. There are, however, several Cucurbitaceae that become moderately woody. Four of these have been selected because they represent divergent habits that may form the basis for correlations between habit and wood anatomy. Acanthosicyos horridus Welw, is a shrub of Namibian sand dunes; the lower stem, usually buried beneath the sand, may develop a woody cylinder 1—2 cm in diameter. Apodanthera undulata A. Gray, from arid areas of New Mexico, has a tuber-like storage root; the base of the stem forms a woody transition to this storage organ. Coccinia grandis J. A. Voigt is a rain forest liana although with moderate woodiness (up to about 10 cm in diameter); the stems at my disposal are 5 cm in diameter. Zanonia indica L. is a rain forest vine in which only a limited amount of secondary growth occurs in the vascular bundles. The features of vessels, imperforate tracheary elements, axial parenchyma, ray parenchyma, and variant cambial types are analyzed with respect to habit of these four species. Although Zimmermann's (1922) neglected but magnificent monograph on Cucurbitaceae contains much anatomical information, the wood histology of the family has needed characterization and analysis.

Wood anatomy of Cucurbitaceae is of interest with respect to systematics. Older systems placed Cucurbitaceae in an order such as Campanulales, along a line

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Figs 1-4. Stem sections of *Acanthosicyos horridus* (Carlquist 8086). - Fig. 1. Transection, showing two zones of secondary phloem (plus a few libriform fibers) produced by a cambium abaxial to intraxylary phloem strands in the pith; at top, multiseriate rays begin abruptly in the two fascicular areas. - Fig. 2. Vascular strand formed by cambium abaxial to intraxylary phloem strand; vessels as well as libriform fibers are in the secondary xylem formed by this cambium. - Fig. 3. Transection of secondary xylem from main woody cylinder, to show perforated ray cells (traversing the ray, above and below), sclerified ray cells, and distribution of thin-walled axial parenchyma. - Fig. 4. Tangential section of wood from main woody cylinder; large multiseriate ray at right, portion of one left; storied nature of the thin-walled axial parenchyma evident. - Fig. 1, scale shown above Fig. 1 (finest divisions = 10 um); Figs 2-4, scale shown above Fig. 2 (divisions = 10 um). - Symbols: cam = cambium, lf = libriform fibers, sap = sclerified paratracheal axial parenchyma; sp = secondary phloem; sx = secondary xylem; tap = thin-walled apotracheal axial parenchyma.
Figs 5-8. Wood sections of Cucurbitaceae. — Fig. 5. Acanthosicyos horridus (Carlquist 8086), transection of cambial region to show contrast between cambium in ray area and in fascicular region; sclereids in ray, below. — Fig. 6. Apodanthera undulata (Fosberg 53738), portion of vessel wall from tangential section, to show wide grooves interconnecting pits apertures. — Figs 7-8. Cocinea grandis (J. B. Fisher 88-23). — Fig. 7. Wood transection; ray cambia have produced two pockets of secondary phloem along the fascicular area in which several vessels and associated libriform fibers are present. — Fig. 8. Tangential section; ray in center; storying evident in axial parenchyma. — Figs 5, 7, 8, scale above Fig. 2; Fig. 6, scale above Fig. 6 (divisions = 10 μm). — Symbols: cam = cambium in fascicular area; lf = libriform fibers; rc = cambium in ray area; sap = sclerified paretreachal axial parenchyma; sp = secondary phloem; tap = thin-walled axial parenchyma.
Fig. 9-12. Wood sections of Cucurbitaceae. — Figs 9-10. *Apodanthera undulata* (Fosberg 53738). — Fig. 9. Transection of wood from lower stem, showing vessels of a fascicular area with rays to the right and left of it. — Fig. 10. Portion of tangential section of wood, showing vessel wall (right), axial parenchyma to the left of the vessel wall, and, at left, two libriform fibers. — Figs. 11-12. *Zanonia indica* (Hartley 10037). — Fig. 11. Vascular strand with secondary xylem (large vessels) from transection of stem. — Fig. 12. Portions of vasicentric tracheids, showing large bordered pits, from tangential section of stem. — Figs 9, 11, scale above Fig. 2; Fig. 10, 12, scale above Fig. 1.
Materials and methods

Wood of Cucurbitaceae offers problems for sectioning in two respects: it is softer than most woods sectioned successfully on a sliding microtome, and the large vessels are likely to fracture during sectioning on a sliding microtome. However, the wood of Cucurbitaceae is hard enough so that it cannot be sectioned successfully by the ordinary paraffin methods that involve sectioning with a rotary microtome. An ideal method that solves these problems involves softening of the wood with ethylene diamine, followed by embedding in paraffin and sectioning on a rotary microtome (Carlquist 1982). A very important element in this method is the soaking in water of exposed surfaces of paraffin-embedded material prior to sectioning; sectioning of tissues that have not been subjected to the soaking process is much less effective.

Sections were stained with safranin and fast green. Macerations were prepared by means of Jeffrey's fluid and stained with safranin.

The material of *Acanthosicyos horridus* was collected in Namibia in 1989, thanks to a grant from the American Philosophical Society. Jack Fisher of the Fairchild Tropical Garden kindly provided the material of *Coccinia grandis*. Material of both of these species was fixed in formalin acetic alcohol. Material of the two other species was dried, and was obtained from specimens in the herbarium of the Rancho Santa Ana Botanic Garden; this material was soaked in water prior to the microtechnique methods mentioned above.

The terms used are according to the IAWA Committee on Nomenclature (1964). The term “vasicentric tracheid” and terms for cambial variants are as in Carlquist (1988); I believe that these usages reflect the intent of the AIWA Committee on Nomenclature (1964), but because few wood anatomists at that time were familiar with these phenomena, the definitions given there for these terms were vague and incomplete. Vessel diameter in the descriptions is computed as lumen diameter at widest point. Very narrow vessels that are similar to vasicentric tracheids and cannot be readily identified in transections are not included in the figures on vessel diameter. Number of vessels per mm² is not computed for Cucurbitaceae because the amount of ray tissue and axial parenchyma differs so much from one species to another or one part of the plant to another, so that calculations do not readily reveal the nature of the wood. Obviously, vessel density drops markedly in the highly parenchymatous stems and roots in which storage of carbohydrates and water is prominent.

Anatomical descriptions

*Acanthosicyos horridus*

Secondary xylem produced by growth that increases the radial extent of the bundles of the primary stem as well as by cambial action adjacent to the strands of intraxylary phloem. Growth rings absent, although mild fluctuation in diameter of vessels evident (Fig. 3). Vessels mostly solitary (Figs 1, 3); mean number of vessels per group, 1.32. Mean diameter of vessels, 128 μm. Mean vessel element length, 89 μm. Mean vessel wall thickness, 5.2 μm. Perforation plates simple. Lateral wall pitting of vessels alternate; pits 6—9 μm in diameter. Pit apertures elliptical or wider; when wider, forming grooves that interconnect pit apertures. Narrow vessels and vasicentric tracheids, often with distorted shapes that are variously rectangular in longitudinal section present, interconnecting vessels or vessel groups radially. All other imperforate tracheary elements are separate libriform fibers with simple pit s. Mean libriform fiber length, 539 μm. Mean libriform fiber diameter at widest point, 32 μm. Mean libriform fiber wall thickness, 5.2 μm. Axial parenchyma of two types: paratracheal thick-walled lignified cells (“sap” in Fig. 4) and thin-walled nonlignified cells that are clearly storied in tangential sections (“tap” in Fig. 3, 4). Paratracheal parenchyma cells distorted in shape by vessel enlargement; pits of paratracheal parenchyma cells bordered (bordered pit pairs) facing vessels, but pits simple on other walls. Thin walled axial parenchyma cells present as variously shaped bands or patches as seen in transection (Figs 3, 5), but fusiform or, less commonly, in strands or two cells as seen in longitudinal section (Fig. 4). Rays all multiseriate, averaging more than 10 cells wide at their widest point (Fig. 4, left and right). A few multiseriate rays originate not by widening of narrow rays, but suddenly (Fig. 1, upper left and upper right). Ray cells predominantly upright; very few square or procumbent cells present. Ray cells thin walled or sclereids; the sclereids isolated or in groups (Fig. 4, upper left, lower right; Fig. 5). Sclerotic ray cells with bordered pits. Storying evident in axial parenchyma and some vessels. Tyloses present in many vessels (Fig. 2, upper left; Fig. 3, upper center).

The strands of intraxylary phloem in *Acanthosicyos horridus* develop at their adaxial faces cambia that produce secondary phloem abaxially and secondary xylem adaxially—an orientation contrary to that produced from a “normal” cambium (Figs 1, 2). The strands produced by the cambium adjacent to intraxylary phloem in Fig. 1 contain mostly secondary phloem, with secondary xy-
lem only as a few libriform fibers. The strand shown in Fig. 2 is characterized by addition of a few vessels as well as libriform fibers. Phloem fibers demarcate the innermost margin of the phloem in these strands (Figs 1, 2), and crushed phloem cells can be found in the older phloem tissue of the strands. There are perforated ray cells in Acanthosicyos horridus, evident by a series of vessel elements derived from ray initials traversing ray areas (Fig. 3, center above and center below). The cambium of the main vascular cylinder shows marked differences between the axial and ray areas (Fig. 5). The ray cambium (“rc”) consists of slow-paced divisions: few but large cells are added to secondary xylem rays and secondary phloem rays in contrast to the numerous narrow cells added by the actively dividing cambium of the axial zones (“cam”).

**Apodanthera undulata**

Wood of lower stem described unless otherwise noted. Wood consisting of plates of vessels (Fig. 9), vessels and their associated lignified paratracheal parenchyma separated from each other by thin-walled parenchyma in the upper root. Vessels solitary (Fig. 9). Mean vessel diameter, 141 μm. Mean vessel element length, 75 μm. Mean vessel wall thickness, 5.4 μm. Perforation plates simple. Lateral wall pitting of vessels consisting of basically alternate circular pits. The shape and arrangement of the pits is altered somewhat by the presence of wide pit apertures which are interconnected by grooves, or coalescent pit apertures (Fig. 6). Wall portions between the horizontal rows of pits are notably thick (Fig. 6; thickenings seen in sectional view, Fig. 10). Vasicentric tracheids are absent. All imperforate tracheary elements are septate libriform fibers with simple pits (Fig. 10, left). Libriform fibers in small numbers are adjacent to some vessels in the lower stem, but are absent from roots. Axial parenchyma of two sorts: lignified thick-walled paratracheal, and nonlignified thin-walled apotracheal. The paratracheal parenchyma forms sheaths two to four cells thick around the vessels (Fig. 9). The thin-walled apotracheal parenchyma forms the ground tissue of the secondary xylem (other than vessels, paratracheal parenchyma), and the very few libriform fibers) and is much more abundant in the root than in the stem base. Apotracheal parenchyma is storied. Rays are all multiseriate, averaging more than 10 cells wide at their widest point. The multiseriate rays are essentially extensions of primary rays. Ray cells are predominantly upright, square or procumbent cells few. All ray cells are thin walled and nonlignified. Tyloses in some vessels.

The gray patches to the left and right of the vessels, lower left, in Fig. 9 are areas of phloem crushed as a result of addition of secondary phloem by ray cambia in much the same fashion as described for Coccinia grandis below. The lignified parenchyma just to the left of the vessel, Fig. 10, appears subdivided into a series of oval cells. In fact, fewer cells than appear present occur here. The vertical walls of the parenchyma cells immediately outside of the vessel are much lobed; a longitudinal section of these interfering lobes results in the appearance shown. The lobed nature of axial parenchyma cells facing vessels was illustrated for Cucurbitaceae by Zimmermann (1922) for wood of Peponium.

**Coccinia grandis**

Secondary xylem in plates representing extensions of the primary stem. Vessels mostly solitary (Fig. 7); mean number of vessels per group, 1.13. Mean vessel diameter, 195 μm. Mean vessel element length, 73 μm. Mean vessel wall thickness, 3.8 μm. Perforation polates simple. Pits of lateral vessel walls alternate, circular, 5-8 μm in diameter, apertures slitlike, some interconnected by grooves. Imperforate tracheary elements consisting of libriform fibers in the vicinity of vessels (“lf” in Figs 7, 8). Libriform fibers sepaete, pits simple. Libriform fibers forming an aliform or paratracheal arrangement with relation to vessels as seen in transverse section, often forming a pair of lateral bands flanking a vessel. Vasicentric tracheids often rectangular in longitudinal section, but variously shape, forming radial interconnections between vessels. Axial parenchyma of two sorts: lignified thick-walled paratracheal, and nonlignified thin-walled apotracheal. The paratracheal parenchyma (Figs 7, 8) forms sheaths two to four cells thick around the vessels. The cells adjacent to the vessels have undulate walls as seen in longitudinal section (Fig. 8, “sap”). Apotracheal parenchyma in the form of bands or variously shaped patches between vessels (and their associated libriform fibers) as seen in transverse section, storied as seen in longitudinal section (Fig. 8, “tap”). Apotracheal parenchyma cells mostly not subdivided, but some cells in strands of two cells. Rays all multiseriate, averaging more than 10 cells wide at their widest points. Ray cells predominantly upright, few square or procumbent cells present. Ray cells all thin walled (Figs 7, 8). Paratracheal axial parenchyma and some vessels conforming to the storied pattern. Tyloses present in some vessels; starch seen in some tyloses.

Ray cambium (term from Carlquist & Hanson, 1991) form along the margins of rays and add, at first, secondary phloem (“sp,” Fig. 7). My material did not show secondary xylem formed by the ray cambia, but Zimmermann (1952) does figure secondary xylem as well as secondary phloem formed by ray cambia in Coccinia engleri; secondary phloem on the distal (ray) side of the cambia, secondary xylem on the proximal side.

**Zanonia indica**

Secondary xylem representing extensions of the primary bundles (in Fig. 11, probably the five largest vessels and
associated imperforate tracheary elements are secondary xylem, the zone with the smaller vessels is primary xylem). Secondary xylem vessels mostly solitary; mean number of vessels per group, 1.10. Mean vessel diameter, 141 \textmu m. Mean vessel element length, 92 \textmu m. Mean vessel wall thickness, 5.0 \textmu m. Imperforate tracheary elements consisting of libriform fibers with simple pits and fusiform vasicentric tracheids (Fig. 12); in my material, the vasicentric tracheids are more abundant than the libriform fibers. Axial parenchyma of two sorts: paratracheal cells with thick lignified walls, and aprotarchal cells with thin nonlignified walls. Paratracheal parenchyma forming a sheath one to three cells thick around vessels. Axial parenchyma present only as strands near the periphery of the vascular strands; the aprotarchal parenchyma is evident as indentations in the outline of the vascular strand shown in Fig. 11. Paratracheal parenchyma either not subdivided or in strands of two cells. Little secondary growth present in ray areas, which are little more than the primary rays, compressed somewhat by the expansion of the vascular bundles by their secondary xylem additions (Fig. 11).

Conclusions about wood histology and its relation to habit

The various features of the wood of Cucurbitaceae can almost all be related, directly or indirectly, to the scandent habit characteristic of the vast majority of the species. The wood feature most often cited as characteristic of scandent plants is wide vessel diameter, which tends to compensate for the small transectional area of secondary xylem (considering the amount of foliage supplied) in climbing plants (see literature cited in Carlquist 1985b). Cucurbitaceae are notable for wide mean lumen diameter (average of the four species, 164 \textmu m). Note should be taken that narrow vessels, comparable in diameter to vasicentric tracheids, were not included in vessel diameter measurements in Acanthosicyos horridus or Coccinia grandis because in transection narrow vessels cannot readily be distinguished from libriform fibers. The vessel elements in the Cucurbitaceae surveyed here are notable for having greater average diameter than length (average length for the four species, 82 \textmu m, exactly half the average vessel diameter of the four species). The shortness of vessel elements is primarily an expression of the high degree of specialization of wood features in Cucurbitaceae. The wall thickness of vessels in the species studied (mean = 4.9 \textmu m) is approximately twice the thickness typical in dicotyledons as a whole. Thick vessel walls seem related to the great diameter of the vessels. The band-like thickenings on vessel walls (Fig. 10) may be another indication of enhanced wall strength that compensates the great diameter of the vessels in woods of vines. The abundance of parenchyma in wood of scandent plants has been cited as a feature that may, by virtue of the flexibility parenchyma confers, protect large and therefore vulnerable vessels against torsion (Carlquist 1985b, 1991; Putz & Holbrook 1991). The stems of Zanonia (Fig. 11) are understandable in this regard: the strands of secondary xylem are arranged in background of soft parenchyma, and the vessels are sheathed in thick walled libriform fibers and vasicentric tracheids.

The dimorphism of axial parenchyma in woods of Cucurbitaceae studied here, as well as those described by Zimmermann (1922), may be correlated to the scandent habit. The lignified thick walls of the paratracheal parenchyma may prevent damage to vessels by enhancing their mechanical strength while the patches of thin-walled aprotarchal parenchyma may offer enhanced flexibility to the stem and may thereby protect vessels when torsion occurs. The wide, tall rays composed of thin-walled parenchyma in Cucurbitaceae, like those in woods of other scandent plant, may be of greater significance than axial parenchyma by offering a tissue that can yield to twisting and protect the plates of axial xylem (which include vessels) against fracture. Perhaps quite significant in this regard is that the only new rays initiated in Cucurbitaceae are wide and tall (Fig. 1), an unusual mode of ray origin because in most dicotyledons, rays originate as narrow (often uniseriate) and gradually widen ontogenetically. Exactly the same phenomenon of sudden origin of wide, tall rays from the cambium occurs in another family with a similar range of habits, Aristolochiaceae (Carlquist, unpubl.). These examples, in turn, remind one of the overrepresentation of successive cambia and other cambial variants that provide abundance of parenchyma in lianoid dicotyledons (for listing, see Carlquist 1991). The distribution of libriform fibers in Coccinia grandis (Fig. 7) suggests enhanced strength and protection of the integrity of vessels without loss of flexibility in stems.

The presence of vasicentric tracheids was reported earlier in Zanonia (Carlquist 1985); they are abundant in secondary xylem of this species. Vasicentric tracheids are less abundant in Acanthosicyos horridus and Coccinia grandis, and are similar enough in transection to narrow vessels and libriform fibers so that the vasicentric tracheids could not be illustrated photographically so as to distinguish them from these other cell types. The distribution of vasicentric tracheids in Acanthosicyos horridus and Coccinia grandis is much like that figured by Zimmermann (1922) for the secondary xylem of Peponium: radial plates of vasicentric tracheids wind through the radial bands of secondary xylem, interconnecting vessels. Note should be taken that narrow vessels may be intermixed with these vasicentric tracheids, but probably have much the same physiological significance. The interconnection of vessels by means of vasicentric tracheids in lianoid woods was cited earlier as a structural mode potentially offering conductive safety in that conductive pathways could be maintained even if particular vessels were embolized (Carlquist 1985,
of occurrence of successive cambia. The three cambial variants may have similar topographic and physiological significance: providing strands of vascular tissue that do not increase the thickness of a single woody cylinder but, instead, form vascular strands separate from the main cylinder. The net effect appears to be provision of a greater flexibility by means of dispersion of vascular strands in a background of soft parenchyma likely to protect the integrity of vascular tissues during torsion (Carlquist 1985b, 1991; Putz & Holbrook 1991).

Systematic conclusions

If Cucurbitaceae belong to Violales, as modern phylogenetic systems claim, the family is different from most others in the order in its vining and lianoid habit. Passifloraceae are the only other violaceous family in which these habits are common. Obviously, wood features that represent modifications of the wood plan to suit the scandent habit cannot be used to construe relationships of Cucurbitaceae. Wood features of Cucurbitaceae worthy of consideration as indicators of relationship are: septate libriform fibers; vasicentric tracheids; and storying of wood. In the following listings, only families commonly assigned to Violales according to the phylogenetic systems cited in the Introduction are mentioned. Septate libriform fibers are found in Begoniaceae, Flacourtiaeae, Lacistemaceae, Passifloraceae, and Violaceae (Carlquist 1988); all families of Violales possess the three features cited, however. This distribution provides sufficient resemblance among the families so that each of these features should be considered as potential indications of relationship. None of the three features cited characterizes the majority of families of dicotyledons; widespread features (e.g., simple perforation plates) are not good indicators of relationship.

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