Successive cambia revisited: ontogeny, histology, diversity, and functional significance

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CARLQUIST, S. (Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105). Successive cambia revisited: ontogeny, histology, diversity, and functional significance. J. Torrey Bot. Soc. 134: 301–332. 2007.—Plant anatomists are generally agreed on the histological products of successive cambia: bands of secondary phloem and associated secondary xylem (“vascular increments”) embedded in a background of conjunctive tissue (parenchyma, sometimes fibers). Interpretations have varied widely on the ontogeny of this plan. Studies have usually involved one or a few species. The study of numerous taxa, especially in centrospermoid families, leads to the conclusion that there is a common plan, although variations on it are manifold. A master cambium produces secondary cortex externally and, internally, rays, conjunctive tissue, vascular cambia, secondary phloem, and secondary xylem. Secondary phloem and especially in centrospermoid families, leads to the conclusion that there is a common plan, although variations on it are manifold. A master cambium produces secondary cortex externally and, internally, rays, conjunctive tissue, vascular cambia, secondary phloem, and secondary xylem. Secondary phloem and secondary xylem are formed from the vascular cambium in each vascular increment. Vascular cambia function indefinitely, so that a master cambium and a series of vascular cambia (each in a vascular increment) function indefinitely. The master cambium either remains active as long as an axis is actively growing (although it may become quiescent following the initiation of each vascular increment and associated conjunctive tissue), or, less commonly, may be reinvented in the secondary cortex. In order to establish a framework for interpretations, the varied appearances of each of these tissues in genera that have successive cambia is discussed. Themes that particular genera represent are then examined: diversification in ray types and raylessness (Nycataginaceae); diversification in conjunctive tissue (Aizoaceae); rays as key structural elements (Cinetaceae); successive cambia as an apomorphy (Chrysanthenoides); protraction of cambial activity (Menispermaceae); and cambial fracture and parenchyma proliferation (Bauhinia, Mendencia). In some taxa, such as Gnetum africanum and the large tropical lianas (Bauhinia, Menispermaceae) a master cambium is absent; new vascular cambia arise by one or a few cell divisions in cortical parenchyma, followed by rapid tangential widening of the vascular cambium. Pervasive ecophysiological themes in plants with successive cambia are examined: storage and retrieval; promotion of mechanical strength and longevity of vascular tissues; and modes of lianoid structure. Because the background tissue in plants with successive cambia is conjunctive tissue, not secondary xylem, the terms “included phloem” and “interxylary phloem” are inapplicable. The term “lateral meristem” is abandoned in favor of “master cambium.”

Key words: anomalous secondary growth, cambial variants, Caryophyllales, Centrospermae, interxylary phloem, lateral meristem, lianas, master cambium.

Successive cambia are familiar as the cause of concentric rings in a beet. They also occur in stems and roots of such familiar plants as Amaranthus, Atriplex, Bougainvillea, Chenopodium, Cycas, Mirabilis, Phytolacca, and Welwitschia. They occur in the flattened or variously shaped forms of the giant lianoid stems of Bauhinia, Gnetum, and numerous Menispermaceae. Successive cambia occur in bands or strands of secondary phloem and secondary xylem (vascular increments), which are embedded in a background of parenchyma or fibers (conjunctive tissue). Schenck (1893) and Pfeiffer (1926) used the term; the latter accurately applied it to many of the genera in which the phenomenon is known today. Others have referred to successive cambia under the vague terms “anomalous secondary thickening” or “included phloem.” The secondary phloem of successive cambia is not included within wood at all, a point made by Stevenson and Popham (1973). Maintenance of such terms may have been furthered by those who are involved with wood identification (IAWA Committee 1989) and who therefore want simple terms. The distinctive appearance of successive cambia and their products can easily be learned by wood anatomists, however. The desire to use such a term as “included phloem” probably indicates a desire to consider the background tissue of plants with successive cambia as “wood,” but although often woody in texture, this background tissue is not wood in the ordinary sense. Wood anatomists who have dealt in detail with plants with successive cambia have used the term conjunctive tissue for the background of fibers and/or parenchyma in which vascular increments are embedded.

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Terminology is only one symptom of the problems involved in analysis of successive cambia and their products. Although various authors describe the histology of species involved with reasonable accuracy, understanding of the ontogeny of successive cambia has been troublesome. One cause is that soft and hard tissues are intermixed in stems and roots with successive cambia. Soft tissues and stages in their development are frequently damaged and uninterpretable when such axes are sectioned untreated on a sliding microscope. One solution to this problem is the use of a softening agent followed by paraffin embedding and sectioning on a sliding microscope (Carlquist 1982). This is best applied to liquid-preserved material. With material from xylaria, the drying process has damaged soft tissues prior to sectioning. Unfortunately, xylaria have served as a primary basis for materials studied by wood anatomists. However, once liquid-preserved materials have been studied successfully, the appearances of those materials based on dried specimens can be interpreted successfully. All of the illustrations in the present study are based on liquid-preserved materials.

A third cause of misinterpretation can be likened to the parable of the blind men and the elephant. Most wood anatomists who have looked at successive cambia have studied only a single genus, sometimes only a single species. Although I believe, as obviously did Pfeiffer (1926), that a common plan underlies the various cases, the differences in expression when one looks at such extremes as Stayneria, Gnetum africatum, or Mendocia may offer problems in interpretation. Over the past 25 years, I have attempted to analyze instances of successive cambia in most clades in which they occur. The value of comparative studies is, I believe, considerable in providing necessary insights.

The complexity of wood produced by a single (“normal”) cambium is daunting, so neglect of successive cambia, which represent an intricate series of histological phenomena, has become commonplace. This is unfortunate, because successive cambia occur in a wide diversity of plants, and represent a fascinating alternative pathway of secondary growth. Successive cambia are known in 34 families of dicotyledons (Carlquist 2001; number of families varies with taxonomic practice). Although the caryophyllalean families (especially the “centropermoid” families) form a prominent nexus on the list, successive cambia must have arisen in about 15 other clades. Welwitschia and all species of Gnetum (Carlquist 1996a) contain successive cambia, and they have been reported in several species in each of the cycad genera Cycas, Encephalartos, and Macrozamia (Greguss 1968). The listing of successive cambia genera represents a small proportion of vascular plants at large, but it poses an evolutionary question out of proportion to numbers: why should this mode of structure have been evolved repeatedly, and what are its adaptive values? The picture of how successive cambia arise evolutionarily and how they are correlated with particular modes of habit, ecology, and physiology has been blocked by failure to understand the ontogeny of these histological systems. Various ontogenetic interpretations have led to thickets of terminology and controversy, which in turn have led to marginalization and avoidance of successive cambia in plant anatomical studies and teaching.

In order to counter widespread neglect, I am attempting to present a template for how successive cambia at large originate and operate. A consistent terminology that can be uniformly applied is offered. Interpretations together with the evidence for them are offered. Those who wish more extensive citations of literature on successive cambia can consult Stevenson and Popham (1973), Costea and DeMason (2001), and Carlquist (2001).

The concept of successive cambia differs from manifestations that are called “interxylary phloem formed from a single cambium” (Carlquist 2001). These instances occur in such groups as Combretaceae (van Vliet 1979), Onagraceae (Carlquist 1975a), and Strychos and allied genera of Loganiaceae (Cockrell 1941, Mennega 1980). Interxylary phloem strands or bands formed from a single cambium do not form pairwise relationship to strands or bands of vessels or vessel groups; the vessels are distributed within secondary xylem. In instances of successive cambia, the strands or bands of secondary phloem occur external to strands or bands of secondary xylem, respectively. These strands or bands, considered vascular increments here, are separated from each other by conjunctive tissue. Because conjunctive tissue is not secondary xylem, the term “interxylary” is not permissi-
ble in plants with successive cambia. This fact was noted by Stevenson and Popham (1973) and others.

Materials and Methods. Comments on Forchhammeria (Brassicaceae) are based on my unpublished data; work on the stem anatomy of this genus is in progress. The slides of Bougainvillea spectabilis were given to me by Vernon I. Cheadle. They represent the slide set on which the paper by Esau and Cheadle (1969) was based. With the exception of these materials, specimens and nomenclature representing the taxa mentioned below are cited in the following papers: Carlquist 1966, 1981, 1995, 1996a, 1996b, 1999a, 1999b, 1999c, 2000, 2002, 2003, 2004, 2007; Carlquist and Robinson 1995; Carlquist and Zona 1988. The microtechnical methods used and documentation of the specimens studied can be found in those papers. Most of the photographs in the present study represent new photomicrographs based on the slides prepared for those studies. Liquid-preserved material was used for most of the species illustrated; exceptions occur in Gnetum schwackeanum and Mendoncia giga., which were studied on the basis of xylarium specimens.

Terminology is similar to that in Carlquist (2004), except that "master cambium" is substituted for the relatively vague "lateral meristem" used in that study. Because interpretations and thus terminology have been so varied, terms and synonyms of them are explained in the contexts below. On photomicrographs, the "pointers" (,<, >) indicate master cambia, whereas arrows indicate vascular cambia. The term "vascular cambium" is used in a restricted sense here: a meristematic layer that produces phloem to the outside and xylem to the inside; this usage excludes production of conjunctive tissue from a vascular cambium. A vascular cambium can include ray initials and produce phloem rays and xylem rays. In some instances, as in Pisonia, rays are produced by the master cambium.

Ontogeny and Products of Successive Cambia

The drawings in Fig. 1 represent a series of stages beginning with the origin of what is termed the master cambium here. This series of drawings is designed to introduce concepts and developmental stages. These present a generalized plan, many features of which are observable in the species discussed. Because it is a generalized plan, any given genus will depart in various ways, discussed below.

As far as is known, the first vascular cambium in species with successive cambia produces secondary xylem and secondary phloem in the same fashion as does the vascular cambium in vascular plant species that have only a single vascular cambium during the secondary growth of stems or roots. The master cambium forms from a periclinal division in cortical cells of stems (pericycle in roots). Although a single cortical cell is shown in Fig 1A, divisions in a series of cortical cells form a band of indefinite circumference, or a cylinder around the entire axis (Kirchoff and Fahn 1984). There has been general agreement about this since De Bary (1884). The parenchyma between the secondary phloem of the first vascular cylinder and the master cambium is parenchyma from the primary cortex (in stems). Conjunctive tissue is produced from the master cambium, as shown by the radial alignment of its cell files. Conjunctive tissue is not formed adjacent to the first vascular cylinder, but is formed interior to each subsequent vascular increment. Conjunctive tissue is easily distinguished from cortical parenchyma not only because conjunctive tissue is in radial rows but because cortical parenchyma cells are wider in diameter (Fig. 22). Note should be taken that after origin of the master cambium, each vascular cambium continues to add secondary xylem and secondary phloem to its own vascular increment. Secondary xylem and secondary phloem continue to be added to the original vascular cylinder (see lower row of drawings in Fig. 1). The master cambium and an indefinite number of the vascular cambia coexist. The master cambium may be active or quiescent at any given time. In some cases a master cambium may be reinvented further out in the cortex or (more likely) secondary cortex, but this is considered less common than maintenance of the master cambium at its original site. Secondary cortex (identifiable by its radial lines of cells) is produced externally by the master cambium.

The Master Cambium. The term master cambium is offered here hesitantly. A plethora of terms for this layer is encountered, including anomalous cambium, lateral meristem, primary thickening meristem, second
The origin of the master cambium is seen in a hypothetical stem transection, followed by stages in the production of cell types (including a vascular cambium produced from that master cambium). Stage H represents a stage just prior to origin of a second vascular cambium from the master cambium. The drawings in the lower row are schematic and indicate the location of the cellular progressions depicted in the upper row. This series of drawings, although based on centrospermoid genera with rays such as Charpentieria and Stegnosperma, is intended for orientation purposes and may not correspond in detail to what is observed in any given species. Labels: c = cortex, ct = conjunctive tissue, mc = master cambium, pd = periderm, pp = primary phloem, pr = primary ray, r = ray, rc = ray cambium, sc = secondary cortex, sp = secondary phloem, sx = secondary xylem, vc = vascular cambium.

Cambium, and supernumerary cambium. Perhaps even more dangerous is to refer to this layer merely as "cambium," as Esau and Cheadle (1969) do. Esau and Cheadle (1969) use the terms "old cambium" and "new cambium" in Bougainvillea, not realizing that the master cambium and the vascular cambium (which may correspond to their "old" and "new" cambia respectively) have quite different extents and actions. Esau and Cheadle (1969) contrast their use of the term vascular cambium with the results of other workers. In
fact, Esau and Cheadle (1969) are inconsistent, because they claim that a vascular cambium (in plants with successive cambia) produces phloem to the outside and xylem to the inside (p. 807), but later state (p. 815) that each of the “cambia” produces “xylem and conjunc­tive tissue to the inside and phloem and conjunctive tissue to the outside.” Esau and Cheadle (1969) attempt to contrast their interpretation with that of workers (e.g., Studholme and Philipson 1966) who find that there is a “self-perpetuating meristematic zone.” This pervasive contrast is unjustified. The concept of a master cambium giving rise to conjunctive tissue and vascular cambia internally is the concept that consistently explains what is observed in diverse centro­spermoid Caryophyllales and most other cases.
Figs. 2–5. Transections of stems. Figs. 2–3, Stegnosperma halimifolium (Stegnospermaceae). Fig. 2. A zone that includes cortical sclereids and the products of two vascular increments; note that the older increment has accumulated more secondary xylem than the upper. Fig. 3. Area showing secondary cortex, a master cambium, and tissues produced by the most recently formed vascular cambium. Figs. 4–5. Bougainvillea spectabilis (Nyctaginaceae). Fig. 4. Area near the outside of the stem, showing the coexistence of a master cambium (several recent divisions to the right of the pointer) and a vascular cambium. Fig. 5. An
In the examples cited here, a master cambium is lacking only in *Gnetum africanum* and the large tropical lianas, such as *Bauhinia*. These lianas show rapid lateral widening of vascular cambia; they also show proliferation of parenchyma that form sites for initiation of new cambia. The important feature to be noted is that two types of cambial action in a single stem are envisioned in the present paper (as in earlier work, Carlquist 2004), whereas those who have dealt with successive cambia mostly have attempted to think in terms of a single type of cambium.

The master cambium is most easily visible when actively dividing (Figs. 3, 24). The radial rows of conjunctive tissue between a master cambium and the preceding vascular increment (ct. Fig. 22) make the master cambium readily distinguishable. If the master cambium is actively dividing, it may appear to consist of several layers. The term “diffuse lateral meristem,” inadvisably applied to this phenomenon, was used earlier (Carlquist 2001). The concept presented here is that the master cambium is functionally a single layer in thickness. As in an “ordinary” vascular cambium in most woody plants, the sequence of products is not disorderly—a fact, together with radial alignment of cells and observations on cambium in winter condition, that has led to the idea that a vascular cambium is a single cell in thickness. In some species with successive cambia, a master cambium never ceases to function. Although the occurrence of marked discontinuity in radial cell alignment in some axes and stems may be evidence that one master cambium has ceased to function and a new one has formed. In most species, however, the master cambium apparently functions over a long period of time. It can become quiescent, and after being quiescent, may regain activity, a condition shown in Fig. 1. In most species with successive cambia, the master cambium does not relocate; this concept is in contrast to the idea that the [master] cambium “moves outward” as expressed by several authors, such as Costea and DeMason (2001). There may be exceptions in some lianas, such as *Gnetum africanum* (Figs. 28, 29) and *Mendoncia* (Figs. 32, 33), in which new master cambia do form de novo in cortical cells.

In some species, the constraints imposed by the existence of a cylinder of cortical fibers prevents origin of a master cambium further outwards. This is shown clearly (Fig. 27, upper right). In this instance, one may regard the master cambium as the outermost layer of thin-walled cells shown. In that case, no secondary cortical cells are produced. Esau and Cheadle (1969) and Costea and DeMason (2001) devote much space to a discussion of whether a “cambium” is bidirectional or unidirectional. The confusion on which such discussions are based may relate to varied concepts of what cells a master cambium produces outwardly, but more likely the cause is a conflation of a master cambium and a vascular cambium and their products before two types of cambia were recognized. Esau and Cheadle (1969) claimed that their study of *Bougainvillea* “revealed no uniform continuous perpetuation of a meristematic zone. Instead, a sequence of cambia were found arising outside each successive growth increment.” This statement is at odds with what is seen in *Pisonia* and allied genera, also of Nyctaginaceae (Carlquist 2004). Esau and Cheadle (1969) claim that conjunctive tissue is an abaxial product of each “successive cambium” (which they say also produces conjunctive tissue inwardly). The origin of each “successive growth increment” in such alleged outer conjunctive tissue is at odds with the histology. Esau and Cheadle (1959, Plate 2A) show this tissue to consist of raphide idioblasts and of parenchyma cells subdivided transversely into strands of several cells. My study of the Cheadle slides confirms the histological nature of this tissue (which I would call secondary cortex). Obviously, the fusiform cells from which both the master cambium and the vascular cambium are composed in *Bougainvillea* could not have their origins in such a tissue.
Figs. 6–9. Tangential (Figs. 6–8) and radial (Fig. 9) sections of stems. Figs. 6–7 *Bougainvillea spectabilis* (Nyctaginaceae). Fig. 6. Section from a relatively small (ca. 1 cm diameter) stem, showing secondary phloem (at right) and secondary xylem (left) from a vascular increment. Fig. 7. Section from a relatively large (ca. 16 cm diameter) stem showing rays (center) and other tissues of a vascular increment. Fig. 8. *Heimerliodendron brunonianum* (Nyctaginaceae), showing rayless condition, with a single vessel traversing the fibrous xylem. Fig. 9. *Nototrichium sandwicense* (Amaranthaceae), showing that vessel elements and
In some species with successive cambia, the long and clearly radially aligned files of cells demonstrate the existence of a master cambium with prolonged activity. The long radial series of cells that are figured by Lev-Yadun and Aloni (1991) for Suaeda suggest this. Other examples are shown here in the cases of Pisonia (Fig. 10), Guapira (Figs. 12, 13), and Stayneria (Fig. 25). There is probably little or no quiescence in the activity of the master cambium of these species, in keeping with the relatively nonseasonal nature of their habitats. The vascular cambia are active in these at the same time that the master cambium is active, so that these above examples form strong evidence for the co-existence of two types of cambia. 

Pisonia forms a critical example, because the illustration by Solereder (1899, 1908; reproduced in Metcalfe and Chalk 1950, p. 1064) for Pisonia nigricans Swartz, which is much like the material studied here for P. rotundata, cannot be explained in terms of the action of a single cambium. Solereder's illustration has never received the comment and interpretation it so obviously invites. There are a few flaws in the illustration: crushed secondary phloem is not shown (and therefore the action of vascular cambia in producing secondary xylem and secondary phloem is not illustrated), and there should be radial alignment of the fibers with the immature cells between fibers and the master cambium (see Fig. 17). But the central issue at hand is clearly figured by Solereder: there is a master cambium that extends around the stem: it produces rays, vascular cambia, and most of the fibers internally. The strands of vessels and associated phloem (Fig. 17) contain vascular cambia, a feature not considered by Solereder: these produce phloem externally and vessels and fibers associated with the vessels internally. Although the master cambium extends around the stem, the vascular cambia are narrow strips, each perhaps 10-12 cells wide tangentially. Because the background of the stem is fibrous, few if any vessels are added by any given vascular cambium once the fibers have matured around a given vascular increment. Secondary phloem is added by each vascular cambium, as is seen by crushing of earlier-formed secondary phloem and a degree of compression of the arcs of parenchyma cells exterior to the secondary phloem.

Vascular Cambium. A vascular cambium originates from a master cambium which can, in the process, retain its own identity (Fig. 1D as in Pisonia and allied genera). The criterion for the origin of a vascular cambium here is no different from that in most vascular plants: cells are produced externally and internally, and these products mature into identifiable mature cell types. At the point indicated, division of an initial cell into a sieve tube element and a companion cell is evident (Fig. 15; the letters po are superimposed over these cells). The cell below those is a vascular cambium cell. In addition, the cell below the vascular cambium cell is probably an immature conjunctive tissue cell. Divisions leading to the formation of a sieve tube element and a companion cell are evident (Fig. 15; the letters po are superimposed over these cells). The cell below those is a vascular cambium cell. In addition, the cell below the vascular cambium cell is probably an immature conjunctive tissue cell. Divisions leading to the formation of a sieve tube element and a companion cell are readily evident because of the narrowness of phloem cells: production of conjunctive tissue is not so easily ascertained. The master cambium has produced conjunctive tissue initials before the origin of sieve tube elements. An anticlinal division is implicated in the origin of a vascular cambium (Fig. 1D). This is shown in photomicrographs in (Fig. 15, the three pairs of files above the letter d; Fig. 29). Why should one expect an anticlinal division?

The master cambium cells, because they are initiated by periclinal divisions in cortical parenchyma cells, tend to have tangential cell widths like those of such parent parenchyma cells. Phloem cells and xylem cells, in accordance with their functional nature, tend to be cells much narrower than parenchyma cells. Thus, for a vascular cambium to produce xylem and phloem, periclinal divisions must occur (Fig. 1D). We find, in fact, that the number of files of vascular cambium cells and derivatives thereof is greater than the number of files of master cambium cells and deriva-

conjunctive tissue, and sieve elements have similar lengths, although some files of conjunctive tissue subdivide. Labels: ct = conjunctive tissue, fx = fibrous xylem, jr = juvenilistic (paedomorphic) ray, pb = band of axial parenchyma, sp = secondary phloem, v = vessel. Figs. 6-8, scale in Fig. 2; Fig. 8, scale in Fig. 3.
FIGS. 10–13. Sections of stems of Nyctaginaceae. Figs. 10–11. *Pisonia rotundata*. Fig. 10. Transection, showing three vascular increments in a fibrous background. Fig. 11. Tangential section, showing vessel (far left), uniseriate rays, and a biseriate ray (lower right) in a background of fibrous tissue. Figs. 12–13. *Guapira discolor*. Transections from a large stem (ca. 4 cm diameter). Fig. 12. Area showing three vascular increments; five fibers delimit primary cortex, outside of stem (top), from secondary cortex. Fig. 13. Area from cortex (top) to secondary xylem of outermost vascular increment. Labels: c = primary cortex, ctf =
tives thereof—often two times as great. For example, in Stegnosperma (Fig. 3), the ratio of vascular cambium cells to master cambium cells in the area shown is about 18:11; in Heimerliodendron (Fig. 14) about 17:11. One must be careful not to count fiber tips (which are intrusive, of course) in estimating the number of cells in the vascular cambium and its derivatives. The process of conversion of master cambium derivatives to vascular cambium initials has not been mentioned in the literature, evidently because authors have depended on the concept of a single kind of operative cambium.

A fascinating exception to the above is in Pisonia and allied genera (Guapira, Neea, Torrubia). In these genera, fibers form the background tissue of the stem. This also occurs in Aizoaceae, in Stayneria (Fig. 25). Thus, the master cambium must consist of tangentially narrow cells from the outset in these particular genera, and it does. Vascular cambia do arise from master cambia in Pisonia and allied genera, but anticlinal divisions do not occur in that process, because they have occurred earlier. Note should be taken that in the Pisonia group of genera and in Stayneria, fibers are derived from both master cambium and vascular cambia, with no boundary indicating which fibers are derived from which cambium. This is completely understandable, because tangential cell diameter is the same in both types of cambia.

The sequences of divisions and their products in the schematic drawing (Fig. 1) do not apply to all species, but can serve as a way of demonstrating common conditions. Materials that show these division stages are very difficult to obtain. Microtechnical preparations that reveal divisions in tissues with delicate thin walls but also reveal hard tissues (such as cortical fibers or conjunctive tissue fibers), necessary to identification of meristematic cells, are extraordinarily difficult to make. More importantly, active division in meristematic tissues of a species with successive cambia may well not be occurring at a given time in a given piece of stem or root.

Preparations that reveal divisions in cambia in plants with single vascular cambia are by comparison much easier to obtain.

As in vascular plants with a single cambium, there is no evidence in the plants considered here to counter the idea that a vascular cambium is functionally more than one cell layer thick. The fact that secondary phloem is always produced outward and secondary xylem is always produced inward in plants with a single vascular cambium is cited as one line of evidence that these should be termed vascular cambia (instances of interxylary phloem, as in Combretaceae, Onagraceae, and Loganiaceae, are an obvious exception in plants with a single cambium). In all of the genera considered here, each vascular cambium produces secondary xylem inwardly and secondary phloem outwardly, a fact that I believe supports the recognition of the concept of a vascular cambium functioning separately from (but ontogenetically derived from) a master cambium.

Frequency of initiation of vascular cambia over time is omitted from most studies, perhaps because most anatomists do not know the age of the stems or roots they study. The roots of Beta show that numerous vascular cambia can be formed per year, and more than one per year is probably the prevailing condition in successive cambial plants. The longevity of each vascular cambium can extend over a series of years. The sympodial nature of shoots in Phytolacca dioica can be used as a marker for number of vascular increments produced per season; in Phytolacca dioica, several vascular increments are produced per season (Bruce Kirchoff, personal communication).

The period of viability of vascular cambia is a separate issue from number of vascular cambia formed per season. Length of viability of the vascular cambia has not been specifically studied in any plant, as far as I know Studies that show whether vessels in earlier vascular increments are still conducting are needed. Vascular cambia are not alike in all species that have successive cambia. These

conjunctive tissue fibers, ctp = wide zone of conjunctive tissue parenchyma, ft = fibrous tissue, pet = narrow band of conjunctive tissue parenchyma, r = ray, sc = secondary cortex, sp = secondary phloem, sx = secondary xylem, v = vessel, arrow = vascular cambium, pointers = master cambium. Figs. 10, 11, 13, scales in Fig. 3; Fig. 12, scale in Fig. 2.
FIGS. 14-17. Transections of stems of Nyctaginaceae. Figs. 14–16. Heimerliodendron brunoniaum. Fig. 14. Area showing, from top to bottom, secondary cortex, master cambium, a band of fibers abaxial to which no phloem is evident; conjunctive tissue parenchyma; and a portion of an older vascular increment. Fig. 15. Master cambium and its products; origin of a phloem strand (po, superimposed on the phloem cells) and divisions indicative of vascular cambium origin (three pairs of cells above the letter d) are indicated. Fig. 16. Section showing origin of secondary phloem from vascular cambium; note the relative number of
differences, most readily determined by examining the products of the vascular cambia, are detailed in the taxonomic groups considered in the second major section of this paper.

Note should be taken that when vascular cambia form, the fusiform cambial initials are longer and narrower than are cells of the master cambium, conjunctive tissue cells, or secondary cortex cells. This is one obvious correlation with the fact that conjunctive tissue and secondary cortex tissue are not produced by vascular cambia. Radial sections show that the fusiform cambial initials remain fusiform cambial initials and do not subdivide or change shape.

Secondary cortex. The master cambium produces radial files of parenchyma to the outside (Figs. 2, 3). Only a single layer of secondary cortex is present in some preparations, although a second layer may be formed (Fig. 1H). Esau and Cheadle (1969) apparently regard the secondary cortex as "conjunctive tissue," an interpretation that is not supported here. The term conjunctive tissue implies used by most authors denotes tissue that lies between one vascular increment and the next.

Secondary cortex may, in fact, not be present in some species with successive cambia. In an illustration of *Pisonia* (Fig. 17), the layer just inside the fibers and sclerenchyma shows periclinal divisions that indicate the existence of a master cambium. There are about three or four layers of secondary cortex in the stem of *Guapira* illustrated (Fig. 13). A scattering of divisions in various planes may be seen in the secondary cortex of *Stegnosperma* (Fig. 3). Such divisions are generally not common in the species with successive cambia, because the radial rows of cells in the secondary cortex are usually conspicuous (Figs. 14, 16, 24).

The large tropical lianas (e.g., *Bauhinia*) form new vascular cambia frequently, and such events can be detected by the appearance of vascular strands, isolated within a parenchyma background. Most other species with successive cambia innovate master cambia infrequently, often only once in the life of an axis. Reasons for this interpretation include the following:

1. *Beta* produces numerous vascular increments ("rings") in a single season, each vascular increment with its own vascular cambium. The examination of Artschwager's (1926) photographs and drawings is compatible with the idea of a single master cambium, with very little secondary cortex production. To imagine otherwise, we would have to imagine the numerous vascular increments produced from two or more origins of a master cambium, and more than one master cambium would be an uneconomical way to achieve that.

2. Those who have successfully prepared extensive transactions of Chenopodiaceae (Lev-Yadun and Aloni 1991) show unbroken radial seriation of segments of vascular cambium, rays, etc. One would expect disjunctions (offsets, discontinuities) in radial seriation if master cambia were innovated continually.

3. The centrospermoid families mostly have a distinctive cylinder of cortical fibers (Figs. 2, 12, 13) that delimit inner from outer cortex. If new master cambia were continually produced outwardly, one would expect to see some of these fibers incorporated into secondary tissues of the stem (or root), but in fact, that has never been reported. A master cambium may be present in the cell layer just interior to such fibers (Fig. 17).

4. While there may be shifts in successive cambial schemes within centrosperms and between centrosperms and the other clades in which successive cambia occur, one would not expect radical departure from a basic plan unless there were some histological evidence (as there is in *Gnetum africanum* and certain woody tropical lianas) that master cambia are absent.
FIGS. 18–21. Transections of stems of Aizoaceae. Figs. 18–20. *Trichodiadema bulbosum*. Fig. 18. Area from secondary cortex (top) inward showing a series of vascular increments (looking like but not equivalent to vascular bundles) in a background of conjunctive tissue parenchyma. Fig. 19. A portion of a vascular increment, showing fibrous secondary xylem (bottom) adaxial to parenchymatous secondary xylem. Fig. 20. A strand of fibers formed by vascular cambial action that has produced no vessels and no secondary phloem. Fig. 21. *Aptenia cordifolia*. Area showing, from top to bottom: active divisions in master cambium cells,
Numerous innovations of master cambia would present problems in forming interconnections between a series of vascular increments; such interconnections do occur (Fahn and Schchori 1967, Kirchoff and Fahn 1984).

**Conjunctive Tissue.** A master cambium is most frequently separated from the secondary phloem of the previous vascular increment by about four cells of conjunctive tissue (Fig. 22), although there are more numerous layers in those species that have bands of sclerenchyma in conjunctive tissue. As a master cambium becomes active, at first few or no layers of conjunctive tissue are evident between the master cambium and the secondary phloem of the preceding increment (Fig. 21). Quiescence of the master cambium may obscure this at times (Fig. 4). When several layers (the approximate number is characteristic of particular species) have been formed, no more layers are added to that band, as study of stems with numerous vascular increments (Fig. 22) shows. The fact that several layers of conjunctive tissue may be seen internal to a master cambium before other tissues are appear (Fig. 15) is taken as evidence that conjunctive tissue is the first product of a master cambium (Figs. 1C, 1D).

Some conjunctive tissue consists wholly of parenchyma, as in *Beta*. The familiarity of this example may lead some to consider conjunctive tissue always to be parenchyma. However, in addition to parenchyma, fibers, sclereids, and occasionally idioblasts may be present in conjunctive tissue. The distribution of these cell types in amount and in spatial relationship to each other within conjunctive tissue varies markedly in species with successive cambia. The distinctive expressions of conjunctive tissue are considered in the second major section of this paper. Artschwager (1926) claims that in a photomicrograph of numerous vascular increments of *Beta* (that illustration inverted with relation to drawings in the paper) that these rings are “composed mostly of undifferentiated cambium and some phloem.” There is phloem in all of the vascular increments, as his drawings show, but the “undifferentiated cambium” proves to be mostly parenchyma of secondary xylem. The cell layer identified as by Artschwager (1926) as cambium elsewhere in his paper would support the idea that the vascular cambium is functionally only a single layer in thickness.

**Secondary Phloem.** The phloem produced by vascular cambia is by definition secondary phloem, and this holds in plants with successive cambia. Radial files are readily evident in secondary phloem of these species (Figs. 15, 16). In successive cambial species studied to date, secondary phloem differentiates before secondary xylem in any particular vascular increment (Artschwager 1926, Esau and Cheadle 1969). Secondary phloem may contain fibers (Fig. 27). It may consist mostly of parenchyma, as in the roots of *Beta* (Artschwager 1926) or *Mirabilis* (Mikesell and Popham 1976).

A feature of successive cambia not often mentioned in the literature is the prolonged production of secondary phloem by each vascular cambium. Earlier-formed secondary phloem is crushed (Figs. 5, 10, 17, 19, 25).

**Secondary Xylem.** Amounts of secondary xylem produced by a vascular cambium vary from a few cells (Fig. 22) to increments several cm wide, as in some Menispermaceae (Carlquist 1996c). Distinctive parenchyma bands (Fig. 19) or various distributions of parenchyma and fibers beside the vessels may occur (Figs. 4, 5). These represent characteristics of particular genera, as discussed later.

If growth rings occur in plants with successive cambia, they will be evident in secondary xylem. An instance of these is illustrated here (Fig. 31), and they have been identified in *Charpentiera densiflora* of the Amaranthaceae (Carlquist 2003). The mention of “annual rings” in *Beta* by Artschwager (1926: 168, 175) is presumably a wording error.

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secondary phloem, a vascular cambium, and secondary xylem. Note that about four files of master cambial cells are evident, whereas about nine or ten files of vascular cambium cells can be identified. Labels: csp = crushed secondary phloem, ct = conjunctive tissue, ctp = background of conjunctive tissue parenchyma, f = fibrous conjunctive tissue, psx = parenchymatous secondary xylem, sp = secondary phloem, sx = secondary xylem, vl = vessel, arrow = vascular cambium, pointers = master cambium. Fig. 18, scale in Fig. 2; Figs. 19-20, scale in Fig. 3; Fig. 21, scale = 30 μm.
Figs. 22–25. Stem transections of Aizoaceae. Figs. 22–23. *Aptenia cordifolia*. Fig. 22. Area showing primary cortex (top) and portions of two vascular increments. Although secondary phloem is present in both increments, no vessels have formed at this stage. Fig. 23. Area showing portion of an older vascular increment, showing vessels. Fig. 24. *Marlothistella uniondalensis*. Most of the secondary tissue consists of conjunctive tissue parenchyma. Fig. 25. *Stayneria neillii*. A pair of vascular increments in a rayless fibrous background tissue. Labels: c = cortex, csp = crushed secondary phloem, ct = conjunctive tissue, f = fibrous
(annular would be correct). Although the idea that one vascular increment per year would be produced by a successive cambial plant may be appealing, it does not seem to be true. More than one vascular increment per year seems the common condition.

One feature that has not been expressly addressed when analyzing secondary xylem in plants with successive cambia is how to describe it separately from conjunctive tissue. If the scheme proposed in the present paper is followed, secondary xylem is always defined as the internal product of a vascular cambium. This becomes significant in families where some genera have successive cambia while others do not, such as Phytolaccaceae (Carlquist 2000). Secondary xylem in genera with successive cambia can have distinctive axial parenchyma distributions (e.g., scanty vascentric in Caryophyllales: Fig. 11, cells to the right of the vessel) that should not be confused with conjunctive tissue parenchyma.

**Rays: paedomorphosis and raylessness.** If one is familiar with ray types in typical dicotyledonous woods produced by a single cambium (the "Kribs Ray Types": Carlquist 2001), one finds that such rays are not common in species with successive cambia. Instead, one tends to find such conditions as (1) permanently juvenilistic rays; (2) raylessness; or (3) rays produced from a master cambium rather than from a vascular cambium. Occasionally, one sees the occurrence of unusually wide rays in species with otherwise rayless secondary xylem. In *Suaeda* (Lev-Yadun and Aloni 1991). This assemblage of ray phenomena has provoked diverse reactions. Baird and Blackwell (1980) refer to "radial conjunctive tissue" (as opposed to "tangential conjunctive tissue") in *Halosgeton* (Chenopodiaceae), although they figure (p. 271) what any wood anatomist would identify as biseriate and triseriate rays. In *Beta*, Artschwager (1926) does not mention rays in vascular increments after the first one. Similarly, rays are not mentioned by Esau and Cheadle (1969) in *Bougainvillea*. Esau and Cheadle are evidently unaware of the concept of paedomorphism (juvenilism) in rays, although that concept had been enunciated earlier (Carlquist 1962). Paedomorphic rays consist wholly or predominantly of upright cells, not just at the beginning of secondary growth, but indefinitely thereafter (Carlquist 2001). *Bougainvillea* has rays, as defined the rays usually are, radial sheets of parenchyma, which take the form of elliptical zones one to several cells wide as seen in tangential section. These can be seen in the preparations of Cheadle (Fig. 6 here; Plates 1A, B and Plate 3C in Esau and Cheadle 1969) and, more clearly, in some of my preparations (Fig. 7). In the latter, the rays are distinct from parenchyma bands (pb) of conjunctive tissue. Metcalfe and Chalk (1950) term the rays of *Bougainvillea* "raylike radial sheets of conjunctive parenchyma."

The occurrence of paedomorphic rays in species with successive cambia should not be a surprise. The nature of a master cambium is distinctive in that it makes repeated copies (the vascular cambia) of its cells. Because each of the vascular cambia is of relatively short duration compared to that of a normal woody dicotyledon, the changes seen in fusiform cambial initials (Bailey and Tupper 1918) and rays (Barghoorn 1941) do not have time to occur. In fact, there is little change in fusiform cambial length (as judged from vessel element lengths observed in study of radial sections) over time in species with successive cambia (Carlquist, unpublished data). Similarly, there is little change in type (procumbent, square, upright) of ray cells over time. In most species with successive cambia, each vascular cambium undergoes little tangential increase cell number because of its limited life span (although *Gnetum africanum*, Fig. 29, is an exception). The limited tangential increase of the vascular cambium is associated with the phenomenon that vascular cambia are so frequently juvenilistic in species with successive cambia. Increase in tangential extent of meristematic layers occurs mostly in the master cambium. Tangential sections of cambia in plants with successive cambia are
Figs. 26–29. Stem transections of *Gnetum* (Gnetaceae). Figs. 26–27. *G. schwackeana.* Fig. 26. Area showing portions of two vascular increments; there is a marked disjunction in the histological composition of the two increments (in ray number and size, for example). Fig. 27. Outer portion of a vascular increment; a probable master cambium forming just outside of the phloem fibers. Figs. 28–29. *G. africanum.* Fig. 28. A single vascular increment, showing marked dilation in both ray and fascicular tissue with secondary growth. Fig. 29. Origin of a new vascular increment (narrow cells) by subdivision of a few (perhaps two) cortical
infrequently illustrated: Esau and Cheadle (1969, P. 3) present an excellent section. A section of a master cambium should look much like a section of a vascular cambium where lengths of fusiform cells are concerned.

Raylessness in woods is a form of paedomorphosis, or protracted juvenilism (Carlquist 1970, 2001) in which rays may never develop, or, if they do, are characterized by mostly upright cells. Not surprisingly, raylessness occurs in a number of species with successive cambia, especially in Caryophyllales. Virtually the entire family Aizoaceae is rayless (Carlquist 2007).

The ontogeny of rays in Pisonia and allied genera (Guapira, Neea, Torrubia) is unusual in that rays are formed from the master cambium, not from the vascular cambium (Carlquist 2004). The rays in these genera are narrow (uniseriate or biseriate), well defined (Fig. 11), and not like the rays of other Nyctaginaceae. Vessels and some fibers but no rays are produced by the vascular cambium in the Pisonia alliance (Figs. 10, 12, 13). This division of labor between master cambium and vascular cambium is one clear line of evidence for the existence of both a master cambium and vascular cambia, rather than a single cambium, in species with successive cambia. This interpretation should have been offered long ago, because the figure of the stem of Pisonia nigricans by Solereder (1899, 1908, 648; reproduced by Metcalfe and Chalk 1950, p. 1064) has stood without comment or explanation for about a century.

Ray cambium is difficult to discern in species with successive cambia that do have rays. Divisions are relatively few (Fig. 3) compared with divisions in fascicular areas. Much radial growth is accomplished by radial cell elongation in rays, hence the infrequency of periclinal divisions.

Although the rays of species with vascular cambia are predominantly upright, leading them to be termed paedomorphic, exceptions can be found in the genera Guapira, Neea, Pisonia, and Torrubia (Nyctaginaceae). Metcalfe and Chalk (1950) refer rays in these genera to Homogeneous Type II of Kribs (1935). There is a notable correlation involved. In Guapira and allied genera all rays are produced from the master cambium, not from vascular cambia.

Three-Dimensional Aspects. The discussion to this point is based mostly on transactions, with passing reference to tangential or radial sections. The tissues in successive vascular increments, in order to be function, must be connected with each other, but single sections do not illustrate this well. Only a few workers have examined the three-dimensional patterns involved in species with successive cambia. Fahn and Schchori (1967) have made a notable contribution based on study of Chenopodiaceae. Conceivably, there are different patterns in different families. Three-dimensional patterns can be studied with a variety of techniques, ranging from serial sections (Fahn and Schchori 1967, Fahn and Zimmermann 1982) to dye injection (Fisher and Ewers 1992). Fahn and Schchori (1967) make the fascinating observation that the pathways of phloem strands are not identical with those of xylem strands in a given axis, but run independently of each other in the material they study. The degree to which this is widespread in plants with successive cambia needs studied.

Esau and Cheadle (1969) note points of fusion between "old" cambia and "new" cambia in transactions of Bougainvillea. Their figures suggest that what they are describing may represent ontogenetic starting points in formation of anastomoses between vascular increments.

In my account of cambial variants (2001), I made a distinction between instances of "successive cambia" and examples of "wood portions dispersed or separated in divisions in parenchyma or parenchyma expansion." The latter list, in fact, contains a number of examples in which formation of successive cambia is present in addition to other meristematic phenomena. One genus notable in this regard is Bauhinia of the Fabaceae (Handa 1937, Wagner 1946, Machado et al. 1966, Basson and Bierhorst 1967, Roth and Ascenscio 1977, Fisher and Ewers 1994, Vieira...
FIGS. 30–33. Stem transections of species with successive cambial activity. Fig. 30. *Chrysanthemooides monilifera* (Asteraceae). Portions of two vascular increments and the conjunctive tissue between them. Fig. 31. *Anamirta cocculea* (Menispermaceae). A vascular increment and the preceding and following bands of conjunctive tissue, which contain tangential bands of sclereids. Figs. 32–33. *Mendoncia gigas* (Acanthaceae). Fig. 32. Area representing most of a vascular increment, radiating from point of origin (osx) and an isolated vessel with associated fibers at top, left of center. Fig. 33. Area from outside of stem...
To this may be added Rourea of the Combretaceae (Fisher and Ewers 1992), Mendoncica of the Acanthaceae (Carlquist and Zona 1988), and *Triphyophyllum* (Dioncophyllum) of the Dioncophyllaceae (Gottwald and Parameswaran 1968). There is little or no action of a master cambium in these examples, because origin of new vascular cambia occurs as points (single cells) rather than as sheets of parenchyma.

**Comparative Themes**

**Simmondsia and Stegnosperma: symplesiomorphies in the centrosperms.** Downie and Palmer (1974) and Downie et al. (1997) have presented DNA-based trees of Caryophyllales. These trees refine the phylogenetic constructions by Rodman et al. (1984). The positioning of the monogenic families Simmondsiaceae and Stegnospermaceae in these trees suggests that one might expect character states primitive for Caryophyllales in these two families. Indeed, tracheids, a feature symplesiomorphic for dicotyledon woods at large (Carlquist 2001), occur in these two genera but in few other centrospermoid Caryophyllales. In contrast, Phytolaccaceae (Carlquist 2000) and Amaranthaceae (Carlquist 2003) have libriform fibers in wood. *Simmondsia* (Bailey 1980, Carlquist 2002) and *Stegnosperma* (Carlquist 1999a) have uniseriate to triseriate rays, as well as a few wider rays (Fig. 2). The rays in both genera are paedomorphic in having a preponderance of upright cells, they are otherwise not unlike those of other dicotyledon woods (most of which have Heterogeneous Type II rays of Kribs, 1935), and thus are best interpreted as symplesiomorphic for the centrospermoid Caryophyllales. This contrasts, for example, to the raylessness that predominates in Aizoaceae (Carlquist 2007). Both genera have diffuse axial parenchyma (Carlquist 1999, 2002), a primitive condition in dicotyledons (Kribs 1937). The majority of Caryophyllales have scanty vasicentric parenchyma (original data). These several wood symplesiomorphies in *Simmondsia* and *Stegnosperma*, as well as evidence from molecular studies (Downie and Palmer 1994, Downie et al. 1997) reinforce the idea, presented earlier, that the plan of master cambia and vascular cambia in the two genera, represents a basic condition in centrospermoïds with successive cambia. There has been no previous evolutionary sequence of successive cambia types within Caryophyllales hitherto proposed.

**Nyctaginaceae: apomorphies in master cambia and rays.** Esau and Cheadle (1969) do not mention rays (or for that matter, raylessness) in their account of *Bougainvillea*, and thus present an incomplete picture of meristematic activity in the genus. In the transaction shown here (Fig. 5), the right five radial cell files are best interpreted as a ray. The area in a tangential section (Fig. 6) designated "f" forms an elliptical area typical of rays, and since there is radial continuity of such areas (Fig. 5), they should be considered as rays. Ray cells (Fig. 7, r) embedded in a background of fibers (Fig. 7, fx) are readily identifiable as rays, certainly, even though most of the ray cells are upright. The presence of upright cells and storying does not disqualify these structures from being rays. Paedomorphosis in ray cells has long been recognized (Carlquist 1962). Storying is evident in all cell types in *Bougainvillea*. This is the action of increase in girth by the master cambium rather than the vascular cambium. Attention should be drawn to this phenomenon because accounts of storying in vascular plants are based on "normal" vascular cambia rather than on plants with successive cambia (e.g., Bailey 1923). Areas of fiberlike parenchyma in *Bougainvillea* (Fig. 7, pb) and thin-walled conjunctive tissue (ct) are distinguishable from ray areas. There is some division of labor in parenchyma cells in *Bougainvillea*. Some have thin secondary walls and contain starch (Fig. 5, upper left).

**Pisonia** (Figs. 10, 11, 17) and *Guapira* (Figs. 12, 13) are genera of Nyctaginaceae including periderm (top), showing two vascular increments that have formed recently from cortical parenchyma. Labels: ct = conjunctive tissue, ctp = conjunctive tissue parenchyma, cts = conjunctive tissue sclerenchyma, osx = origin of secondary xylem increment, pb = parenchyma band, pe = periderm, rs = ray sclereid, sp = secondary phloem, spf = secondary phloem fiber area, ssc = sclerified secondary cortex, sx = secondary xylem, sxf = fibrous secondary xylem, sp = secondary xylem parenchyma, v = vessel, arrow = vascular cambium, pointers = master cambium. Figs. 30, 32–33, scale in Fig. 2; Fig. 31, scale in Fig. 28.
that represent a greater degree of differentiation, compared to *Bougainvillea*, between axial and radial tissues. In these genera, there are no ray initials in the vascular cambia and thus no rays in secondary xylem and secondary phloem. Examination of the sections of *Guapira* (Figs. 12, 13) makes this especially clear. Rays occur only in the background tissue of conjunctive tissue, which consists mostly of fibers. The arcs of thin-walled parenchyma around the secondary phloem of the vascular increments also contain rays (Fig. 13), but rays do not occur in the thin-walled parenchyma directly external to the secondary phloem. Distinctive rays may be seen in tangential sections (Fig. 11). No plant anatomist would fail to recognize these as rays. The reader may note that the term “vascular ray” is avoided here, and may not be applicable because the rays do not originate from a vascular cambium. The distribution and nature of the rays in *Pisonia* is not entirely clear in the drawing of *P. nigricans* by Solereder (1899, 1908), and has not received comment by other workers. Metcalfe and Chalk (1950) accurately describe the rays of *Neea*, *Pisonia*, and *Torrubia* without noticing their distinctive distribution within the stems of these genera. The production of rays by a master cambium, which is the meristematic layer that drives increase in girth of the axis, and their absence in the vascular cambia shows a fascinating division of labor.

The observant reader will have noticed that there are a few fibers in secondary xylem areas, adjacent to vessels in these genera (Fig. 10), fibers identical to those in the “background” fiber tissue. How can there be two sources for fibers, with such precise and seamless coordination of production of the fibers from the two sources? The answer is that unlike the master cambium in most species with fusiform cambia initials, the master cambium in *Guapira* (see points in Fig. 13) consists of narrow fusiform cells like those of the vascular cambia. Thus both master cambium and vascular cambia have a template for production of fibers. In most species with successive cambia, the cells of the master cambium are tangentially wider than cells of a vascular cambium, and production of vascular cambia from the master cambium therefore involves anticlinal divisions (e.g., Fig. 15 above the letter d). Thus the coordination of simultaneous production of conjunctive tissue fibers with production of a relatively small number of secondary xylem fibers is not a morphogenetic problem. The use of the term “fiber” here contains some intentional vagueness. If fibers are formed from a vascular cambium, they should be termed libriform fibers if they have simple pits—as do they in *Pisonia* and allied genera. Because fibers formed from vascular cambia and from the master cambium are identical in *Pisonia*, there is no contrast that can be made, and there is no reason why the term “fiber” should not be used. However, the terminological consequences of shift in mode of ray origin and fiber origin in Nyctaginaceae have not been noted by plant anatomists—who are likely to neglect such minor problems.

The presence of arc-like zones of conjunctive tissue parenchyma in *Guapira* (Fig. 12; Fig. 13, top) and *Pisonia* (Fig. 10, pet) represents an interesting division of labor in conjunctive tissue. The arcs of parenchyma contrast markedly with the fibers. The walls are thin, and a few raphide idioblasts may be found in this tissue. The parenchyma cells do not have intrusive growth, as do the fibers. The arcs of parenchyma are not part of the secondary phloem and do not contain any sieve elements. The parenchyma arcs do contain rays (but not opposite the strips of vessels). The parenchyma arcs are derived from the master cambium, not from the vascular cambia.

An obvious corollary to the above is that in *Guapira* and allied genera, the master cambium extends in a cylinder around the stem, whereas the vascular cambia are tangentially narrow strips. A single master cambium per stem (or root) is active indefinitely in *Guapira*, *Pisonia*, etc., whereas the vascular cambia, although they may produce secondary phloem for indefinite period of time, very likely eventually cease functioning in older parts of a stem or root. The production of vessels plus a few fibers by vascular cambia is limited by the fact that the vascular increments are encased in fibers. Although a vessel or two may be added over time (see vascular increment, Fig. 10, upper right), such additions are very minor.

The sequence of events hypothesized by Esau and Cheadle (1969) in *Bougainvillea* (a single cambium giving off conjunctive tissue and secondary phloem externally, conjunctive tissue and secondary xylem internally) is
inapplicable to Guapira, Neeea, Pisonia, and Torrubia. Their proposed interpretation is, in fact, inapplicable to Bougainvillaea. The condition represented by Bougainvillaea may be considered apomorphic to those in Phytolacca or Stegnosperma in that near-raylessness is being achieved in Bougainvillaea. This is in line with the ray phyletic plan hypothesized earlier (Carlquist 2001, p. 188).

Heimerliodendron of the Nyctaginaceae (Figs. 8, 14–16) has achieved complete raylessness, which is clearly an apomorphy as well as a form of permanent juvenilism, or paedomorphosis. The lack of rays can be clearly seen in a tangential section of fibrous tissue (Fig. 8, fx). Derivatives of the master cambium (pointers, Fig. 14) subdivide antically, thereby creating narrow cells destined to become fibers. Subdivisions in the derivatives of the master cambium also lead to fusiform cambial initials (Fig. 15 above the letter d) and to secondary phloem (Fig. 15, po). Early stages in maturation of fibers around vessels or vessel groups (Figs. 15, 16) appear as islands or strands in a background of undifferentiated cells. Strands of secondary phloem are present radially outside of these zones of vessels (Figs. 15, 16), but not at all points opposite fibers (Fig. 14). In the mature stems of Heimerliodendron, concentric rings of conjunctive tissue fibers (about seven to eight cells thick) alternate with cylinders of parenchymatous conjunctive tissue fibers about four or five cells thick. This situation has been excellently illustrated by Meylan and Butterfield (1978).

A terminological question is presented by the bands of conjunctive tissue fibers: Do fibers originate from a vascular cambium or a master cambium in areas where no secondary phloem is evident (Fig. 14)? The answer is that they are derived from the master cambium. Vascular cambia are claimed here to be operative only where strands of secondary phloem and vessels are evident. Thus, Heimerliodendron (sometimes regarded as a species of Pisonia) is really very similar to Pisonia, differing only in raylessness and in differentiation of conjunctive tissue parenchyma into concentric bands of fibers and parenchyma rather than a background that consists almost entirely of fibers. As shown by Meylan and Butterfield (1978, Fig. 198), radial chains of vessels and associated fibers are produced as radial flanges, much like the curious radial strips of vessels figured for Charpentiera of the Amaranthaceae (Carlquist 2003, his Figs. 23, 24). In Charpentiera, the radial vascular flanges are interconnected laterally by ray cells with lignified cell walls.

Amaranthaceae (including Chenopodiaceae) are like Nyctaginaceae in that some genera, such as Nototrichium (Fig. 9) and Grayia are entirely rayless, whereas others may have some wide ray areas (Lev-Yadun and Aloni, 1991). The conjunctive tissue of Nototrichium (Fig. 9) could easily be confused with ray tissue in radial sections because horizontal subdivision of ray cells occurs. The master cambium of Nototrichium consists wholly of fusiform cells, as does that of Heimerliodendron.

Aizoaceae: diversification of conjunctive tissue within a rayless clade. The structural mode of alternating concentric rings of fibrous conjunctive tissue and parenchymatous conjunctive tissue, and with localized strands of xylem and phloem, as seen in Heimerliodendron, occurs in many Aizoaceae. This condition is readily seen in Aptenia (Fig. 22). All of the Aizoaceae illustrated in the present paper are rayless, as are those figured earlier (Carlquist 2007). As in Heimerliodendron, master cambium derivatives in Aizoaceae, at first tangentially wider (Fig. 21), subdivide to become much narrower tangentially (Fig. 22).

In stems of Trichodiadema, a master cambium (Fig. 18, top) yields radial rows of secondary cortical cells to the outside. Inwardly, it produces radial rows of parenchyma, some of which are raphide idioblasts (Fig. 18, cells with gray contents). Here and there, vascular increments are evident. These vascular increments mostly have fiber strands on their inner faces (Figs. 18–20). The radial rows of vessels are not embedded in fibers, but rather in axial parenchyma produced from the vascular cambium (Fig. 19). As more secondary phloem is added, earlier secondary phloem is crushed (Fig. 19). A small number of vessels (with associated axial parenchyma) are added by vascular cambia, although no fibers are added. As with Pisonia, the master cambium extends around the stem, whereas vascular cambia are, tangentially, narrow strips. The vascular strands appear almost randomly distributed (Fig. 18), so that the origin of vascular cambia from the master cambia must vary spatially through time. In a very small
number of fiber strands, no vessels or phloem are present (Fig. 20). Just to the inside of the master cambium in *Trichodiadema*, fiber bands are evident (Fig. 18). I am interpreting these, and therefore the fiber strands elsewhere, as conjunctive tissue. Phloem is not associated with the fibers at all points in *Trichodiadema*, nor are vessels. Thus, the stems of *Trichodiadema* are similar to those of *Heimerliodendron* in histology, except for the fact that the fibers strands do not extend tangentially for indefinite distances around the stem.

In *Aptenia* (Figs. 21–23), the master cambium derivatives subdivide into more numerous cell files as fibers, secondary xylem, and secondary phloem. The conjunctive tissue differentiates not as parenchyma and fiber strands associated with secondary xylem, as in *Trichodiadema*, but as alternating concentric bands of fibers and thin-walled parenchyma, as in *Heimerliodendron*. The strands of secondary xylem and phloem are formed on the abaxial faces of the fiber bands. As with *Heimerliodendron*, the most obvious interpretation is that the there is a master cambium around the stem that produces conjunctive tissue. The conjunctive tissue shows distinct patterns, and the vascular strands are produced by tangentially narrow bands of vascular cambial cells. *Heimerliodendron* and *Aptenia* do show a specialized placement of vascular cambia: always along the abaxial face of the fiber bands, whereas vascular cambia are spatially scattered in *Trichodiadema*.

*Marlothistella* (Fig. 24) provides an example of absence of mechanical tissue. A small strand of fibers (fsx) is present in the transsection illustrated, but fiber strands are extremely infrequent in this plant. Vascular increments, looking like small vascular bundles, are scattered widely throughout the conjunctive tissue parenchyma background. A few raphide idioblasts (ri) are present in the conjunctive tissue parenchyma. The stem of *Marlothistella* represents a maximization of parenchyma and a minimization of fibers and of vascular tissue.

*Stayneria* (Fig. 25) shows a pattern that contrasts markedly with that of *Marlothistella*. Almost the entire conjunctive tissue consists of fibers. Vascular increments, like the one (arguably two close to each other) shown. Two chains of vessels can be seen in Fig. 25. As in *Pisonia*, there is no difference between fibers derived from a vascular cambium and those derived from a master cambium. As in *Pisonia*, the master cambium consists of narrow cells. The only change in derivatives of these cells is vertical (intrusive) elongation, no lateral subdivision is required as they mature into fibers. There are a few thin-walled parenchyma cells external to the secondary phloem in *Stayneria* (Fig. 26). Interestingly, the stem of *Stayneria* is thus identical to that of *Pisonia* in histological patterns except for the absence of rays in *Stayneria*. *Stayneria* represents a maximum of mechanical strength in stem structure in Aizoaceae, *Marlothistella* a minimum. These patterns are best interpreted in terms of habit and ecophysiology (below).

*Gnetum*: parenchyma as a stem patterning device. *Gnetum schwackeanum* (Figs. 26–27) is typical of New World species of *Gnetum* (Carlquist 1996b) in having wide bands of conjunctive tissues and wide rays. The patterns of development in stems of these species suggest that a given master cambium may not function indefinitely, but may be supplanted by a new master cambium formed by tangential divisions in parenchyma outside of the secondary phloem of the secondary phloem fibers (Fig. 27). This pattern is not markedly different from those of the families and genera considered before, because even in them, master cambia can sometimes cease functioning and can be supplanted by others. The idea that master cambia may be formed more frequently in *Gnetum* is based on apparent disjunction in cell lineages involved in one or more bands of vascular increments. Such a disjunction may be present between the two vascular increments shown in Fig. 26, although identifying such a disjunction is not easy. These might merely be distinctive products of a single master cambium over time. More study of the meristematic action in stems of *Gnetum* is needed, but is hindered by the lack of availability of liquid-preserved material and of workers interested in studying ontogeny of successive cambia. Amazingly, the sections of *G. schwackeanum* were derived from dried specimens, treated so that soft-walled tissue would remain intact. In any case, the basic pattern in *G. schwackeanum* is the point at hand: strands of secondary xylem plus fibers and secondary phloem (capped by fibers) are isolated from each other by thin-walled ray parenchyma and conjunctive tissue parenchyma, a kind of cable construction.
Parenchymatization in *Gnetum africamum* (Figs. 28–29) takes the form of rays, which become dilated as growth proceeds (Fig. 28). The African species of *Gnetum* thus contrast with the New World species by having several long-lived cambia per stem (Carlquist and Robinson 1995). As the rays dilate and the outer surface of the vascular tissue increases, the vascular cambium splits into fragments (Fig. 28, arrows), each of which may survive and produce an ever-widening wedge of vascular tissue. There are occasional bands of axial parenchyma in the fascicular xylem of *G. africamum* (Fig. 28). These bands, which represent secondary xylem not conjunctive tissue, are much less pronounced than are the conjunctive tissue parenchyma bands in *G. schwackeanum*. One can say that there are no master cambia in *G. africanum*. However, there is division in cortical parenchyma cells. At infrequent intervals, new vascular cambia arise as a group of cells, rather than a sheet, in the cortical parenchyma (Fig. 29). As seen in three dimensions, there are interconnections between the vascular increments, but such interconnections are not apparent in a single transaction.

Thus, the rapid increase in tangential extent of the a cambium in *G. africamum* achieves a broad wedge of vascular tissue, a mechanism at a polar opposite from the development of a master cambium that extends around a stem (or root) in a complete cylinder (*G. schwackeanum* or a series of interconnected arcs (*Bougainvillea*), followed by production of vascular cambia. *Gnetum africamum* and represent different ontogenies, but both exemplify the idea that more than one cambium—and thus successive cambia—are functioning in a given stem at any particular time.

**Chrysanthemoideos and Chloanthaceae (= Dicrastylidaceae): examining apomorphies.** Successive cambia have originated in about 15 clades. The numerous occurrences of successive cambia in families of centrosperms Caryophyllales suggest that in that order, successive cambia might not be apomorphies—the number of reversions one must hypothesize to explain the single-cambium taxa as the primitive state may be fewer than the number of conversions from a single cambium to successive cambia in the centrosperms. Perhaps the centrosperms contain a gene system in which switching from one condition to the other can be readily achieved.

In any case, successive cambia clearly have occurred as apomorphies in some clades, so one must ask why they arise, why they do not arise more often (or less frequently, for that matter), and whether they all represent a single plan. The first two questions relate to function (analyzed in the last section of this paper). The second question probably cannot be answered, except for the speculation that successive cambial plans are modifications (from a single-cambium plan) that are generally not easily achieved in genetic terms. But the third question can be answered affirmatively although one must take into account some very diverse examples, and explain that diversity. Apparently there is a limited number of ways in which vascular cambia can be formed and included within the structural plan of a stem or root.

*Chrysanthemoideos* is a genus of calenduloid Asteraceae. It was formerly considered a species of *Osteospermum*. When it and its closest relatives are analyzed, all of the Calenduleae chosen (Nordenstam et al. 2006) prove to be basal to *Chrysanthemoideos*. Thus, with *Chrysanthemoideos* the only genus of Asteraceae in which successive cambia are known to exist (Adamson 1934, Carlquist 1966), successive cambia are clearly an apomorphy in Asteraceae. Wood of all genera and species close to *Chrysanthemoideos* (using the tree of Nordenstam et al. 2006) has not been examined yet, but even if some of these prove to have successive cambia, the situation remains the same. Fibers occur in secondary phloem (Fig. 30, spf) of *Chrysanthemoideos*. Secondary xylem, however, is like that of other Calenduleae (Carlquist 1966). The growth form of *Chrysanthemoideos* may demonstrate an interesting correlation with presence of successive cambia. A young plant of *Chrysanthemoideos* has a single terminal head, as though it were an annual. Then, by lateral branching it can become a large shrub or, if water is available, a small tree. Thus, successive cambia may represent a mechanism for innovation of secondary growth in a non-woody lineage.

A second family of dicotyledons suggests a similar story. Chloanthaceae (= Dicrastylidaceae), an Australian family of plants (sometimes subfamily Chloanthoideae of Verbenaceae), have successive cambia (Carlquist 1981). As in *Chrysanthemoideos*, young plants in
Chloanthaceae have terminal inflorescences and increase in size (some of them are shrubs to 1 m or so) by lateral branching. Why Chryanthemoides and Chloanthaceae have developed successive cambia, rather than mere protracted secondary xylem production from a single cambium, is an intriguing question. Worth noting is that even if included in Verbenaceae, Chloanthaceae probably do not form a sister group to Avicennia, which has traditionally been thought to be close to or included within Verbenaceae. Recent results show that Avicennia is in the same clade of Acanthaceae that includes thunbergioids, to which Mendocia belongs (Schwarzbach and McDade 2002). The types of successive cambial activity of chloanthoids, Mendocia, and Avicennia, respectively, are rather different, and conceivably each of these instances of successive cambial occurrence could represent an apomorphy.

Menispermaceae: cambial protraction; sclereids. Successive cambia in Menispermaceae (Carlquist 1996c) doubtless represent an apomorphy in the ranunculoid (“basal eudicot”) clade. Some Menispermaceae, such as Legnophora moorei Miers, although woody, have only a single cambium as far as known, whereas others have numerous successive cambia. Some vascular increments in Menispermaceae can develop several centimeters of secondary xylem, but others are much thinner. Unfortunately, these patterns and their potential correlations can be clarified only when more extensive material is collected in the field. Information on stems of Menispermaceae has been derived almost exclusively from xylarium material. We need liquid-preserved material from field-collected specimens. The improved histological results are less important than the documentation of habit, size, etc., of the specimens. There is virtually no such information on xylarium specimens, and thus we have no key to possible correlations between extent of secondary xylem within each vascular increment and other histological features of stems as they might be related to plant size and habit.

The tangential bands of sclerenchyma in Anamirta cocculus (Fig. 31) are considered here to be the last-matured cells of an increment of conjunctive tissue between vascular increments. Only a few other species with sclerenchyma bands in conjunctive tissue are known: Avicennia (Studholme and Philipson 1996, Carlquist 2001) and Forchhammeria pallida (Carlquist, original data). Most species of Forchhammeria lack such sclereid bands.

Mendocia (Acanthaceae) and other lianas: cambial fracture and parenchyma proliferation. The portion of a Mendocia gigas stem (Fig. 32) shown here is not unlike that figured earlier (Carlquist and Zona 1988, Fig. 29); it is, however, more extensive and includes most of a secondary xylem increment that began (center left) with a small number of cambial initials and then widened markedly. This increment in that respect resembles the secondary xylem illustrated for Gnetum africanum (Fig. 28). The widening of the vascular increment, achieved by increase in number of fusiform cambial initials and ray initials, frequently results in fragmentation of the cambium (Fig. 32). Thus, the vascular increment becomes lobed as seen in transection. From bands of parenchyma within the increment of secondary xylem (Fig. 32, pb), new parenchyma may develop. A single isolated vessel, with associated fibers (Fig. 32, top) is associated with long files of parenchyma in two directions; this isolated strand does not seem like a typical vascular increment. Xylary expansions are permitted by the compressibility of older secondary phloem, which may be identified by scattered fibers (Fig. 32, spf; Fig. 33, sp). What was not noted by Carlquist and Zona (1988) is the innovation of new cambia in Mendocia gigas. By definition these are successive cambia (Fig. 33). The radial files of cells involved in the origin of vascular cambia, Fig. 33, suggest that limited portions of master cambium activity may be involved. However, origin of vascular cambia without master cambial activity appears to be characteristic of lianas such as Mendocia and Bauhinia, just as it is in Gnetum africanum.

Ecophysiological Themes

The majority of genera and species with successive cambia belong to the centrospermoid clade of Caryophyllales. The growth forms and habitats of these genera are so highly varied that correlations might not seem possible. However, individual genera offer possible interpretations. When one adds examples from outside of Caryophyllales, correlations become clearer. Caryophyllales are used as a prime example
here, after which comparisons from other groups with successive cambia are added.

**Storage and Retrieval of Photosynthates and Water.** The alternation of vascular increments with parenchyma provided by the successive cambial mode of construction offers an ideal histological plan for storage and retrieval of photosynthates and water. The roots of *Beta* (Artschwager 1926) and *Mirabilis* (Mikesell and Popham 1976) have thin cylindrical vascular increments spaced from each other by relatively wide zones of parenchyma. Sugar is stored abundantly in roots of *Beta,* starch in those of *Mirabilis.* In both genera, more recent vascular increments lack vessels, although vessels do eventually differentiate in earlier-formed vascular increments. This seems clearly correlated with adaptation to photosynthetic storage and retrieval rather than water storage.

Some Aizoaceae, such as *Mestoklema* and *Trichodiadema,* have thick tuberlike roots but relatively slender stems. The vascular increments are more widely spaced from each other in stems of those two genera than they are in roots (Carlquist 2007). Unlike *Beta* and *Mirabilis,* *Mestoklema* and *Trichodiadema* have xylem as well as phloem in all increments. This seems to be correlated primarily with storage of water in the underground structures, although small amounts of starch can be observed in the roots.

*Marlothistella* is an interesting example of adaptation by the successive cambial plan to water storage in a stem. The stems of *Marlothistella* are short and thick, and bear numerous very short branches. The main stem is clearly succulent. The vascular increments are slender and sparsely distributed (resembling vascular bundles) in a background tissue that consists almost entirely of thin-walled parenchyma. The stem of *Marlothistella* represents a version of the successive cambial plan in which water storage is maximized and mechanical strength is minimized. The occurrence of similar configurations in roots (*Beta, Mirabilis*) is not unexpected, because roots show minimal adaptations for mechanical strength.

An interesting confirmation of the suitability of the successive cambial plan for storage is found in genera of Caryophyllales that have a single cambium in the stem but successive cambia in the root. This condition has been reported for several genera of Caryophyllaceae (Pfeiffer 1926, Carlquist 1995). Labbe (1962) reported this condition in *Limoniastrum, Limonium,* and *Plumbago* (Plumbaginaceae). A few genera in these two families have successive cambia in both roots and stems (Pfeiffer 1926, Labbe 1962).

Dispersion of vascular tissue throughout storage organs does occur in plants that do not have successive cambia: examples from monocots (*Dioscorea*) and dicots (*Ipomoea, Solanum*) are familiar. The vascular plan of the typical monocotyledon needs no modification other than increase in parenchyma amount to achieve such a configuration. In dicotyledons with storage organs that do not have successive cambia, diversification of bundle placement or vascular tissue placement within a stem or root (e.g., pith bundles) has achieved results similar to those than that can result from slight alteration of the successive cambial template.

**Promotion of Mechanical Strength: a Paradigm for Prolonged Conductive Capabilities.** *Guapira,* *Neea,* *Pisonia,* and *Torrubia* are tropical or subtropical nyctaginaceous trees. All of these genera have slender vascular increments embedded in a background of fibers. This configuration suggests optimal mechanical strength. Even the rays in these genera contribute to mechanical strength by having secondary walls and by being vertically short and laterally narrow, so that they occupy a small proportion of stem tissue. To be sure, there are arcs of parenchyma around the phloem strands in these four genera, and these arcs would represent a slight departure from a plan of optimal mechanical strength. These parenchyma arcs could provide zones that could accommodate increased volume of secondary phloem as it is produced outwardly from vascular cambia. The parenchyma arcs are somewhat larger in *Guapira* than in *Pisonia,* but these arcs contain raphide idioblasts that could afford protection from predation of phloem.

Phloem in dicotyledons with a single cambium mostly lasts only a single season. Functional phloem is represented in the newest bark tissue. This is matched by the fact that, as dye analyses show, only the current year’s accumulation of secondary xylem is functional (Braun 1970). However, in a tree such as *Guapira,* each of the numerous strands of secondary phloem, scattered throughout the stem (or root) is functional, as evidenced by
the continued production of secondary phloem in each of these vascular increments. A logical corollary is that secondary xylem the vascular increments in which vascular cambia are continuing to form secondary phloem is also functional. Thus, a much greater area of the stem is potentially available for conduction by secondary phloem and secondary xylem than in a dicotyledon with a single cambium.

The consequences of prolonged conductive activity in the vascular increments are manifold. All of a stem’s vascular increments are potentially conductive, especially in species where water stress from drought or freezing does not disable earlier-formed vessels. Certainly in Guapira and allies, the warm humid habitats without strong extremes in moisture availability make vessel embolism occurrences relatively unlikely. The capability for prolonged conductive activity of vessels, matched as it is by continual production of secondary phloem by vascular cambia means that production of large numbers of vessels, especially narrow ones that would have greater embolism resistance (a phenomenon established by Hargrave et al. 1994 in *Salvia*) is unnecessary. Indeed, the vessel density of Guapira and allied genera is very low compared with vessel density in wood of dicotyledons with a single cambium. In turn, this permits a higher proportion of the stem tissue to be devoted to mechanical tissue. This situation actually represents a maximum economy in use of photosynthates to produce wall material, because fibers represent a kind of mechanical strength superior to vessels; in vessels, mechanical strength is present, but is much less than that of fibers. In a sampling of species with successive cambia, vessel density was shown to be lower than in woody dicotyledons with a single cambium (Carlquist 1975).

The vascular cambia of *Charpentiera* (Amaranthaceae) produce not only radial rows of vessels over a prolonged period, they produce associated fibers as well, resulting in the formation of radial flanges of vessels sheathed in fibers (Carlquist 2002, his Figs. 22, 23). The occurrence of wide concentric bands of conjunctive tissue parenchyma permits these additions of secondary xylem, which intrude outwardly into the conjunctive tissue. This tendency can also be observed in older parts of *Heimerliodendron* stems. In both of these genera, addition of fibers alongside vessels by the vascular cambium assures increase in mechanical strength as well as prolonging the activity of the vascular pathways formed earlier in the stem. Each of these radial flanges is capped by secondary phloem, formed for an indefinite period of time by each vascular cambium.

Fahn and Schchori (1967) claim that phloem strands of Chenopodiaceae are long-lived. Presumably the basis for that statement could be found in continued production of secondary phloem by vascular cambia, a characteristic of numerous species as noted above. This is true of the Californian desert shrub *Grayia spinosa* of the Chenopodiaceae as well (original data). The secondary xylem strands of *Grayia spinosa* probably have considerable duration and resistance to embolism formation, because they have not only narrow vessels, but vasicentric tracheids as well (Carlquist 1985).

Some Aizoaceae, such as *Aptenia*, have extended secondary xylem production from each vascular cambium, as noted above for *Charpentiera* and *Heimerliodendron*. In *Aptenia*, very few fibers are produced in this later-formed secondary xylem (Carlquist 2007). Thus, mechanical strength is not increased, but xylem conductive area is either maintained or increased. This structural mode seems related to the flexibility of the sprawling stems of *Aptenia*.

Interestingly, *Stayneria* of the Aizoaceae has a stem anatomical plan virtually identical to that of *Pisonia*, except that *Stayneria* lacks rays. *Stayneria* even has small arcs of conjunctive tissue parenchyma abaxial to phloem strands. *Stayneria* is a shrub larger than most other Aizoaceae, and thus a structural mode that features mechanical strength is adaptive.

The various anatomical plans above have obvious correlations with respect to mechanical strength and longevity of conductive tissues in stems (and presumably roots, which are studied much less frequently than are stems). These distinctive plans have not been studied by plant physiologists. Such study would reveal whether anatomical formulations offer differences from those of single-cambium species in their conductive and their mechanical characteristics. If successive cambial species were more common in dicotyledons at large, they would doubtless have received such study. The fact that successive cambial species are not sources of lumber does not make them of less physiological interest, but it may be one reason why wood physiologists have studied them so little.
The Liana Syndrome: Flexibility and Fiber Distributions That Protect Vessels. Lianas have less mechanical tissue per unit transaction than self-supporting woody plants (Schenck 1893, Carlquist 1991). They do have appreciable quantities of fibers in stems, however. Transections of lianas show that the fibers are often disposed as sheaths of individual vessels or sheaths of a group of vessels—often vessels with relatively large diameter. Conflerring mechanical strength that safeguards the integrity of water columns by preventing rupturing of vessels may be the primary function of these vessel sheaths. Jacobsen et al. (2005) find that presence of fibers around vessels contributes to cavitation resistance.

Successive cambial modes of structure make possible various patterns of fiber disposition with respect to distributions of thin-walled parenchyma. Some of these predispose toward flexibility of stems simultaneously with sheathing of vessels. The centrosperm families Agdestiaceae (Carlquist 1999b) and Basellaceae (Carlquist 1999c) are lianoid families that satisfy that description, but in different ways. In Amaranthaceae, Bosea has thin-walled parenchyma in ray areas as well as thin-walled conjunctive tissue between vascular increments (Solereder 1908, Metcalfe and Chalk 1950). Bosea is a shrub that can become markedly scandent (to 10 m). The fact that Charpentiera densiflora, also of Amaranthaceae, has lignified ray cells interconnecting plates of fibrous secondary xylem (Carlquist 2007) correlates with the fact that Charpentiera densiflora is a tree, whereas Bosea is lianoid. Soft (parenchymatous) conjunctive tissue between successive vascular increments offers flexibility, even to the point of tearing while vascular tissues remain intact. That this happens has been shown experimentally by Putz and Holbrook (1991) in Securidaca.

Bougainvillea offers wide ray areas, as well as parenchymatous conjunctive tissue, that seem to correlate with potential flexibility of this lianoid plant. The starch-rich nature of the parenchyma of rays and of conjunctive tissue, as well as the storage of starch in fibrous tissue, suggests a distinctive function that can be related to its habit: rapid seasonal production of large inflorescences at tips of branches that reach the canopy or similarly sunny sites.

There are a number of lianas (Bauhinia offers the best known example), as mentioned above with respect to three-dimensionalization, in which successive cambia are accompanied by other phenomena: rapid dilation of vascular increments through tangential expansion of cambia, fracturing of vascular cambia into segments, production of axial parenchyma bands, production of wide rays, and proliferation of cells in the axial parenchyma and ray areas. The result of this syndrome of interrelated ontogenetic changes is production of anastomosing strands of wood varied with respect to transactional area and shape. One advantage where habit is concerned seems to be mechanical flexibility, as hypothesized long ago by Schenck (1893) and experimentally demonstrated by Putz and Holbrook (1991). Stems of lianoid Bauhinia species, as well as those of other lianas, frequently deviate from a cylindrical form and often assume a flattened, bandlike form (Vieira 1994). The adaptation represented by this widened form may represent a conformation suited to maximal surface contact with the surface of the branch of the supporting tree. Such a possibility is difficult to demonstrate experimentally. The multiplicity of ontogenetic actions, which make a stem transaction of a liana seem irregular with comparison to that of a self-supporting tree, may also be a more rapid way to achieve change in three-dimensional stem shape and achievement of the advantages of cable construction than would eccentric growth of a single cambium.

Although not lianoid, the structure of sprawling stems in Apenia, Carpobrotus, and Tetragonia is instructive. These plants have strong but very flexible stems that feature concentric cylinder of alternating thin-walled and fibrous conjunctive tissue, with vessels abaxial and secondary phloem on the abaxial faces of the fiber cylinders (Carlquist 2007). Some of these genera grow on sand dunes or other places subject to soil level shift: Carpobrotus is often planted in order to stabilize sand dunes. Another correlation of this kind of stem structure in Aizoaceae is with the tendency of sprawling plants in this family to be able to bend toward the ground without damage and thereby reroot. This strategy enlarges the plant without the expenditure involved in mechanical strength production such as one finds in a typical shrub.

In all of the examples of lianoid or sprawling plants cited above, one can consider the various anatomical plans to represent
kinds of “cable construction,” as opposed to
the rodlike or cylindrical structure we associate
with dicotyledons that have a single cambium. In addition to combining flexibility
with increased strength, cable construction
offers the potential advantage of redundancy.
Because lianoid plants and sand dune plants
are subject to torsion, and thus to potential
injury, ground plans that feature redundancy
in conductive pathways and spatial separation
of those pathways are of special value.
Disposition of fibers as sheaths around vessels
is a mechanism that helps safeguard water
columns from embolism formation. Successive
cambial plans may prove to offer degrees of
redundancy safety equal to if not greater than
those of woods of single-cambium species
when comparable materials of each are studied
experimentally. Although successive cambia
are represented by a relatively small number of
species compared with the number of species
with single cambia, the multiple origins of
successive cambial plans within vascular
plants—and the varied growth forms represented
by successive cambial plants—provides
a kind of circumstantial evidence of the
adaptational values of these plans.
The lesson provided by the many above
examples that tend to show sensitive adapta-
tions to habit, ecology, and physiology is
obvious: they should be studied in those
contexts. Too often, comparative studies in
plant anatomy are limited to a description of
the histology of the group of species under
study and have recognition of diagnostic
features as the sole goal. Potential structure-
function correlations are all too frequently
avoided, and thus comparative anatomy fails
to provide questions worth answering. In the
case of plants with successive cambial struc-
ture, the problems have been compounded
because of the complexity of the histological
patterns, their microtechnical difficulty, and
the strong desirability of liquid-preserved
material. Although these may be considered
reasons for avoiding study of successive
cambial plants, they are precisely reasons
why study of these plants offers so many
opportunities.

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