Successive cambia in Aizoaceae: products and process

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The transverse and longitudinal sections of the stems and roots of 11 genera of Aizoaceae, representing a wide range of growth forms from hard fibrous stems to fibre-free roots, were studied using light microscopy and scanning electron microscopy. In most of the genera, fibres are the first xylary product of each vascular cambium, followed by vessels in a parenchyma background. Variations on this pattern help to prove that fibres are produced by vascular cambia, except in Ruschia and Stayneria, in which both the lateral meristem and the vascular cambia produce fibres.

Cylinders of conjunctive tissue parenchyma that alternate with the vascular cylinders are produced by the lateral meristem. The concept that the lateral meristem gives rise to the vascular cambia and secondary cortex is supported by photographic evidence. Radial divisions occur in the origin of the lateral meristem, and then again as vascular cambia arise from the lateral meristem; these radial divisions account for storing in fibres and conjunctive tissue. Raylessness characterizes all Aizoaceae studied, with the exception of Tetragonia, which also differs from the remaining genera by having vasicentric axial parenchyma, a scattering of vessels amongst fibres, and the presence of druses instead of raphides. Several vascular cambia are typically formed per year. Several vascular cambia are active simultaneously in a given stem or root. Roots have fewer fibres and more abundant conjunctive tissue parenchyma than stems. Successive cambia result in an ideal dispersion of vascular tissue with respect to water and photosynthate storage and retrieval capabilities of the parenchyma, and to liana stem plans. The distribution and relative abundance of fibres, vessels, secondary phloem, and conjunctive tissue parenchyma relate primarily to habit and are not a good source of systematic data, with the probable exception of Tetragonia. The general pattern of lateral meristem and vascular cambial ontogeny is the same as in other families of the core Caryophyllales, although the patterns of the tissues produced are diverse. © 2007 The Linnean Society of London, Botanical Journal of the Linnean Society, 2007, 153, 141–155.

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INTRODUCTION

The phenomenon of successive cambia, recognized many years ago by Schenck (1893) and Pfeiffer (1926), is characteristic of Aizoaceae (Caryophyllales) with perennial stems. Successive cambia occur in all of the families of the ‘core Caryophyllales’ (the Centrospermae of Eichler, 1876), with the exception of Achatocarpaceae, Cactaceae, Didiereaceae, Halophytaceae, Hectorellaceae, Portulacaceae, and some Phytolaccaceae (Gibson, 1994). Successive cambia occur in more than 20 families outside of the core Caryophyllales (Carlquist, 2001), as well as in Gnetum and Welwitschia (Carlquist, 1996).

Successive cambia represent a mode of structure that has been variously interpreted with respect to how successive cambia are formed, and therefore how the histology of what is produced should be interpreted. The terminology applied to stem and root histology in species with successive cambia is as amazingly diverse as the interpretations. Each family with successive cambia potentially offers important data on this phenomenon. This information can be divided into two categories. First, the nature of the products of the successive cambia and how they relate to features such as habit and texture. Second, and a potential result of such studies, an understanding of the origin and nature of successive cambia. Is a single plan involved, or are there several plans? Nyctaginaceae proved to be a seminal group with respect to both structural diversity and the analysis of ontogenetic processes (Carlquist, 2005). However, a wide range of families that have successive cambia must be analysed to bring clarity and
Aizoaceae form a key group, because successive cambia (as 'ein abnormen Dickenwachstum') have been claimed to be present in the perennial species of Aizoaceae (Pax & Hoffmann, 1934). Although Aizoaceae can be characterized as succulent to various degrees, there is a wide range of habits within the family. An attempt has been made here to select diverse growth forms in order to reveal a wide range in the products of secondary activity. These include acaulescent perennials (Lithops), perennials with condensed prostrate stems that root (Faucaria, Glottiphyllum), mat-like perennials with elongate prostrate stems that branch from a central stem (Aptenia, Tetragonia), a mat-like perennial with elongate prostrate stems that root readily (Carpobrotus), a small shrub with thick roots (Mestoklema), a subshrub with carrot-like tuberous roots (Trichodiadema), a subshrub with numerous short branches from a thick succulent base (Marlothistella), and small shrubs with dense, fibrous stems (Ruschia, Stayneria).

The histology of the species sampled appears to be highly diverse, although more patterns doubtless remain to be described in this large family. Are all of these plans attained with much the same ontogeny? Attention is focused here on the details of ontogeny in the successive cambia and the divisions antecedent to the successive cambia. Although the mature tissues of the stems and roots of Aizoaceae have received attention (Pax & Hoffman, 1934; Gibson, 1994), a more detailed knowledge of ontogenetic events leading to these mature products is desirable.

The terminology of the stem and root histology of Aizoaceae and of the ontogenetic processes that lead to these tissues is difficult. For example, are fibres in these axes secondary xylem fibres or are they extraxylary fibres? Even with ontogenetic studies, these designations may not seem obvious to all students of plant anatomy. There has been a tendency by some workers who desire simple histological identifications to equate the ground plan of axes with successive cambia as comparable with the ground plans of secondary xylem produced by vascular plants with a single cambium. Such workers misapply the term ‘interxylary phloem’ in the former cases. Indeed, in axes with successive cambia, a phloem strand cannot be interxylary because, on its adaxial face, secondary xylem derived from a vascular cambium is present, whereas, on its outer face, there is no secondary xylem, but conjunctive tissue derived from the lateral meristem (Carlquist, 2005). Likewise, the term ‘anomalous secondary thickening’ must be rejected when describing the phenomenon of successive cambia, because the actions of the lateral meristem and the successive cambia related to it are just as orderly and precisely organized as the happenings in axes of vascular plants with a single cambium. The visual cues by which successive cambia can be recognized and understood are not formidable and can be mastered readily. Likewise, the lateral meristem that leads to the formation of successive cambia has not been clearly understood, and has been variously termed (anomalous meristem, primary thickening meristem, secondary meristem, etc.). The term ‘lateral meristem’ may seem vague, but precise alternatives would be ponderous (e.g. ‘lateral meristem leading to the formation of successive cambia’). The present study, like an earlier report (Carlquist, 2005), represents an effort to clarify and simplify the phenomenon of successive cambia so that accurate and consistent interpretations can be reached, and therefore a terminology reflecting such an interpretation can be attained.

**MATERIAL AND METHODS**

The collections studied are as follows: *Aptenia cordifolia* (L.f.) Schwantes, cultivated, Santa Barbara, California; *Carpobrotus edulis* (L.) L.Bolus, Arroyo Burro Beach, Santa Barbara, California; *Faucaria tigrina* Schwantes, cultivated, Huntington Botanical Gardens, San Marino, California; *Glottiphyllum linguiforme* N.E.Br., cultivated, Huntington Botanical Gardens, San Marino, California; *Lithops turbinifloris* (Haw.) N.E.Br., cultivated, Santa Barbara, California; *Marlothistella uniondalensis* Schwantes, cultivated, Huntington Botanical Gardens, San Marino, California; *Mestoklema tuberosum* N.E.Br., cultivated, Santa Barbara, California; *Ruschia multiflora* (Haw.) Schwantes, between Swellendam and Rivieronderend, Cape Province, South Africa, *Cariquist 4556* (RSA); *Stayneria neillii* (L.Bolus) L. Bolus, cultivated, Rancho Santa Ana Botanic Garden, Claremont, California; *Tetragonia tetragonioideus* (Pall.) Kuntze, *Cariquist 8202* (SSBG), adventive, Santa Barbara, California; *Trichodiadema bulbosum* Schwantes, *Cariquist 8201* (SSBG), cultivated, Santa Barbara, California.

The only material in which a dried specimen was used was *Ruschia multiflora*; portions of this were boiled in water and stored in 50% aqueous ethanol. Material of the other Aizoaceae studied was fixed in 50% aqueous ethanol. The specimens of *Ruschia* and *Stayneria* stems were sectioned on a sliding microtome without prior softening. The remainder of the genera, except *Lithops*, were softened for various lengths of time in an ethylendiamine solution, embedded in paraffin, and sectioned on a rotary microtome, according to the schedule of Carlquist (1982). This method proved successful, but the presence of idioblasts containing raphides caused some tearing of the sections. All sections of the above were...
stained with a safranin–fast green combination. Although most of the sections illustrated are transections, tangential and radial sections were also prepared. Both stems and roots were sectioned for \textit{Marlothistella} and \textit{Trichodiadema}. Stems, roots, and the transition between stems and roots were sectioned for \textit{Mestoklema}. The \textit{Lithops} material did not section well with paraffin techniques because of resistance of the corky layers to paraffin infiltration. Consequently, the hypocotyls and upper roots of \textit{Lithops} were hand sectioned with a razor blade; sections were dried between glass slides, sputter coated with gold, and examined with a Hitachi S2600N scanning electron microscope. The scanning electron microscopy photographs of \textit{Lithops} provided an opportunity to demonstrate the bordered nature of perforation plates and rounded nature of pit borders in sectional view. In addition, the idea that \textit{Lithops} has only helical thickenings in vessels (Gibson, 1994) could be re-examined. The portions selected for all species studied were those judged to have the maximal accumulation of secondary tissues.

In the accompanying photographs, wide pointers have been used to denote lateral meristems. Arrows demarcate vascular cambia. The terminology follows Carlquist (2001, 2005).

**RESULTS**

**MATURE PATTERNS**

The plan of the stems of \textit{Trichodiadema bulbosum} (Figs 1, 2) can be regarded as fibrovascular strands embedded in a parenchymatous background. There is no differentiation of the parenchymatous background into rays vs. axial tissue, and all of the background tissue is regarded as conjunctive tissue here: all parenchyma cells conform to a single pattern of length to width proportions. The fibrovascular strands of the stem, examined in detail (Fig. 2), are each composed of several layers of fibres, followed by several layers of vessels intermixed with parenchyma. Strands increase in radial extent through cambial action (note the crushed phloem in Fig. 2). Thus, more recently formed strands (Fig. 1, top) are radially shorter than older strands. The fibres have simple, slit-like pits and are easily distinguished from vessel elements, which have simple bordered perforation plates and alternate circular pits with pit cavities round in face view. These vessel characteristics hold for all of the genera studied, with the exception of \textit{Lithops}.

In \textit{Trichodiadema bulbosum} (Figs 3, 4), the fibrovascular strands of the roots are much more slender and sparse than those of the stems. The fibrous parts of adjacent strands are tangentially intercontinuous in the stems (Fig. 1, top left), but the narrower strands of the roots are well separated from each other (Fig. 3). The fibrovascular strands of the root, if tangentially narrow (Fig. 4), are just as long radially as those of the stem.

The stems of \textit{Aptenia cordifolia} (Figs 5–8) are constructed of concentric fibrovascular cylinders separated from each other by cylinders of conjunctive tissue parenchyma (Figs 5, 6); the illustrations show only limited portions of each of these cylinders. In the more recently formed cylinders of a basal part of an \textit{Aptenia} stem, vessels are lacking (Fig. 5, top). The cylinders are progressively wider towards the stem interior (Fig. 5). However, in the central part of the stem, fibrovascular cylinders have numerous vessels, which are mixed with parenchyma and scattered fibres abaxial to each fibre cylinder (Fig. 6). Vessels are most abundant abaxial to the older fibre bands (Fig. 6, top).

The lateral meristem of \textit{Aptenia} can be readily located (Fig. 5, top; Fig. 7, above centre). Abaxial to the lateral meristem are several layers of secondary cortex, outside of which are the much larger cells of the primary cortex (Fig. 7, top). Secondary phloem and secondary xylem are produced by each cambium (Fig. 8). However, in more recent fibrovascular cylinders, cambia have thus far produced only fibres internally and only parenchyma externally (Fig. 8, left; Fig. 7, centre).

\textit{Mestoklema tuberosa} stems (Figs 9, 10) have fibrovascular cylinders of moderate width near the outside (Fig. 9). As in \textit{Aptenia}, abaxial to the fibrous cylinders are strands of vessels intermixed with parenchyma and a few fibres. Cylinders of conjunctive tissue parenchyma alternate with the fibrovascular cylinders (Fig. 9). As the bands age, they produce more secondary phloem, which crushes the earlier produced phloem (Fig. 9, bottom). The earliest formed vascular tissues in the stem show primary xylem, then secondary xylem, in which fibres are scarce; no fibrous cylinder adaxial to the vessels is present (Fig. 10, bottom). There are fibres in the next vascular increment (Fig. 10, centre and above) and subsequent increments.

\textit{Mestoklema tuberosa} upper root portions (Figs 11, 12) have fibrovascular cylinders that are radially narrower, and conjunctive parenchyma bands that are radially wider, than those of the stems. Vessels are scarce in the outer cylinders of the root (Fig. 11, top) and only occasional in inner cylinders (Fig. 11, bottom). The lateral meristem (Fig. 12, pointer) is associated with only one or two layers of secondary cortex, external to which lie cortical cells (some with divisions in various planes) (Fig. 12, top). The vascular cambium is adjacent to one to three layers of fibres in the portion illustrated in Figure 12 (arrow). External to the vascular cambium, conjunctive tissue is present, and secondary phloem has developed (as of the time.
Figures 1–4. Transections of Trichodiadema bulbosum. Wide pointers indicate lateral meristems; arrows denote vascular cambia. Fig. 1. Portion of stem, showing that vascular strands are relatively dense; large cells with grey contents are raphide idioblasts. Fig. 2. A vascular strand and portions of two others from a stem; formation of fibres precedes the formation of vessels. Fig. 3. Portion of root, showing relatively sparse vascular strands; thin-walled tissues from top to bottom are periderm (barely seen, top left), primary cortex, secondary cortex, and the conjunctive tissue parenchyma (which contains the vascular strands). Fig. 4. Vascular strand from root; strand is tangentially narrower, parenchyma cells larger than in the stem. Scale bars, 10 µm.
Figures 5–8. Transections from basal stem of *Aptenia cordifolia*. Wide pointers indicate lateral meristems; arrows denote vascular cambia. Fig. 5. Outer portion of stem, showing that the outer fibrovascular cylinders have accumulated less secondary xylem at the time of harvesting. Fig. 6. Inner portion of stem; the innermost fibrovascular cylinders (below) show many more vessels than the later formed cylinders. Fig. 7. Outer portion of stem (primary cortex at top, and secondary cortex above pointers); each of the two vascular cambia has produced secondary phloem and, in the secondary xylem, fibres but no vessels. Fig. 8. A vascular cambium (arrow) and its products: secondary phloem (top right), a pair of vessels (near centre), and fibres (bottom). Figs 5, 6: scale in Fig. 1; Fig. 7: scale in Fig. 2; Fig. 8: scale bar, 20 μm.

Figures 9–12. Transections from stem (Figs 9, 10) and upper root (Figs 11, 12) of Mestokiema tuberosum. Fig. 9. Outermost fibrovascular cylinders; fibres form continuous bands tangentially, vessels occur in groups. Fig. 10. The two innermost fibrovascular cylinders (and portion of a third, top). The innermost cylinder is devoid of fibres; the next oldest contains about equal amounts of fibres and vessels. Fig. 11. Relatively large and radially elongate conjunctive tissue cells between two fibrovascular bands. Fig. 12. Part of outer portion of stem; primary cortex (with recent divisions in random planes at top), a layer or two of secondary cortex and, within the lateral meristem, three or four layers of conjunctive tissue parenchyma. Figs 9–11: scale in Fig. 1; Fig. 12: scale in Fig. 2.
the material was fixed) only in isolated strands adjacent to the fibrovascular band.

The lower portions of the root of Mestoklema are similar to the upper portions. However, radial elongation of conjunctive parenchyma is more prominent in the upper root portions (Fig. 11, centre), accounting for the tuberous appearance of the roots. In older fibrovascular cylinders of the lower root, phloem strands are more common than in the root portion illustrated in Figure 11, but in neither upper nor lower root is there much secondary phloem produced, and crushed secondary phloem is infrequently observed.

The stems of Mestoklema, as seen in tangential section (Fig. 16), exemplify the raylessness of secondary growth. What appears to be a ray-like structure (Fig. 16, near left) is actually a strand of vessels mixed with parenchyma (corresponding to the areas of the transactions shown in Fig. 9, bottom, or Fig. 10, top). The right three-quarters of Figure 16 consists of fibres. Storeying can be seen in some of these fibres.

In Stayneria neillii (Figs 13–15), the background tissue consists wholly of fibres. Parenchyma is present as strands abaxial to secondary phloem (Figs 13, 14). Radial chains of vessels are adaxial to each strand of secondary phloem (Figs 13, 14). Vessels are thus embedded in fibres which contain no parenchyma. A few radial chains of vessels occur in an isolated fashion in the fibrous background. Crushed secondary phloem is evident abaxial to functioning secondary phloem. Although not illustrated in Figure 13, growth rings (fibres narrower in late wood) are present in the fibrous background, and bear no relationship to the distribution of strands of secondary xylem and secondary phloem. In a tangential section, the parenchyma adjacent to the phloem strand proves to be storeyed (Fig. 15). Some of the fibres are also storeyed. Rays are absent.

Transsections of the stem of Ruschia multiflora show a structure identical to that of Stayneria neillii, except that no vessel chains isolated in the fibrous background are observed.

Mariothistella uniondalensis (Fig. 17) shows maximal parenchymatization of the stem and root. Vascular strands, each produced from a vascular cambium, are scattered within the parenchymatous conjunctive tissue. Only a few fibres are present in the fibrovascular strands. Vessels mixed with parenchyma occur within the fibrovascular strands. Idioblasts bearing coarse raphides are common within the conjunctive tissue parenchyma (grey spots in Fig. 17).

In Glottiphyllum linguiforme (Fig. 18), stems have only one to five cylinders of fibrovascular tissue within a parenchymatous background. The first cylinder is inverted (Fig. 18, centre right). Subsequent increments are normally orientated, and are often dissected, the portions separated from each other by ray-like bands of thin-walled parenchyma (Fig. 18, top). Within the secondary xylem, fibres may be preceded by vessels intermixed with parenchyma (Fig. 18, bottom), or the reverse may be true.

The stems of Fauaria tigrina are the same as those of Glottiphyllum in all respects, except that the innermost cylinder of vascular tissue does not have an inverted orientation of xylem and phloem.

Carrobrothus edulis (Fig. 19) begins secondary growth with a cylinder of bundles that is four-angled in transsection. These bands, adjacent to the pith, consist of radial strands of narrow vessels and fibres that interconnect the radial strands of the vessels (Fig. 19, bottom). Subsequent secondary activity consists of secondary phloem (with adjacent parenchyma) opposite the radial chains of the vessels, embedded in a fibrous background. The fibrous tissue is rayless. Thus, the histological plan subsequent to the first cylinder of bundles is the same as that of Stayneria or Ruschia. However, the stems of Stayneria and Ruschia produce indefinite amounts of fibrous tissues, whereas, in Carrobrothus, only a few millimetres of such tissue are produced.

The stems of Tetragonia tetragonioioides show a distinctive pattern (Fig. 20). Increments of vascular bundles are separated from each other by thin-walled parenchyma. Ray-like plates of parenchyma separate the vascular portions, which consist of secondary xylem and secondary phloem. Rays are also present within the secondary xylem portions (Fig. 20), although not abundant. The secondary xylem consists of vessels that are often solitary, embedded in a background of fibres. Scanty vasicentric axial parenchyma is associated with the vessels. Druses are present in some pith cells; there are no crystals in conjunctive tissue parenchyma.

Lithops (Figs 21–25) apparently lacks fibres in the xylem of the hypocotyl and upper root. The secondary wall portions of the vessels in sectional view (Fig. 21) form round outlines (notice that the pits of the two adjacent vessels in Fig. 21 are offset rather than opposite each other as one would expect). Perforation plates are round in face view (Fig. 22). The perforation plates have borders, although the borders are round in sectional view rather than sharp as in most dicotyledons (Fig. 24). The lateral walls of the vessels (Figs 23, 24) mostly do not have circular pits. Rather, the pits are elongate and slit-like. The term pseudoscalariform is applicable to this pattern, or they may be considered to be intermediate between helical and scalariform. The vessels are mostly separated from each other by parenchyma (Fig. 25), so that the matrix of the secondary xylem is, in fact, parenchyma.
Figures 12–16. Sections of stems of *Stayneria neilli* (Figs 13–15) and *Mestoklema tuberosum* (Fig. 16). Fig. 13. Transection, showing vascular strands scattered within a background of fibres. Fig. 14. Transection, showing an adjacent pair of vascular strands; in the strands, from top to bottom, parenchyma, crushed secondary phloem, active secondary phloem, cambium (arrow), and radial chains of vessels. Fig. 15. Tangential section; a vessel runs from top to bottom, centre; to right of the vessel, parenchyma of vascular strand (storeyed); to left of vessel and at right of photograph, fibres, vaguely storeyed. Fig. 16. Tangential section through fibrovascular cylinder; left one-quarter of photograph shows vessels and parenchyma of the cylinder; right three-quarters shows fibres (some storeyed) of the cylinder. Figs 13, 16: scale in Fig. 1; Figs 14, 15: scale in Fig. 2.

Figures 17-20. Transections of stems of Aizoaceae. Fig. 17. Marlothiella uniondalensis; one vascular strand (top left) in a background of conjunctive tissue parenchyma; dark grey spots are raphide idioblasts. Fig. 18. Gliottiphyllum linguiforme; centre of stem; the earliest formed vascular cylinder, centre, has an inverted orientation of xylem and phloem. Fig. 19. Carpobrotus edulis; first fibrovascular cylinder (below) and subsequent densely fibrous stem tissue (top half of photograph). Fig. 20. Tetragonia tetragonioides; portions of two fibrovascular cylinders; vessels are scattered throughout the secondary xylem. Figs 17-20: scale in Fig. 1.

Figures 21–25. Tangential sections (Figs 21–24) and transection (Fig. 25) of upper root of Lithops turbiniformis. Fig. 21. Portions of two adjacent vessel elements, with secondary wall portions offset from each other rather than opposite each other. Fig. 22. Outer surface of tip of vessel element, showing perforation plate. Fig. 23. Longisections of two adjacent vessel elements, showing the non-extensible pseudoscalariform pitting. Fig. 24. Longisection of vessel, showing the perforation plate (slightly above centre) with borders rounded rather than sharp, between which is a thin layer of primary wall material. Fig. 25. Transection. Vessel elements (rounded lumina) are separated from each other by parenchyma (angular cells). Scale bars, 10 μm.

ONTOCENETIC DETAILS

The stems of *Aptenia cordifolia* (Fig. 26) clearly reveal the developmental details. The lateral meristem is not shown in Figure 26; at the top of this photograph are radial rows of large cells, the innermost conjunctive tissue parenchyma, which is derived from the lateral meristem. Secondary phloem, as well as fibres (Fig. 26, bottom half) of the secondary xylem, are shown, and, between them, a vascular cambium (arrow). The vascular cambium is a single cell in thickness. A significant detail is the fact that the number of cell files (counted tangentially, left to right in Fig. 26) in the phloem, cambium, and fibres is approximately double that in the conjunctive tissue parenchyma.

The photograph of *Mestoklema* (Fig. 27) shows a lateral meristem (pointers). There are about five layers of conjunctive tissue between the lateral meristem (and in radial seriation adaxial from it) and the secondary phloem. Abaxial to the lateral meristem are one or two layers of secondary cortex, produced by the lateral meristem and therefore with a radial seriation in line with cells of the lateral meristem. The number of primary cortical cells (Fig. 27), counted left to right, is approximately half the number of cell files in the conjunctive tissue parenchyma.

*Trichodiadema* roots (Figs 28, 29) have a lateral meristem. It is close to the vascular tissue in Figure 28, because this strand and the cambium from which it is derived are relatively recent products of the lateral meristem. At other points along the circumference of the lateral meristem, several layers of conjunctive tissue parenchyma lie between the vascular tissue and the lateral meristem. In the enlarged portion shown in Figure 29, there is only a single layer of conjunctive tissue parenchyma between the lateral meristem and the vascular tissue. More layers of conjunctive tissue would be expected to be deposited abaxial to the vascular tissue before another vascular cambium is derived from the lateral meristem, and such a vascular cambium forms another vascular strand. As with the *Mestoklema* section, the root of *Trichodiadema* (Fig. 29) shows many more tangential rows (counted tangentially) of vascular cambium, indicated by the arrow (and products of the vascular cambium, such as fibres), than there are initials in the portion of lateral meristem (pointers).

DISCUSSION AND CONCLUSIONS

Of prime importance in reaching conclusions about how the lateral meristem and the vascular cambia derived from it operate in Aizoaceae is a clear reading of the histology of the products. Implicit in the preceding sentence is the assumption that the lateral meristem, which first originates in the cortex of a primary stem, is the source of vascular cambia, which develop on its inner face, and that each of the vascular cambia produce secondary xylem and secondary phloem. This concept also presupposes that at least one layer of secondary cortex is produced by the lateral meristem, and that numerous layers of conjunctive tissue, mostly in the form of parenchyma, originate adaxially from the lateral meristem. These concepts appear to be validated by an earlier study (Carlquist, 2005), as well as the present one. The evidence lies in the histology of the products. The lateral meristem in the above concept can become quiescent, although in the actively growing Aizoaceae studied, recent cell divisions indicating its presence could frequently be seen. The same applies to the vascular cambia. Both secondary phloem and secondary xylem provide evidence that not only the outermost series of vascular cambia, but several cycles, are active simultaneously. The occurrence of crushed phloem, more of which can be found in the inner vascular tissues than in the outer ones, provides clear evidence of this. Successive cambia have no relationship to annual events, and the known chronological age of a plant, as well as growth rings (*Styneria*), shows that, typically, several cycles of vascular cambia and therefore several cylinders of vascular tissue are produced in a year by a stem or root. In Aizoaceae, as well as in other plants with successive cambia, a boundary can often be seen between late wood and early wood in the middle of a secondary xylem cylinder or band.

What is produced by the lateral meristem, what is produced by the vascular cambia, and how can one distinguish between these activities and products? The lateral meristem produces one to several layers of secondary cortex on its exterior face. The demarcation between secondary cortex and primary cortex is based on three characteristics. Primary cortex cells are randomly arranged, whereas secondary cortex cells are in radial series extending outward from the lateral meristem. The lateral meristem is distinguishable because of recent tangential divisions. The radial rows of secondary cortex cells are aligned with and have the same number as the rows of conjunctive tissue parenchyma. The secondary cortex cells also tend to be tangentially narrower than the primary cortex cells, suggesting that radial divisions take place during lateral meristem origin, whereas primary cortex cells divide less actively (and in various planes). Radial divisions of lateral meristem origin and tangential expansion are responsible for the storeyed nature of conjunctive tissue parenchyma, as seen in tangential divisions.

Are the fibres of stems of Aizoaceae produced by vascular cambia or by lateral meristems? As a prelude to answering this question, note should be taken that a vascular cambium need not give rise to equal amounts of secondary xylem and secondary phloem at any
Figures 26–29. Transections of stem (Fig. 26) and roots (Figs 27–29) of Aizoaceae, showing ontogenetic details. Fig. 26. *Aptenia cordifolia*; the vascular cambium (arrow) has produced secondary phloem (above cambium) and fibres (below cambium). Fig. 27. *Mestoklema tuberosum*; there are four or five layers of conjunctive tissue parenchyma between the lateral meristem (pointers) and the secondary phloem; cambium indicated by arrow; secondary xylem fibres at bottom. Fig. 28. *Trichodiadena bulbosum*, outer portion of root; inside about four layers of primary cortex (top) are about four layers of secondary cortex, which have been produced by the lateral meristem (pointers). Fig. 29. Same, enlarged. Recent divisions of the lateral meristem (pointers) indicate recent divisions of the lateral meristem, which is just beginning to form conjunctive tissue parenchyma subsequent to the production of secondary xylem (bottom) and secondary phloem by the vascular cambium (arrow). Figs 27, 28: scale in Fig. 2; Figs 26, 29: scale in Fig. 8.
particular locus. In recently formed vascular cambia of Nyctaginaceae, secondary phloem production often precedes secondary xylem production. Bands or cylinders of fibres are produced by vascular cambia before vessels are produced in Aptenia and Mestoklema. One may ask whether these fibres in Aptenia and Mestoklemareally are produced by vascular cambia or are part of the conjunctive tissue. The fact that the radial files of fibres (and secondary phloem cells) are fewer than the files of conjunctive tissue parenchyma in a given species is one line of evidence that fibriform cells are derived from vascular cambia. Another line of evidence is conveniently provided by the vascular increments of Glottiphyllum. In this genus, vascular bands may begin with fibres, outside of which zones of vessels plus parenchyma are produced. In other vascular bands, the reverse sequence occurs. In Glottiphyllum stems, it is also possible to find some increments composed wholly of fibres, and other increments composed wholly of vessels plus parenchyma. Longitudinal sections permit a distinction to be made between fibres and vessel elements, even though their diameters, as seen in transsections, may be similar.

In the fibrovascular cylinders of Mestoklema, secondary phloem may be produced in strands adjacent to fibrous tissue that forms continuous tangential bands rather than strands. Thus, at any given place, the vascular cambium may be producing sieve tubes but no vessels, only fibres. Such an inequality in vascular cambial products was observed in Simmondsia (Carlquist, 2002). In Simmondsia, the vascular cambium produces phloem strands externally; internally, it produces a tangentially continuous cylinder consisting of vessels and tracheids.

As mentioned above, storeying can occur in conjunctive tissue, but storeying can also occur in fibres of the secondary xylem (visible to various degrees in the Aizoaceae studied). The number of radial files of secondary xylem fibres and secondary phloem cells is greater than the number of radial files of conjunctive tissue parenchyma. This indicates that, in the process of origin of vascular cambia from a lateral meristem, radial divisions occur. The slender nature of vascular cells seems to be related to this phenomenon. An increase in the circumference of the vascular cambium was cited by Bailey (1923) as the reason for storeying in dicotyledons with storeyed cambia. This activity may account for some of the storeying seen in tangential sections of Aizoaceae, but the origin of lateral meristems from cortical parenchyma and the origin of vascular cambia from lateral meristems are mechanisms for the production of storeying that have not been discussed hitherto in the literature on plant anatomy.

The only exceptions in Aizoaceae to the above account of what tissues are produced and by what meristemtic activity are Ruschia and Stayneria. In these genera, fibres occur as a background in which vascular strands (which are the result of the formation of secondary xylem and secondary phloem from each of the numerous vascular cambia) are embedded. Secondary xylem consists of a single radial chain of vessels in each strand, and the addition of more vessels apparently ceases at the point at which each vascular strand becomes encased in fibres. Secondary phloem can be added because earlier formed phloem is crushed as new phloem is formed. The point of interest is that, if the origin of the fibres is traced, it must be concluded that most originate as conjunctive tissue, but the position of others adjacent to the vessels suggests an origin from the vascular cambium, an interpretation supported by the examination of cells maturing into fibres. Such an occurrence is not unprecedented, for this situation also appears to occur in Guapira and Pisonia of the Nyctaginaceae (Carlquist, 2005).

Conceding that fibres in most Aizoaceae are the product of vascular cambia, can the term ‘libriform fibres’ be applied? That term would probably be misleading because of the problem presented by Ruschia and Stayneria of the Aizoaceae and Guapira and Pisonia of the Nyctaginaceae. The remainder of Aizoaceae could be said to have libriform fibres. The vaguer term ‘fibre’ has been used in the account above. Those seeking definitions that have no exceptions may be dismayed by such a situation, but the exceptions in this case are very few.

Raylessness occurs in all of the Aizoaceae studied, with the exception of Tetragonia. Tetragonia also lacks the band-like distributions of fibres seen in Aizoaceae. Instead, Tetragonia has vessels scattered amongst fibres, and vasicentric axial parenchyma adjacent to the fibres. These are all symplesiomorphies for the wood of core Caryophyllales. Therefore, the opposite conditions in groups of Aizoaceae other than Tetragonia are synapomorphies, although the sampling in the present study is inadequate to reveal precisely where in the tree for Aizoaceae (using that of Klak et al., 2003) these synapomorphies are located. Tetragonia is placed in the subfamily Aizoideae by Klak et al. (2003), who regard Aizoideae as an outgroup to the remainder of Aizoaceae. The wood features of Tetragonia are phylogenetically congruent with this interpretation.

The similarity in the fibrous background tissue of the secondary xylem between Carpobrotus, Ruschia, and Stayneria is reflected in the tree of Klak et al. (2003), in that Carpobrotus and Ruschaipair together. From this tree, it can be concluded that thick fibrous stems are an apomorphy in Aizoaceae, and that herbaceous stems with relatively less secondary activity, such as those of Aizoon or Sesuvium, represent an ancestral condition.
The suborder Phytolaccoideae, as described by Behnke (1997), receives support from the phylogeny of Cuvéoud et al. (2002). In their tree of Caryophyllales, a clade is formed by Gisekiaceae, Phytolaccaceae, Agdestidaceae, Sarcobataceae, Aizoaceae, and Molluginaceae. In Phytolaccaceae, Gallesia and Seguiera have rays (Carlquist, 2000a), but the monogenic families Agdestidaceae (Carlquist, 1999) and Sarcobataceae (Carlquist, 2000b) do not. The phylogenetic status of ray presence remains an interesting problem that requires further investigation. Rays are present in Guapira and Pisonia of the Nyctaginaceae, but they originate from the lateral meristem (Carlquist, 2005), not from the vascular cambia, a departure that shows the complexity of this situation. Metcalfe & Chalk (1950) considered ray-like formations in some Nyctaginaceae, such as Bougainvillea, and some Amaranthaceae, such as Bosea, to be 'radial plates of conjunctive tissue', which is a possible designation, although they recognized rays in other genera of these two families. To base the definition of rays on either topography or ontogeny exclusively would result in awkward situations, although these two categories coincide in the definition of rays in the majority of cases.

Habit bears a relationship to stem and root histology in Aizoaceae. The highly fibrous stems and roots of Ruschia multiflora and Stayneria neilii correlate with the shrubby stature of these two species, which reach 2 m (Goldblatt & Manning, 2000). Mestoklema tuberosum, which has tough fibrous cylinders alternating with conjunctive tissue parenchyma, is a shrub to 70 cm (Goldblatt & Manning, 2000). The roots of Mestoklema have fewer and thinner fibrous cylinders than do the stems. The anatomy of the basal stem of Aptenia cordifolia, which has long sprawling branches, is very similar to the stem anatomy in Mestoklema, which has shorter upright branches. The prostrate stem of Carpobrotus may not seem congruent with its dense cylinder of fibres, but the cylinder may resist well the torsion to which Carpobrotus edulis plants, which grow on shifting sandy substrates, are subjected.

Lithops is acaulescent; all vascular structures studied were from the upper root (and possibly some from the hypocotyl). The external surfaces of the roots do not suggest a contractile capability; they have fissures that correlate with expansion and contraction related to moisture availability extremes. The fact that no fibres were observed in the roots of Lithops correlates with the shrinkage capability. The vessel walls, reported to have helical thickenings (Gibson, 1994), actually prove to have pseudocalariform pitting, which may be regarded as an expression of paedomorphosis (Carlquist, 1962). Pseudocalariformly pitted vessels do not have the capability to shrink and expand as do vessels with helical thickenings, such as those in the primary xylem. However, the vessels in Lithops are spaced apart from each other by parenchyma cells that do have the ability to shrink or expand.

Stems and roots with successive cambia have great adaptive potential. The relative amounts of parenchyma, fibres, vessels, and sieve tubes can easily be reallocated by this ontogenetic system so as to provide more mechanical strength, more flexibility, or more storage capacity. Aizoaceae have an enormous range of diversity in this respect. The stems of Ruschia and Stayneria have great mechanical strength, the stems of Carpobrotus and Tetragonia have great flexibility, and the roots of Mestoklema and Trichodiadema have plans related to storage ability. In another family of core Caryophyllales, Amaranthaceae, the successive cambial plan shows a great range of variations in histology (Carlquist, 2003) related to arboreecence (Charpentiera, Nototrichium), scapent shrubs (Bosea, to 10 m), and storage (Beta). Likewise, the successive cambia plan shows multiple structural adaptations to habit in Nyctaginaceae (Carlquist, 2005), including trees (Charpentiera, Guapira, Pisonia), lianas (Bougainvillea), and storage roots (Boerhavaia, Mirabilis). In Aizoaceae, water storage in leaves is obviously a strategy. However, the preservation of water columns in perennial axes, the loss of which would result in significant diminution of the plant body, is doubtless aided by the succulence of the stems and roots in many genera. The plan of successive cambia, in which vascular strands can be scattered throughout a storage structure, predisposes species with successive cambia to efficient storage plans, in which conducting strands are not far from any parenchyma cell in which starch or water can be located. This is clearly evident in the roots of Trichodiadema and in both the roots and stems of Marlothiella. Dicotyledons with a single cambium per axis achieve this by the lateral displacement of bundles and much branching of vascular strands; the single cylinder of bundles typical of dicotyledon stems cannot otherwise be dispersed well into storage organs.

The successive cambial plan can also be readily modified so as to achieve the separation of larger portions of vascular tissue by means of radial and tangential bands of parenchyma, a plan suited to lianas in which torsion is frequent. A much higher percentage of the dicotyledons with successive cambia are lianoid (Icacinaeae, Menispermaceae, etc.; Carlquist, 2001) than are dicotyledons with a single cambium. The fact that several cylinders of vascular cambia within a given stem can be active simultaneously in the production of fibres, secondary phloem, and secondary xylem is a fact that has not been appreciated where conduction and mechanical strength is concerned.
the ontogenetic patterns of plants with successive cambia become better understood, we can expect studies on physiology to follow. Although few of the plants with successive cambia have much economic importance, this does not make them less interesting scientifically. Solving the technical and conceptual difficulties that plants with these structures possess should lead to fascinating new perspectives.

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REFERENCES


