Living cells in wood. 2. Raylessness: histology and evolutionary significance

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Raylessness occurs in several hundred species belonging to about 40 families (fewer depending on taxonomic delineation). Fibre distribution (raylessness at first, followed by origin of rays), fibre wall thickness and sclerenchyma at pith margins support the idea that rapid acquisition of mechanical strength is basic to most instances of raylessness. Raylessness may be the most readily available process for achieving mechanical strength in ancestrally herbaceous groups lacking large amounts of phloem and cortical fibres. Raylessness is not a uniform phenomenon and a small number of instances suggest alternative causation, as in two lianas (Cobaea, Thunbergia). Raylessness occurs in only a small number of trees and annuals, but is found in woody herbs, subshrubs and some shrubs. It is indicative of secondary woodiness and wood paedomorphosis. Raylessness would seem to block the radial flow that rays typically provide, but a surprising number of rayless woods have moderately pitted fibres (indicative of flow) and septate or non-septate living fibres. Three-dimensional networks of conjunctive tissues in rayless species with successive cambia (Aizoaceae, Amaranthaceae, Nyctaginaceae) could also provide radial flow avenues. Ontogenetic changes from raylessness to ray presence within the stem of a given species are described and illustrated. Pseudo-raylessness, late-onset raylessness and early-onset raylessness are recognized. Systematic distribution and pertinent literature are given for known instances of raylessness and pseudo-raylessness. Raylessness shows that wood evolution involves not merely change in the abundance and position of cell types, but also redesign and diversification in cell types. © 2015 The Linnean Society of London, Botanical Journal of the Linnean Society, 2015, 178, 529–555.


INTRODUCTION

The inclusion of a study on rayless woods in a series of papers devoted to various aspects of parenchyma may seem ironic, given that rays are one kind of parenchyma in wood. However, in perhaps the majority of species with rayless woods, rays and (often at the same time) axial parenchyma develop after the first year, indicating that parenchyma does have a significant selective value. These instances also suggest that raylessness has value during the first year of the development of a stem. In fact, more than a few rayless woods have living fibres (which have a close similarity to parenchyma in aspects other than cell shape and wall thickness) and such rayless woods are composed mostly of living cells.

Raylessness in wood proves not to be a uniform phenomenon and thus this essay explores the diversity of expressions that can be described within that term. We are only just beginning to appreciate this diversity. Wood anatomy is still a field governed by an interest in arboreal species. Even those workers reasonably familiar with wood anatomy may never have looked at wood sections that are rayless. The most species-rich rayless genera that are rayless are probably Atriplex L. (chenopodioid Amaranthaceae), Cyrtandra J.R. Forst. & G. Forst. (Gesneriaceae), Hebe Comm. ex Juss. (= Veronica L. p.p., Plantaginaceae) and Silene L. (Caryophyllaceae). Rayless trees are few: Heimerliodendron Skotts. (Nyctaginaceae) is one. Few annuals have been reported to be rayless; Halophytum Speg. (Halophytaceae; Gibson, 1978) is one, but Brassicaceae are likely to offer more numerous examples than the genus cited. Investigations of
the secondary xylem of annual angiosperms are still few.

Recognition of raylessness in angiosperm wood is certainly not recent. Solereder (1908: 1144) listed 27 families in which raylessness has been reported; nearly all of these are confirmed by the systematic distribution list in the present essay, which expands that listing appreciably. Ontogenetic dimensions remained to be explored, and these were considered by Barghoorn (1940, 1941a, b) in his studies on ray ontogeny. The cells in potential ray areas (and their precursors in the vascular cambium) do not subdivide horizontally, but instead elongate into fusiform cells which mature into libriform cells indistinguishable from the libriform fibres in a fascicular zone. This similarity between fibres in potential ray areas and those in fascicular areas is possible only in woods with more numerous apomorphic cambial features, so that there is minimal disparity between height of ray cells and length of fusiform cells. Raylessness is commonly found in clades with more herbaceous species.

Raylessness is a form of paedomorphosis, or protracted juvenilism, in woods (Carlquist, 1962, 1970). Raylessness, although not common in woody angiosperms as a whole, is notable in secondarily woody plants (e.g. the Hawaiian species of Caryophyllaceae, Geraniaceae, Plantaginaceae, Primulaceae and Violaceae; Carlquist, 1974).

These generalizations lead us to the question of why raylessness develops. Is there a single unifying explanation? In turn, this question leads us to ask what diversity rayless woods show, and the types of diversity are explored in the present essay. The number of rayless species is small enough so that this group can be sampled sufficiently to monograph the phenomenon and give the systematic occurrence at the level of families and genera.

MATERIAL AND METHODS

Most sections were derived from dried specimens, but some stems were fixed in 50% aqueous ethanol. Methods are described in the papers cited in the Systematic Distribution section of the paper. The figures are arranged mostly in terms of systematic groupings. (e.g. Figs 2 and 3 show Asteraceae, Figs 5–8 represent Lamiales and Figs 10–12 feature Caryophyllales). Smaller family units are used in the running text, but with recognition of more comprehensive recent treatments (e.g. epacrid Ericaceae). A similar convention is followed in the systematic listing. The diverse kinds of raylessness are presented as a series of 22 points that are exemplified by these systematic groupings.

The term ‘fascicular xylem’ refers to secondary xylem other than rays. The term ‘vascular cambium’ is now preferred to merely ‘cambium’ for the meristematic layer in woody plants, thereby permitting ‘monocot cambium’, ‘master cambium’ (in species with successive cambia) and other types of cambial activity to be recognized more clearly.

The present essay is a review, a presentation of original observations and an offering of hypotheses and questions. As such, the organization departs from the usual sharp division between presentation of results and conclusions, because that would involve constant separation of observations from the interpretations of what is seen in species after species. However, the paper does conclude with 12 summations of what is evident when one takes the totality of knowledge of this phenomenon into account and constructs generalizations based on the survey of groups. The presentation does not describe rayless species sequentially, but examines questions and concepts about raylessness. The illustrations are based on systematic groupings, but these groupings lend themselves to the 22 phenomena seen in those groupings.

OBSERVATIONS ON RAYLESSNESS AS SEEN IN ILLUSTRATED SPECIES

1. DEFINING AND CHARACTERIZING RAYS AND RAYLESSNESS

A ray consists of a radial sheet of parenchyma cells in secondary xylem. To be more inclusive than that, one must note rather particular conditions and include or exclude them from that definition. For example, rays may be only one cell wide and one cell high, as in certain epacrids (Solereder, 1908; Lens et al., 2003) or Setchellanthus Brandegee (Carlquist & Miller, 1999), or they can be indefinite in extent vertically (Piperaeaceae). Rays may be augmented by progressive addition of (chiefly uniseriate) rays in the case of aggregate rays in Fagaceae, the ray margins of which can therefore be difficult to define.

A serious challenge to ray definition is implicit in Metcalfe & Chalk (1950), who designated rays in stems of certain species with successive cambia as ‘radial plates of conjunctive tissue’. This has been countered by evidence from Amaranthaceae (Carlquist, 2003) and Nyctaginaceae (Carlquist, 2007a). If the rays in these families do not qualify as rays, then we must recognize two categories which are, in fact, indistinguishable in terms of anatomy. My usage follows that of Solereder (1908), who recognized raylessness in some but not all chenopods (Amaranthaceae s.l.), such as Atriplex. Radial plates of xylem extend outwardly to a vascular cambium or else a master cambium; in the former case, phloem rays are separated from xylem rays by the cambium.
In the instance of successive cambia, a ray may abut outwardly on a master cambium outside of which there is no phloem (e.g. *Pisonia* L.).

To determine whether rays are present in a given stem, one must view not only tangential sections but also transverse and radial sections. Elliptical groupings of cells as seen in a tangential section may not extend radially, as seen in transverse or radial sections. If such groupings do not extend radially in the form of sheets, they are axial parenchyma rather than rays.

2. PSEUDO-RAYLESS WOODS

This term is hesitantly applied to woods with large multiseriate rays (e.g. Fig. 1A), which when seen in tangential section prove to be composed of upright fusiform cells (Fig. 1B, D) that resemble thin-walled

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**Figure 1.** Sections to show ray ontogeny and histology in woods. A-C, *Begonia parviﬂora* Wall., *Carlquist* 7050 (RSA). A, transverse section. Rays are wide and undivided. B, pseudo-raylessness: ray cells are elliptical-like fibres, but shorter and wider than the libriform fibres in the non-ray (fascicular) areas of the wood. C, radial section: ray cells have blunt rather than fusiform tips. D, *Lactoris fernandeziana* Phil., *Stuessy* 11178 (OS), tangential section. Pseudo-rayless condition. Ray cells about the same height as libriform fibres, but wider than them. E–F, *Diapedium assurgens* Kuntze, SJRw-51436, wood sections to show late-onset raylessness. E, transverse section: a wide multiseriate ray transitions into non-ray (fascicular) secondary xylem. F, tangential section. Potential ray area, composed of fibriform cells, left. Abbreviations: fc = fibriform cells and strands; fx = fascicular xylem composed of fibriform cells; urc = upright ray cells.

fibres. However, in such woods the differences between ray cells and fibres is easy to detect, and both may be storeyed (Fig. 1B, D). Cells along the margins of the rays may be intermediate between ray cells and libriform fibres. In Lactoris fernandeziana Phil. (Fig. 1D), the young stems show fewer differences between cells of fascicular areas and those of rays (Carlquist, 1964), but the differentiation between the two is more pronounced in older stems (Carlquist, 1990).

Ray cells in wood that are pseudo-rayless are all upright, as seen in radial section (Fig. 1C). However, they tend to be somewhat shorter and wider than libriform fibres in the woods in which they occur (Fig. 1B, D). Significantly, the ray cells as seen in radial section are blunt at their ends (Fig. 1C). Thus, their tips are mitred or chisel-like rather than fusiform. In true raylessness, cells in potential ray areas develop acicular (pointed) ends. Such cells are, in turn, intrusive and about as long and wide as the fibriform cells in the fascicular xylem.

In addition to the examples from Begoniaceae (Fig. 1A–C) and Lactoridaceae (Fig. 1D), pseudo-raylessness can be found in Impatiens L. of Balsaminaceae (Lens et al., 2005b, 2012). Impatiens also has true raylessness (Lens et al., 2005b, 2012). Woods like those shown here for Begonia L. are also present in some species of Piperaceae (original data).

3. LATE-ONSET RAYLESSNESS

In some cases of raylessness, wide multiseriate rays begin at the pith of a stem and extend outwards (Fig. 1E). Examples are furnished here in Diapedium assurgens (L.) Kuntze (Fig. 1E, F) and Artemisia pycnocephala DC. (Fig. 2A–D). This ontogenetic process would also probably account for raylessness in Impatiens (Lens et al., 2005b, 2012). In D. assurgens, there is an imperceptible shift from ray cells to fibriform cells in a potential ray area (Fig. 1E). Eventually, the fibriform cells grade into true fascicular xylem, indicated by the presence of vessels (Fig. 1E, top). The intermediate stage, that of fibriform cells without accompanying vessels, is shown for D. assurgens in Figure 1F.

A similar ontogeny was observed in Artemisia pycnocephala. The three stages in conversion of a multiseriate ray to fascicular secondary xylem are indicated in Figure 2A. A tangential section of the wood (Fig. 2B) shows that strands of two cells (cross walls, cw) are scattered in potential ray areas. Radial sections (Fig. 2C) reveal that these are not ray cells with blunt ends; they are isolated strands of parenchyma with fusiform tips. Both axial parenchyma and libriform fibres have nuclei (Fig. 2C, D) and thus A. pycnocephala provides us with an example of living fibres that are non-septate. Admixture of libriform fibres with fusiform two-celled strands of parenchyma characterizes the transitions between rays and fascicular tissue in D. assurgens (Fig. 1F) as well as A. pycnocephala. The conversion of ray areas to fascicular xylem happens gradually, and is not sharply demarcated, in Lysimachia L. (see Fig. 13F). Thus, conversion of ray areas to fascicular xylem in species with late-onset raylessness may proceed transitionally. The transitional zones can feature a mixture of fibres and two-celled strands; the latter are not ray cells (they do not occur in radial sequences) but do qualify as parenchyma strands.

4. EARLY-ONSET RAYLESSNESS

Most instances of raylessness involve early-onset raylessness, and the present essay is designed to show how this ontogeny can be detected. Early-onset raylessness is defined by lack of rays at the pith margins; potential ray areas begin with fibriform elements (mostly libriform fibres). Early in secondary xylem formation, the cambium in potential ray areas therefore consists of fusiform cells. Transverse sections of the wood of Artemisia tridentata Nutt. (Fig. 2E) show an origin of multiseriate rays after the initial raylessness, as do tangential sections (Fig. 2F). The first two years (growth rings strongly demarcated in A. tridentata by interxylary cork) may lack rays entirely (Fig. 3A), as evident by the difference in wall thickness of ray cells and fibriform cells (= libriform fibres).

Other examples of early-onset raylessness illustrated here include Artemisia rothrockii A.Gray (Fig. 3B), Pelargonium hortorum L.H.Bailey (Fig. 4B, C), a species of Cyrtandra section Chaetocalyces (Fig. 7E) and Silene verecunda S.Watson (Fig. 10C). In most of these, after initial raylessness, rays begin a few at a time as multiseriate rays that originate abruptly (Fig. 10C). Pelargonium hortorum is unusual in that the rays first initiated are biseriate or uniseriate (Fig. 4C). The material of Artemisia rothrockii (Fig. 3B) studied shows both conversion of ray areas to fascicular secondary xylem (late-onset raylessness, mro) and the origin of multiseriate rays in fascicular areas (early-onset raylessness, mre). Unless specifically noted otherwise here, the species mentioned may be presumed to have early-onset raylessness.

5. DO RAYLESS SPECIES EXEMPLIFY AN INCREASE OF MECHANICAL STRENGTH OF WOOD?

Rayless species were claimed to represent an increase in mechanical strength (Carlquist, 1988). What is the anatomical evidence for this in the species illustrated...
Early-onset raylessness represents substitution of presumptively mechanically strong libriform fibres (often thick-walled) in place of thin-walled ray cells very early in the development of secondary growth. Certainly, thick-walled fibres characterize species such as *Artemisia tridentata* (Fig. 3A), *A. rothrockii* (Fig. 3B), *Eriocephalus africanus* L. (Fig. 3C), *Geranium tridens* Hillebr. (Fig. 4E), *Penstemon azureus* Benth. (Fig. 6A), latewood of various Polemoniaceae (Fig. 9A, C), portions of growth rings of *Dianthus* L. and *Silene* (Fig. 10A and especially Fig. 10D), *Frankenia* L. (Fig. 12D) and *Lysimachia* (Fig. 13F). This is also true in species with interxylary phloem (*Stylidium glandulosum* Salisb., Fig. 13E) and successive cambia (*Stenneria* L.Bolus, Fig. 11A, B and *Grayia spinosa* (Hook.) Moq., Fig. 12A, B).

By contrast, *Xanthium strumarium* L. (Fig. 3D) is included here to demonstrate libriform fibre thickness.

**Figure 2.** Raylessness in *Artemisia* (Asteraceae). A–D, *Artemisia pycnocephala* DC., *Balls* 19499 (RSA). A, transverse section, showing late-onset raylessness. B, tangential section; at centre, a zone transitional from ray cells to fascicular xylem. C, radial section; fibres are nuculate; cross-wall indicates cell pair is a strand of axial parenchyma. D, tangential section, showing living fibres and axial parenchyma cells adjacent to a vessel (vessel not shown). E–F, *Artemisia tridentata* Nutt., *Carlquist* 1701 (RSA), early-onset raylessness. E, transverse section; ray originates after the rayless condition which begins secondary growth. F, tangential section showing latewood, earlywood, and two multisierate rays. The latewood cells are mostly interxylary cork. Abbreviations: cw = cross walls of parenchyma strands; lw = latewood; mr = multisierate ray; n = nucleus; origin of a multisierate ray.
and pith and ray cell thickness more common in woody angiosperms that are not rayless. Wide multiseriate rays in this species are intercontinuous with thin-walled pith cells, and thin-walled cells can be presumed to have less mechanical strength than sclerenchyma. Sclerenchyma in and bordering the pith would be important if we could correlate it with habit, because it could add as much to mechanical strength of a stem as the substitution of fibres for ray cells that raylessness confers. An increase in thickness of lignified walls of pith sclereids and fibres adjacent to the pith can presumably be achieved without complex genetic changes. Pith sclerenchyma is illustrated here for *Artemisia rothrockii* (Fig. 3B), *Eriocephalus africanus* (Fig. 3C) and *Lysimachia kalalauensis* Skotts. (Fig. 13F).

**Figure 3.** Ray presence (D) and absence (A–C, E, F) in Asteraceae. A, *Artemisia tridentata*, Carlquist 1701 (RSA), transverse section showing two successive years of rayless wood. B, *Artemisia rothrockii* A.Gray, Anderson 2933 (KSC), late-onset raylessness (mre) and early-onset raylessness (mro) in a single transection. Note pith-periphery fibres. C, *Eriocephalus africanus* L., Carlquist 1813 (RSA), transverse section, showing early-onset raylessness. D, *Xanthium strumarium* L., Anderson 2983 (KSC), transverse section, ray cells clearly delineated, ray and pith cells thin-walled. E–F, *Lasthenia macrantha* Greene, Ornduff 4140 (UC). E, transverse section; vessels undetectable because they are the same diameter as the libriform fibres. F, tangential section; fibriform cells are homogeneous. Abbreviations: mre = multiseriate ray ends; mro = multiseriate ray originates; raf = potential ray area converted to libriform fibres.)
Rays often have secondary walls that presumably offer more strength than ray cells that have only primary walls. The mechanical strength of rays with secondary walls is hypothesized here to be less than the equivalent volume of fibres.

Rays undoubtedly function in radial translocation of photosynthates, as has been claimed by various authors (Sauter, 1966a, b; Carlquist, 2007a). The less the accumulation of secondary xylem, the less the amount of radial photosynthetic conduction that would therefore be hypothesized. Also, radial conduction of photosynthates in cell types other than rays may occur.

6. RAYLESS SPECIES WITHOUT MECHANICAL STRENGTH ENHANCEMENT
In considering any hypothesis, explaining exceptions is as important as presenting the supporting

instances. By comparing the exceptions to such factors as habit and ecology, we can often see some compelling correlations. *Xanthium* L. (Fig. 3D), introduced here as an example of a genus of Asteraceae without anatomical mechanisms suggesting enhanced mechanical strength, has rays. *Xanthium* plants attain modest height and grow in open areas. Lower branches are often close to horizontal, and plant height is probably limited by dispersal mode (the ‘cockleburs’ are adaptations for catching on the hair of terrestrial animals).

Although some species of *Artemisia* L. have pith and pith-adjacent fibres or sclerenchyma, *Artemisia pycnocephala* lacks them. The libriform fibres of *A. pycnocephala* wood are also relatively thin-walled (Fig. 2A–D). This species has a sprawling, rhizomatous habit, with upright branches that are short and terminate in inflorescences. Thus, the secondary xylem of the rhizomes (illustrated here) might not be expected to have enhanced mechanical strength.

Likewise, *Lasthenia macrantha* (A.Gray) Greene (Fig. 3E, F) shows no mechanically strong cells in its pith, and secondary xylem consists of wide thin-walled libriform fibres. One cannot, in fact, distinguish vessels from libriform fibres in a transverse section (Fig. 3E). *Lasthenia macrantha* is the only perennial in a genus otherwise composed of annuals. It is a beachside shrub with a lax or spreading habit.

7. **Diversification in Geranium L.: ray elimination or wood adaptation?**

Barghoorn (1941b) used *Geranium tridens* as one of the species in his study of the ontogeny of raylessness. The subtitle of his paper, 'The elimination of rays', suggests that in phylogenetic terms, absence of rays is what we term today an apomorphy. That may be true, but is there evidence that raylessness, rather than being a loss of a feature, represents an innovation, a mechanical enhancement, in most rayless species? Vivianiae, a possibly valid segregate of Geraniae, have rayless woods, perhaps for the entire life of a particular plant (Carlquist, 1985c). In Geraniaeae, so far as is known, woods are rayless to begin with and then develop rays: early-onset raylessness. In *Pelargonium hortorum*, rays are absent at first (Fig. 4A, B) but then uniseriate and biseriate rays develop (Fig. 4C). In *P. domesticum* L.H.Bailey (not illustrated), rays develop after a small amount of rayless wood is formed, and then widen markedly, often breaking open and becoming spaces in the woody cylinder. *Pelargonium domesticum* is a small, sparsely branched shrub. Wood of the Hawaiian species reflects ecology and habit. *Geranium tridens* (Fig. 4E, F) is shrubby, but in a distinctive way. The stems are elongate and little branched, terminating in small leaf clusters. This is in accord with the torsion doubtless created by the winds at upper elevations of Haleakala, Maui. The wood anatomy reflects this habit and ecology. The rays are wide and multiserate, with prominent central gaps, which may reflect constant necrosis related to twisting of the stems. The thick-walled fibres seem ideal adaptations to buffeting in the open alpine conditions. The vessels are notably narrow, and thus less likely to be damaged by torsion, and they also reflect xeromorphy: narrower vessels characterize xeromorphic woods (Carlquist, 1966). *Geranium arboreum* A.Gray (Fig. 4G, H) also grows on Haleakala, but in mid-elevation valleys where it is exposed to less wind and has greater moisture availability. It has less necrosis in multiserate rays. The libriform fibres are wider and thinner-walled than those of *G. tridens* and the vessels are much wider than in *G. tridens*. Wood of *G. cuneatum* Hook. (not illustrated) from exposed slopes of upper reaches of Hualalai, Hawai‘i, has similar wood to that of *G. tridens*.

*Pelargonium hortorum* (a presumptive garden hybrid) has low vessel density (Fig. 4A), suggesting that whatever the ecology of its ancestors, it is now adapted to sites that are not strongly xeric. The libriform fibres of *P. hortorum* (Fig. 4D) are living fibres and are filled with starch. *Pelargonium hortorum* may, in its wood, reflect artificial selection, because such large amounts of water and starch storage in secondary xylem suggest appreciable reserves related to flowering. *Pelargonium hortorum* is able to survive for long periods of time without watering, which may be related to water storage capabilities of the living fibres. Plants leaf out and flower rapidly when moisture becomes available.

8. **Living fibres: more common in rayless woods?**

Septate fibres are commonly thought to be living fibres, and their development of septa is thus evidence of protoplast longevity. We have little knowledge of living non-septate fibres, because most wood studies have been based on wood samples preserved by drying, in which evidence of protoplast presence is no longer visible. The important studies of Wolkinger (1969, 1970a, b, 1971) on living fibres are unfortu-nately not widely accessible to wood anatomists. In the present study, liquid-preserved materials were available for *Artemisia pycnocephala* (Fig. 2C, D), *Pelargonium hortorum* and *Veronica speciosa* R.Cunn ex A.Cunn. (as *Hebe speciosa* (R.Cunn ex A.Cunn.) Andersen) (Fig. 5A–E). Nuclei are present in the non-septate fibres (imperforate tracheary elements) of these species. Interestingly, the imperforate tracheary
elements of *V. speciosa* are not libriform fibres, but fibre-tracheids (Fig. 5E). The pits of the fibre-tracheids vary in size and the degree to which they are bordered, but they are smaller than the bordered pits on vessel-to-vessel faces (Fig. 5D).

The libriform fibres of Plantaginaceae (Fig. 6) may be living fibres, but the wood samples of insular species of *Plantago* L. that have been studied were all from dried material. Septate fibres are common in woods of Gesneriaceae (Fig. 7; notice particularly Fig. 7F) and Acanthaceae (Fig. 8), and have been illustrated for the rayless genus *Alseuosmia* A.Cunn. (Carlquist, 2015).

9. Structure favouring radial conduction in rayless woods

*Veronica* (Fig. 5A) and *Calceolaria* L. (Fig. 5F) show prominent radial grouping of vessels, a feature also evident in *Geranium* (Fig. 4E, G), *Jacobinia* Moric. (Fig. 8A) and, to some extent, most rayless woods. The radial seriation of vessels may account for radial conduction of sap and for connection of the conductive function in recently formed wood with that in older but still functional wood. This is a phenomenon commonly represented in ray-bearing woods also.
Rays account for radial conduction of photosynthates among living cells (Sauter, 1966a, b; Braun, 1970), a phenomenon undoubtedly related to the density of pits, and their frequently bordered nature, on the tangential walls of ray cells (Carlquist, 2007a). In addition, however, is there evidence for radial conduction among libriform fibres, albeit less pronounced than that among ray cells? This question was raised in connection with the rayless genus Alseuosmia, which has prominent pitting on tangential surfaces of the living fibres (Carlquist, 2015), a fact that suggests conductive possibilities; libriform fibres in woods commonly have sparse and small pits on tangential surfaces. Prominent pitting on tangential walls of septate fibres is seen in sectional view in Cyrtandra (Fig. 7F); the tangential walls are much more densely pitted than the radial walls (seen in face view in Fig 7F). The living fibres, noted above for Artemisia pycnocephala, Geranium hortorum and Veronica speciosa, are probably much more commonly represented in living fibres than at present appreciated, but we have reports of non-septate living fibres in only a small number of angiosperm woods.

10. ABSENCE OF TRACHEIDS IN RAYLESS WOODS

Tracheids (sensu Bailey, 1936; Carlquist, 1988; Sano et al., 2011), although present in quite a number of woody angiosperms (instances of vasicentric tracheids not included), do not occur in any of the woods reported here to be rayless, although tracheids might be expected to be of value for radial conduction. The reason for tracheid absence lies in the fact that no instances are known in which upright ray cells mature into tracheids. Ray tracheids have been reported, to the best of my knowledge, only in one angiosperm species, *Tetracentron sinense* Oliv. (Bailey & Thompson, 1918). The conversion of potential ray areas to tracheids could only occur in a clade that characteristically has tracheids in fascicular xylem areas, and no such instances have been reported. The occurrence of fascicular xylem composed of fibre-tracheids in *Hebe* (Veronica) represents only a small divergence in this direction. Occurrence of tracheids in fascicular xylem of rayless species is much less likely than occurrence of libriform fibres or even fibre-tracheids, because tracheids are usually appreciably longer than upright ray cells and thus not likely show similarity in vertical dimensions.


In searching for evidence of radial transport of photosynthates among living fibres, we need to consider possible instances in which the value of mechanical strength outweighs the value of radial conduction of photosynthates. In several instances of early-onset raylessness, the rays that originate after the initial rayless secondary xylem is formed are few in number but multiseriate and moderately large. Such instances are shown here for *Artemisia tridentata* (Fig. 2E, F) and *Cyrtandra anthropophagorum* Seem. (Fig. 7C, D). This is a feature related to raylessness that has not been noted before. One could interpret such ray sparseness as either an instance of slow conversion to a ray-bearing condition, or partial retention of the values of the rayless condition. The rays of *Geranium tridens* are relatively large, and that may be an example of torsion accommodation.
The rays of *Plantago* are also relatively few in number. Michener (1981) noted that in wood of *Keckiella* Straw, various degrees of raylessness occur, and perhaps none of the species is completely rayless. That is very probably true, although particular wood samples of *Keckiella* and the related genus *Penstemon* Schmidel may lack rays entirely.

Various degrees of ray acquisition in Gesneriaceae are illustrated in Figure 7. *Besleria* L. of Gesneriaceae (Fig. 7A) lacks rays entirely. No rays were evident in mature wood samples of four of the species of *Cyrtandra* studied: *C. cordifolia* Gaud., *C. hornei* C.B.Clarke, *C. prattii* Gillespie and *C. victoriae* Gillespie. Wood anatomy of only a small number of *Cyrtandra* species has yet been studied (Carlquist & Hoekman, 1986). *Cyrtandra anthropophagorum* (Fig. 7C, D) has a paucity of rays, whereas other *Cyrtandra* species have more numerous rays (Fig. 7E). These tendencies are not linked to stem diameter, at least not with appreciable exceptions, because some species have few rays even in stems of large diameter (Carlquist & Hoekman, 1986). Other members of Gesneriaceae have numerous rays (e.g. *Coronanthera* Vieill. ex C.B.Clarke) and *Cyrtandra* is thus distinctive in the family. *Cyrtandra* is a large genus, however, and only a small percentage of the species have been examined with respect to wood anatomy. *Cyrtandra* is characteristically found as an understorey shrub in moist forest. The relationship between habitat and raylessness and the thin-walled nature of the (often) septic fibres needs to be studied with respect to ecology.

12. QUANTITATIVE VESSEL FEATURES OF RAYLESS WOODS

The species studied here mostly have notably narrow vessel elements. Citing only the low-power transverse sections here, this tendency is exemplified by *Diape- dium* J.Koenig (Fig. 1E), *Artemisia* (Figs 2E, 3B), *Pelargonium* L’Hér. ex Aiton (Fig. 4A), *Geranium tridens* (Fig. 4E), *Veronica* (as *Hebe*; Fig. 5A), *Calceolaria* (Fig. 5F), *Plantago* (Fig. 6C, E) *Besleria* (Fig. 7A), *Cyrtandra* (Fig. 7E), *Jacobinia* (Fig. 8A), *Leptodactylon* Hook. & Arn. (Fig. 9A), *Eriastrum* Wooton & Standl. (Fig. 9C), *Dianthus* (Fig. 10A), *Silene* (Fig. 10C) and *Kalanchöe* Adans. (Fig. 13A). Vessel density is correspondingly high in most of these. This suggests that these are adapted to relatively dry situations, as with Asteraceae from arid situations (Carlquist, 1966). The correlation seems to be not merely due to xeric conditions *per se*, but to the fact that herbs with secondary woody tendencies occur in disturbed habitats where herbaceous groups have more opportunities to radiate. *Jacobinia* and *Cyrtandra* certainly typify moister habitats. Low vessel density, as in *Cyrtandra* and in *Pelargonium hortorum*, is indicative of more mesic habitats (Carlquist, 1975). Because *Pelargonium hortorum* is a hybrid that has originated in cultivation and been propagated for many years under mesic conditions, we cannot speak with assurance about how quantitative vessel features might match a particular habitat.

The two species with notably large vessels (as well as some small ones) are the lianas *Thunbergia alata* Bojer ex Sims (Fig. 8E) and *Cobaea scandens* Cav. (Fig. 9E). *Bougainvillea* Comm. ex Juss. (Fig. 11E) also qualifies in this regard; it is a scandent shrub. Occurrence of wide vessels has been reported for over a century in lianas by numerous workers. The vessels in two tree species represented here, *Geranium arborescens* (Fig. 4G) and *Heimerliodendron bruni- anum* (Endl.) Skottsb. (Fig. 11C), are relatively wide, as is expected for tree species in groups that have radiated into various habitats (Carlquist, 1966).

13. RAYLESSNESS AND HABIT: SHRUBS VS. LIANAS

An attempt has been made here to study and illustrate rayless woods from plants of diverse habits. The predominant growth form for rayless species is a shrub: more than a few are subshrubs. The correlation here is that with numerous stems branching from the base of a plant, the secondary growth of any particular stem is finite. Presumably increased mechanical strength in such a growth form is important, because large quantities of mechanically strong tissue as a result of prolonged cumulative addition of fibrous tissue, as in a tree trunk, are not available. Among the subshrubs and shrubs branched from the base studied here are the species of *Artemisia, Atriplex, Calceolaria, Cyrtandra, Dianthus, Eriastrum, Erica*, *Eriocéphalus L., Frankenia, Geranium, Grayia Hook. & Arn., Hebe (= Veronica), Jacobinia, Kalancheö, Leptodactylon, Lysimachia, Pelargonium, Penstemon, Plantago, Silene, Stayneria and Stylidium Sw. ex Willd.*

*Hebe* contains a range from subshrubs (including the distinctive ‘whiplash’ species) to large shrubs. The various *Cyrtandra* species represent ‘woody herbs’, understorey shrubs and understorey trees. In view of these ranges in habit, the occurrence of raylessness in two lianas presented here is remarkable. Wide, tall rays have been considered zones in liana stems that provide flexibility related to stem torsion experienced by lianas. Such rays are characteristic of such lianoid genera as *Aristolochia* L. and *Piper* L.

In *Thunbergia alata*, the wood (Fig. 8E, F) is rayless, but it has an alternative plan representing lianoid adaptations. Libriform fibres sheathe the large-diameter vessels that are probably vulnerable to breakage in a liana and thus lessen vessel rupture.
The lateral plate-like extensions of the fibre sheaths is unusual in Acanthaceae (Carlquist & Zona, 1988). Some of these plates are tangentially intercontinuous, which would provide a rigidity counterproductive in a liana (Fig. 8E). This is countered by natural breakages that displace these fibres (df, Fig. 8F) and parenchyma invades the resultant gaps in the fibre bands. These breakages compensate for the lack of rays as flexibility zones. Also important in this regard is the sheathing of interxylary phloem strands (ixp, Fig. 8F) with thin-walled parenchyma. The parenchyma presumably minimizes stress to the phloem strands, which consist of relatively large sieve-tube elements.

*Cobaea* Cav. (Polemoniaceae) has bands of libriform fibres alternating with parenchyma zones (Fig. 9E, F). The parenchyma zones are irregular in shape and cannot be characterized as rays. Most of the zones of thin-walled fibres (Fig. 9E, F) are abaxial to large vessels (Carlquist, Eckhart & Michener, 1984). The amount of wood that consists of thin-walled fibres is less than the quantity of parenchyma and thus flexibility is enhanced.
14. PARENCHYMA ZONES IN RAYLESS WOODS: NATURE AND DIVERSITY

Septate fibres form a background in some woods, such as those of Gesneriaceae (Fig. 7) and Acanthaceae (Fig. 8). Septate fibres can be regarded as a parenchyma substitute: they can store water and photosynthates and transfer liquid cell contents from one fibre to another (presumably at a moderate pace compared with procumbent ray cells, which have densely pitted tangential walls). The phenomenon of fibre dimorphism illustrates that flow of solutes among fibriform cells does occur (Carlquist, 2014). Septate fibres are a convenient combination of storage and mechanical strength functions (Carlquist, 2014, 2015). Another alternative is the formation of parenchyma bands that are continuously formed in the secondary xylem.
of certain woods, the characteristic axial parenchyma patterns (aliform, confluent, etc.). In addition to those patterns, one can find instances of parenchyma bands formed at irregular intervals in rayless woods. These are located primarily in latewood or are of indefinite extent. Good examples of these may be seen in various *Penstemon* species (Fig. 6A) and Caryophyllaceae (Fig. 10A–D). *Dianthus* has irregular concentric bands of fibres alternating with parenchyma (Fig. 10A, B). *Silene* also has parenchyma bands of indefinite extent or fibres interpolated into such bands (Fig. 10C, D). However, *Schiedea* Cham. & Schltdl. (Fig. 10E, F) and other Caryophyllaceae do not have such banding. The parenchyma bands may occur in either latewood or earlywood (Fig. 10B, D) or pervasive parenchyma (Fig. 10C) may be present.
The amount, distribution and wall thickness of fibre bands is probably closely related to growth forms: more studies are needed in this regard. What is the advantage of alternating bands of thick-walled fibres and thin-walled parenchyma, versus fibres with a consistent thickness, as in Veronica or Schiedea? The answer appears to be, on the basis of the material to hand, that the alternative values of fibres (mechanical support) and parenchyma (storage of starch and water; assistance to the conductive system during periods of drought) can be flexibly and maximally patterned. A stem of a ‘woody herb’ such as Penstemon may add few fibres during later years, but may deposit axial parenchyma instead: maximal strength has been achieved during the first year. The habits of Dianthus and Silene species are similar (branched from the base; massive flowering of a particular branch) with concomitant weight confined to the first season. The diagonal nature of some branches may be pertinent to weight distribution also.

15. SUCCESSIVE CAMBIA AND RAYLESSNESS

According to my definition of rays, most species with successive cambia have rays. There are, however, some notable examples of raylessness in species with successive cambia. Stayneria is unusual among Aizoaceae (which are mostly sprawling) in being an upright shrub rather than a sprawling herb or woody herb. In Stayneria (Fig. 11A, B), conjunctive tissue is composed of thick-walled fibres with strands of fibres adjacent to the phloem; rays are absent. In sprawling Aizoaceae such as Carpobrotus N.E.Br. or Lampranthus N.E.Br., there are prominent bands of parenchymatous conjunctive tissue that alternate with fibre bands (Carlquist, 2007b). These topographical plans recall in appearance (but not in ontogenetic origin) the alternating bands of fibres and parenchyma in Dianthus or Silene. Dianthus and Silene have single cambia, but Aizoaceae and Nyctaginaceae mostly have successive cambia (a few species in those families have so little secondary growth that successive cambia do not develop). In Aizoaceae and Nyctaginaceae, successive (vascular) cambia are the products of a master cambium, a meristematic cell layer that produces secondary xylem, which is produced by the successive (vascular) cambia; conjunctive tissue is produced by the master cambium, a meristemmatic cell layer that produces secondary cortex externally (usually very little) and conjunctive tissue and vascular cambia inwardly.

The vascular cambia in species with successive cambia can produce secondary phloem (which contains phloem parenchyma) over long periods of time (multiple vascular cambia in these species can simultaneously produce secondary phloem). In three-dimensional terms, the vascular increments and their associated conjunctive tissue in species with successive cambia are also interlinked; we do not realize these interconnections when we view transverse sections exclusively. Three-dimensional networks of conjunctive tissue and of phloem parenchyma in species with successive cambia can provide radial movement of photosynthates and other solutes.

16. TRANSITIONS TO RAYLESSNESS

Frankeniaceae have been described as being rayless (Metcalf & Chalk, 1950; Whalen, 1987; Olson, Gaskin & Ghahremani-nejad, 2003). This generalization is essentially correct, but there may be some minor exceptions. For example, transverse sections of stems of Frankenia grandifolia Cham. & Schldtl. (Fig. 12D) have what appear to be a few multiseriate rays. In a tangential section of stems of this species, elliptical groups of parenchyma cells, the tips of
which do not conform to the storied pattern of vessels (storeying is typical for the family), may be seen (Fig. 12E). These rays appear to be transitional in nature between rays and axial parenchyma. Tangential sections of stems of *F. palmeri* (Fig. 12F), which has larger stems, and of *Hypericopsis* Boiss., now considered a species of *Frankenia*, do not have discernible rays (Olson *et al.*, 2003). Thus, in *Frankenia*, differentiation between rays and axial parenchyma may be difficult, and careful ontogenetic studies are needed. This also applies to chenopods, in which various degrees of ray differentiation were reported by Heklau *et al.* (2012). Regions transitional in histology between typical ray tissue and fascicular xylem were mentioned above for *Artemisia pycnocephala* and *Diapedium assurgens*.
Barghoorn (1941b) considered woods with uniseriate rays composed of upright cells, such as *Staavia* Dahl. (Bruniaceae), to represent transitions to raylessness. However, this ray type (termed Paedomorphic Type III by Carlquist, 1988) is stable over several years and is characteristic of a number of shrubs that appear to have increased degree of woodiness phyletically.

17. Storeying in Rayless Woods and Its Correlations

Rayless woods are storeyed more often than are woods of angiosperms at large. In the present essay, storeyed wood structure is shown for the rayless species of *Artemisia* (Fig. 2B, F), *Calceolaria* (Fig. 5G), *Besleria* (Fig. 7B), *Stauntonia* (Fig. 11B), *Heimerlidendron* (Fig. 11D), *Bougainvillea* (Fig. 1D), *Grayia* (Fig. 12B) and *Frankenia* (Fig. 12F) and for the pseudo-rayless *Begonia* spp. (Fig. 1B) and *Lactotis fernandeziana* (Fig. 1D). Incipient raylessness is visible in species of other genera illustrated here (e.g. *Plantago*, Fig. 6D, F). There is no cause-and-effect relationship between raylessness and storeying; the relationship is indirect. Rayless woods tend to have storeyed structure because storeyed woods have fusiform cambial initials that are shorter, given that species with storeyed have fusiform cambial initials that divide vertically, rather than obliquely, for multiplication of fusiform cambial initials (Bailey, 1923). Rayless woods tend to have shorter fusiform cambial initials because in order to qualify as rayless, not only must ray cells be fusiform in shape, they must be similar in length to the fibrous cells and vessel elements in a given wood. There is less intrusiveness in fusiform cambial initials that divide vertically. The intrusiveness in the pseudotransverse multiplicative divisions of fusiform cambial initials (which are present in non-storeyed woods) results in irregular length and cell tip placement of the fusiform cambial initials, because intrusiveness of cell tips varies considerably in a cell population.

Ray initials tend to be subdivided horizontally over time, resulting in the procumbent cells of 'truly woody' species (Barghoorn, 1940, 1941a). Axially shorter ray cells achieved by this method are thus an indicator of adulthood in woods. If ray initials subdivide later in the development of a stem, or even not at all as a stem ages, the stems have prolonged or permanent juvenilism (paedomorphosis). Taller ray initials can produce derivatives that are similar in height to derivatives of fusiform cambial initials thereby, provided that little intrusive growth occurs during maturation of derivatives of the fusiform cambial initials. Such limited intrusiveness does occur in species with short fusiform cambial initials as noted above, and described by Bailey (1923). The study of Bailey (1923), however, did not involve rayless species at all, and the concept of prolonged juvenilism in woods (Carlquist, 1962) was not included in Bailey's considerations. Raylessness is a form of wood juvenilism and thus involves changes in wood ontogeny, rather than a phylogenetic change as implied by the subtitle ('The elimination of rays') in Barghoorn's (1941b) paper on the subject.

Fusiform cambial initials tend to be shorter in certain 'herbaceous' species (which usually do have secondary growth) than in 'woody' species. Storeying can occur in some 'woody' groups (notably Fabaceae), but raylessness tends to characterize 'herbaceous' groups that feature secondary woodiness. As noted above, the increase in mechanical strength that raylessness can provide is valuable in groups evolving secondary woodiness.

18. If Rays are Absent, is Axial Parenchyma Also Absent?

*Aeonium* Webb & Berthel., *Kalanchoë* and some other Crassulaceae have rayless woods. This is easily seen in *Kalanchoë* (Fig. 12A–C). *Kalanchoë beharensis* Drake can become a large shrub, up to 5 m in height and with a woody cylinder 5 cm or so thick (pith to cambium) at its base. Both *Aeonium* and *Kalanchoë* have prominent axial parenchyma that has primary walls only (Fig. 13B–D), in contrast to axial parenchyma walls in most angiosperm woods. Some of the axial parenchyma cells in wood of *Kalanchoë beharensis* are subdivided into strands that contain crystals (Fig. 13D) and which can be labelled 'chambered crystals' because of the subdivisions. The majority of axial parenchyma cells in this species, as well as the axial parenchyma cells in *Aeonium* and most other rayless Crassulaceae, are not subdivided into crystal-bearing cells.

Given that both *Aeonium* and *Kalanchoë* are stem and leaf succulents, do axial parenchyma cells without crystals in wood of these genera relate to change in water availability? In both genera, the axial parenchyma cells occur scattered within the vessel groups (Fig. 13C) as well as around them ('intervascular axial parenchyma' of Carlquist, 1988). This suggests a distinct function for the axial parenchyma, as does the fact that lateral walls of the vessels facing the parenchyma have large scalariform to reticulate pits, a condition that is found several succulents. The large pit areas may lend flexibility and permit cell expansion and contraction, reminiscent of the wide-band tracheary elements of Cactaceae and Portulacaceae. Under such a hypothesis, expansion and contraction of the axial parenchyma cells in the genera of Crassulaceae may
compensate for the rigidity of the thick-walled libriform fibres that compose the ground tissue of the wood.

In many rayless woods other than Crassulaceae, axial parenchyma is scarce to absent (e.g. *Justicia* L., Fig. 8D). Exceptions can certainly be found. Axial parenchyma is illustrated here for the rayless species *Artemisia pycnocephala* (Fig. 2D).

**Figure 13.** Wood of Crassulaceae (A–D), Stylidiaceae (E) and Primulaceae (F). A–D, *Kalanchoe beharensis*, cult. Santa Barbara, CA. A, transverse section; vessels narrow. B, tangential section; vessel elements have pseudo-scalariform pitting; parenchyma strand evident by a cross wall. C, transverse section at higher magnification, to show intervacular axilar parenchyma in vessel groups. D, radial section; strand containing rhomboid crystals indicated; dark fusiform objects at right are air spaces in preparation. E, *Stylidium glandulosum* Salisb., *Donner 1569* (RSA). Wood is rayless; small strand of interxylary phloem is indicated. F, *Lysimachia kalalauensis* Skotts., Carlquist 1986 (RSA). Transverse section, various kinds of mechanically strong cells present. Abbreviations: c = vascular cambium; cs = crystalliferous strand; cw = cross wall; fr = potential ray area composed of fibres; sp = secondary phloem; vr = ray ontogenetically converted to vessel-containing tissue.

Axial parenchyma associated with strands of interxylary phloem forms a three-dimensional network in species in which interxylary phloem is present. The amount of parenchyma associated with interxylary...
phloem varies from one or two cells, as in *Stylidium* (Fig. 13E), to large sheaths, as in *Thunbergia* Retz. (Fig. 8F).

Phloem in vascular increments of species with successive cambia has been called ‘included phloem’, but this confusing umbrella term should be abandoned. Phloem in more recently formed vascular increments may be intact and functioning (Fig. 11C), but in older ones, some secondary phloem is crushed (Fig. 11A) as each of the successive vascular cambia produces more secondary phloem. Phloem parenchyma is formed by each vascular cambium, with sieve-tube elements and companion cells. Phloem parenchyma, along with conjunctive tissue, forms three-dimensional networks in a stem or root.

20. Change in Wall Thickness as a Correlate of a Mechanical Strength Hypothesis

In the transverse section illustrated for *Lysimachia kalalauensis* (Fig. 13F), the pith fibrosclereids are larger in diameter and have greater wall thickness than the libriform fibres more distal to the pith. This would seem to represent investment of more photosynthates to secure wall strength earlier in ontogeny. Phloem parenchyma varies from one or two cells, as in *Stylidium* (Fig. 13E), to large sheaths, as in *Thunbergia* Retz. (Fig. 8F).

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21. Systematic Distribution of Raylessness

In the listings below, segregate family names are used as a way of demonstrating the systematic localization of raylessness. More inclusive family designations are given in parentheses. The changes in composition of Scrophulariaceae and allied families are notable in this regard (Olmstead et al., 2001; Oxelman et al., 2005). Families that contain rayless species were given by Solereder (1908: p. 1144), but because genera are not specified, Solereder is not cited below; his list of families, however, is largely congruent with mine. The listing below is more inclusive than my previous listing (Carlquist, 1988), but many more instances probably will yet be discovered. The genera listed contain rayless species, but may also contain some ray-bearing species. They may also have raylessness initially but eventually develop rays.


Aizoaceae: most species (Metcalfe & Chalk, 1950; Carlquist, 2007b).


Amaranthaceae subfamily Chenopodioidae (*Chenopodiaceae*): rays ‘typically absent in the family’ but present in *Camphorosma L.* and *Echinopsilorn* Moq. (Metcalfe & Chalk, 1950); raylessness reported in *Atriplex*, *Eurotia* Adams. and *Grayia* (Carlquist & Hoekman, 1985), for *Hammada Iljin* (Fahn, Werker & Baas, 1986) and for various genera by Hekkau et al. (2012).

Apiaceae: *Pimpinella* L. (Carlquist, 1988).

Aristolochiaceae: *Saruma* Oliv. (Dickison, 1996).

Asteraceae: *Stoebe* L. (this genus has successive cambia: Adamson, 1934), *Lasthenia* Cass. (Carlquist, 1959, and the present essay); and first year (or more) of wood of *Artemisia* (Carlquist, 1988).


Begoniaceae: *Begonia peruviana* A.DC. (Carlquist, 1985a).


Calceolariaceae (in Scrophulariaceae of earlier authors, but now recognized by Olmstead et al., 2001; Oxelman et al., 2005, *inter alia*): Calceolaria (Boureau, 1957; present essay).


Cornaceae: *Cornus sueccia* L. (Olsen, 1914).

Crassulaceae: *Aeonium* (as *Sempervivum* L.: Barghoorn, 1941b), *Kalanche* (Carlquist, 1988) and probably other genera.

Diapensiaceae: *Diapensia lapponica* L. (Petersen, 1908).


Gentianaceae: *Ianthus* Griseb. (Carlquist, 1984a; Lens et al., 2013).

### 22. Artificially Induced Raylessness
Raylessness was induced in *Glycine* Willd. as a result of an application of 4-(2,4-dichlorophenoxy)butyric acid (2,4-DB; Pizzolato, 1982). A rayless individual of *Arabidopsis* Heyn. was produced by Melzer *et al.* (2008) in which two flowering-time genes were knocked out. However, the resulting stem was thick and tuber-like and did not represent a normal growth form that would be functional in a wild-occurring plant.

### CONCLUSIONS
Research into functions of mechanical cells and fibrous cells provides a number of difficulties, so our understanding of physiological function of these tissues is incomplete. By contrast, research on water movement in vessels, which can be done in laboratories by attaching tubes to stems etc. is relatively easy (although interpretations of the results may vary). In the case of parenchyma and mechanically strong tissues (especially those which cannot readily be isolated, such as the rayless cylinders that begin secondary growth in many rayless woods), other methods of inferring function may become important. Studies in comparative anatomy can suggest functions, because evolution of particular structures as autopomorphies in numerous genera independently becomes as compelling as replications of an experiment in a laboratory. Questions will remain, however, regarding many of the hypotheses and ideas expressed here.

1. A transitory increase in mechanical strength is probably the most important functional explanation for raylessness, which has arisen in multiple clades. The evidence for this is:

   (a) Most rayless species develop rays after an initial rayless period; rays in this construct would be considered zones weaker than fibrous fascicular secondary xylem. As a rayless stem increases in diameter, the value of rays presumably becomes greater as a means for radial conduction of solutes, whereas the value of fibrous tissue for mechanical support wanes in proportion to cumulative addition of mechanical tissue. Zones of rays in a state of transition between rayless and ray-bearing may contain a mixture of fibrous cells and strands of twocelled fusiform parenchyma strands.

   (b) In some instances, potential ray areas are converted to fibrous tissue adjacent to the pith of stems abruptly (early-onset raylessness) rather than gradually.

   (c) Sclerenchyma in the pith and pith fibres at the pith periphery often accompany instances of early-onset raylessness.

   (d) Rayless species without pith sclerenchyma are often those in which habits other than upright self-supporting stems occur.
(e) In some instances, a decrease in wall thickness of fibres over time can be seen (Lysimachia). Decrease in wall thickness is correlated with lowered strength of wood per unit transection (Zanne et al., 2010).

(f) Mechanical tissue is greatest in stems that are upright, and is less within rhizomatous stems in the same plant (Artemisia pycnocephala); fluctuations in fibre abundance, position and wall thickness can be correlated with habit features.

(g) Narrow vessels are unusually common in rayless species. There is no cause and effect between raylessness and narrow vessels. Rather, the narrowness of vessels may relate to the open habitats in which herbs can radiate better than they can in saturated mesic habitats. Narrow vessels correlate with greater strength per unit transection and greater wood density (Zanne et al., 2010). Narrowness of vessels, in any case, is caused by hormonal action, and the roles of ecology and growth form are indirect. Vessel narrowness in Hawaiian Plantago species is not correlated with xeric conditions; these species occur in markedly wet habitats.

(h) Experimental evidence for the mechanical function of raylessness is lacking. Making comparisons between rayless and ray-bearing wood (preferably within a single stem) could, in fact, be done. One could do this experimentally by extracting samples of the two kinds of tissues. One could also calculate the transectional amount of wall material per unit transection of a wood sample for the ray-bearing and rayless portions of such a wood. Mathematical formulae for this can easily be constructed, as has been done for studies of density in wood (Martínez-Cabrera et al., 2009). Rays make a contribution to the strength of a wood (Burgert & Eckstein, 2001), but not as much as fibrous tissue, because rays often offer elasticity (Beery, Iflu & McLain, 1983). Heartwood offers more mechanical strength than sapwood (Niklas, 1997), which, if generally applicable, suggests that a wood that begins rayless, as in most cases of raylessness, demonstrates less selective value for mechanical strength as growth proceeds. This is exemplified anatomically in the instances of early-onset raylessness. Rosell & Olson (2007) find that in Pittocaulon H.Robb. & Bretrell (Asteraceae), strength is better predicted by length of stem rather than by age. Conceding that Pittocaulon, a succulent, may have characteristics not applicable to denser woods, increasing strength of a wood according to length would be selectively valuable to woody derivatives of herbaceous clades in which increased woodiness is accompanied by an increase in stem length. There are several kinds of mechanical strength one can measure in woods. Perhaps the most important of these where rayless woods is concerned is provided by Young's modulus, which expresses stiffness of a wood; this and other various measures of wood strength are covered well by Niklas (1992). Stiffness in the first-formed xylem of a stem is the factor that would most readily explain the production of raylessness in longer stems of annual Brassicaceae (e.g. Stanleya) in particular and in woody herbs with long stems in general.

2. Other functions for raylessness may include division of labour (cortex vs. woody cylinder) in species that are succulent (Aeonium, Kalanchoë and other Crassulaceae). In these examples, the weight of foliage at the tips of elongate stems is considerable, and a stronger (= rayless) formulation of xylem would be of selective value.

3. Raylessness may be a modification easier to achieve than increase in stem strength by means of origin of collenchyma, cortical fibres, phloem fibres, pith sclerenchyma and cortical sclerenchyma. Because herbaceous groups often have less cortical sclerenchyma and phloem fibres than do ‘typically woody’ species, conversion of potential ray areas near the pith to fibres may be a modification that can be more readily achieved genetically than strengthening a stem by means of initiation of collenchyma, cortical fibres, cortical sclereids and phloem fibres. Masselter & Speck (2008) stressed the mechanical value of sclerenchyma in stems of Aristolochia; such sclerenchyma, they theorized, may counter the moderate strength of secondary xylem in this species. Following such reasoning, raylessness may be a ‘quick fix’ achieving greater mechanical strength in secondarily woody groups in which there is, in contrast to Aristolochia, minimal cortical or secondary phloem sclerenchyma. Certainly this describes the stems of many predominantly herbaceous genera (Metcalfe & Chalk, 1950).

4. Raylessness is a manifestation of secondary woodiness and reflects juvenilistic ontogeny (e.g. lack of horizontal subdivisions in ray initials as opposed to the commonness of such divisions in truly woody species), but most instances of secondary woodiness do not involve raylessness.

5. Although the majority of genera and species eventually develop rays, some (Hebe/Veronica) do
not, as far as we know, but definitive data are not at hand.

6. Although rayless stems would seem counterproductive because woody cylinders require some form of radial transport of photosynthates and other solutes, an appreciable number of rayless species have septate fibres (or living but non-septate fibres) which potentially could serve for radial flow of photosynthates. The number of species with living but non-septate fibres has been vastly under-reported because wood anatomy is largely based on study of wood samples preserved by drying rather than by means of liquid fixatives. Prominent pitting on tangential walls of living fibres also often suggests a potential route for radial conduction (Acanthaceae, Alseuosmiaceae, Gesneriaceae, Plantaginaceae).

7. Three-dimensional networks of parenchyma occur in rayless species with interxylary phloem or successive cambia. In the case of interxylary phloem, sheaths of parenchyma around the phloem strands weave outwards and laterally, connecting older stem portions with younger ones. In rayless species with successive cambia, the conjunctive tissue forms a network of parenchyma.

8. Multi-stemmed subshrubs and shrubs branched from the base, with branches of finite length, are most common in the roster of rayless species. Only a few rayless species are trees [Haloxylon (Amaranthaceae); Heimerliodendron (Nyctaginaceae)]. Geranium arboreum is a small tree, but raylessness in it occurs only briefly at the onset of secondary growth. Only a few rayless species are lianas: Cobaea (Polemoniaceae) and some Thunbergia spp. (Acanthaceae). Only two annuals [Halophytum (Halophytaceae); Stanleya (Brassicaceae)] have been reported, although other rayless Brassicaceae are likely to be found. Rayless species often have narrow vessels, numerous per unit of transverse sectional area. Raylessness is not caused by xeromorphy, but is a product of a group adapted to disturbed habitats radiating into various growth forms, of which multi-stemmed subshrubs are the most common.

9. Axial parenchyma may be absent when rays are absent (Hebe/Veronica); there may be a functional commonality between the two types of parenchyma (Sauter, 1966a, b; Braun, 1970) and some overlap in function (Carlquist, 2015). There is also a three-dimensional series of contacts between rays and axial parenchyma (Kedrov, 2012). However, there are a few rayless species that have axial parenchyma [Lasthenia macrantha (Asteraceae); Aeonium, Kalanchoë and other Crassulaceae)]. These latter species underline the possibility that rays may differ from axial parenchyma not merely in radial versus axial distribution, but in functional respects as well. Armeria (Plumbaginaceae) is rayless but has pervasive axial parenchyma (Carlquist & Boggs, 1996); thus, in that genus there is no correlation between ray absence and axial parenchyma absence.

10. In the instances in which woods that begin rayless eventually develop rays, the rays that are produced often arise as multisieriate rays and are few in number (Artemisia, Cyrtandra, Geranium).

11. Although the number of species in which rayless woods occur or may be suspected to occur is relatively small, many more are likely to be found. In particular, the herbaceous or ‘woody herb’ species of Lamiales (Olmstead et al., 2001; Oxelman et al., 2005) are likely to include more rayless species. Almost all reports of raylessness involve stems. Some species of Caryophyllales with successive cambia (Aizoaceae, Amaranthaceae s.l. and Nyctaginaceae) are likely to be rayless in roots as well as stems. Research in wood anatomy has favoured species that are arboREAL or large shrubs, whereas raylessness occurs mostly in less woody growth forms.

12. Phenomena such as raylessness, fibre absence (Carlquist, 2015), fibre dimorphism (Carlquist, 2014) and paedomorphosis (Carlquist, 1962, 2009) show that when one cell type changes, there may be concomitant changes in other cell types. Wood evolution is not merely a reassembly of narrowly defined cell types, but usually involves simultaneous changes in several cell types. In the case of rayless woods, septate and non-septate living fibres often occur along with absence of rays, and axial parenchyma absence, pith sclerenchyma and other changes may accompany raylessness. Relative proportions of particular cell types may change during wood evolution: raylessness illustrates this clearly. Wood evolution is not the simple construct we once envisaged; it is a much more complicated and multifaceted process, the diversity of which has become more evident since molecular-based phylogenetic trees have become available.

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