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Wood Anatomy of Darwiniothamnus, Lecocarpus, and Macraea (Asteraceae)

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Introduction

The genera *Darwiniothamnus* Harling, *Lecocarpus* Decaisne, and *Macraea* Hook. f. are endemic to the Galápagos Islands. Although wood anatomy of *Lecocarpus* has been considered by Carlquist (1958) and Eliasson (1971), the material available hitherto has been twigs rather than mature wood. The other two genera have not been studied with respect to wood anatomy. Material of all three genera has been made available through the courtesy of Dr. Uno Eliasson, who collected these in 1981 in the Galápagos Islands.

Darwiniothamnus was described by Harling (1962) as a genus distinct from *Erigeron* L., into which Hooker (1847) had placed *E. lancifolius* Hook. and *E. tenuifolius* Hook. As Harling notes, Hooker had scanty material available to him, and his assignment of these two species to *Erigeron* was rather provisional at that time. Harling's studies do place *Darwiniothamnus tenuifolius* (Hook.) Harling (in which three subspecies are recognized) in the tribe Astereae. Harling notes closest similarities between *Darwiniothamnus* and *Conyza* Less. as well as with the shrubby species of *Erigeron* in Chile and the Juan Fernandez Islands.

Lecocarpus consists of three species (Asderson 1980), *L. darwinii* Asderson (I. San Cristobal), *L. lecocarpoides* (Robins. & Greenm.) Cronquist & Stuessy (I. Española and I. Gardner) and *L. pinnatifidus* Decaisne (I. Santa María). *Lecocarpus* belongs to tribe Heliantheae, subtribe Melampodinae, a small and distinctive assemblage of genera (Eliasson 1971). Only the species *L. pinnatifidus* is studied here, but Eliasson's data on wood of twigs suggests little variation among the species is likely to be found.

Macraea laricifolia Hook. f., sole species of its genus, occurs on eight of the Galápagos Islands (Wiggins and Porter 1971). Although once merged with *Lipochaeta* DC., *Macraea* has been reestablished as a genus (Harling 1962). The assignment of *Macraea* to Heliantheae subtribe Helianthinae (formerly subtribe Verbesininae) is clear. Within that subtribe, the relationships of *Macraea* appear to lie with *Aspilia* Thou., *Wedelia* Jacq., or *Zexmenia* La Llave rather than with *Lipochaeta* according to Harling (1962).

With respect to ecology, all three genera can be said to be lowland (below 900 m) shrubs of open lava. In fact, Eliasson (1971) figures the three genera growing together at Cerro Pajas, 420 m, I. Santa María (Floreana).

The present study seeks to discover whether wood anatomy is illustrative of the taxonomic relationships of the genera less than to what ecological factors it might be related. Wood anatomy in the family seems closely and sensitively related to ecological factors, but not clearly related to any hierarchies within the family (Carlquist 1966). The ecological features revealed by wood anatomy of the genera are therefore considered below. In addition, wood anatomy of the genera relates to habit, especially in the case of *Lecocarpus*, where possibly juvenilistic wood features occur.

Materials and Methods

The wood samples were collected by Dr. Eliasson in the field and air dried. Locality data are as follows: *Darwiniothamnus tenuifolius* subsp. *tenuifolius, Eliasson 14,* NE of Cerro Brujo, 50 m, I. Santa María, 9 Jan. 1981, sample from base of 2.5-m tall shrub; *Lecocarpus pinnatifidus, Eliasson 10,* Black Beach, 10 m, I. Santa María, 8 Jan. 1981, sample from base of 60-cm tall shrub; *Macraea laricifolia, Eliasson 11,* Black Beach, 10 m, I. Santa María, 8 Jan. 1981, sample from base of 2-m tall shrub. These samples all represent mature wood patterns for their respective species, because care was taken to select a basal portion of a mature specimen.

Woods were softened according to the method of Kukachka (1977). This was found to improve sectioning despite the fact that none of the woods is notably hard. Woods were sectioned on a sliding microtome; sections were stained with safranin. Macerations were prepared with Jeffrey's fluid and stained with safranin. Slides were prepared by the junior author; data and text are the work of the senior author.

Anatomical Results

Darwiniothamnus tenuifolius (Fig. 1–4).—Growth rings are absent or nearly so (Fig. 1). Vessels are round in outline, chiefly grouped in pore multiples. The mean number of vessels per group is 2.06. Mean vessel diameter is 54 μm, mean vessel wall thickness is 5.3 μm. The mean number of vessels per mm^2 is 50.3. Vessel elements have simple perforation plates, somewhat oblique end walls (Fig. 2, 4) and average 221 μm in length. Pits on lateral walls of vessels are about 3 μm in diameter; pits are alternate on vessel-parenchyma contacts and on intervascular faces (Fig. 4). Libriform fibers average 493 μm in length, 18.5 μm in diameter at the widest point, and 4.5 μm in wall thickness. Axial parenchyma is of two types, vasicentric and banded. The vasicentric parenchyma consists of two to four (mostly three) cells, formed as a sheath most commonly one or two cells in thickness around vessels or vessel groups. Banded parenchyma occurs as tangential bands of varying width (Fig. 1). These bands were present, in the sample studied, only near the periphery of the stem. Cells of the banded paren-
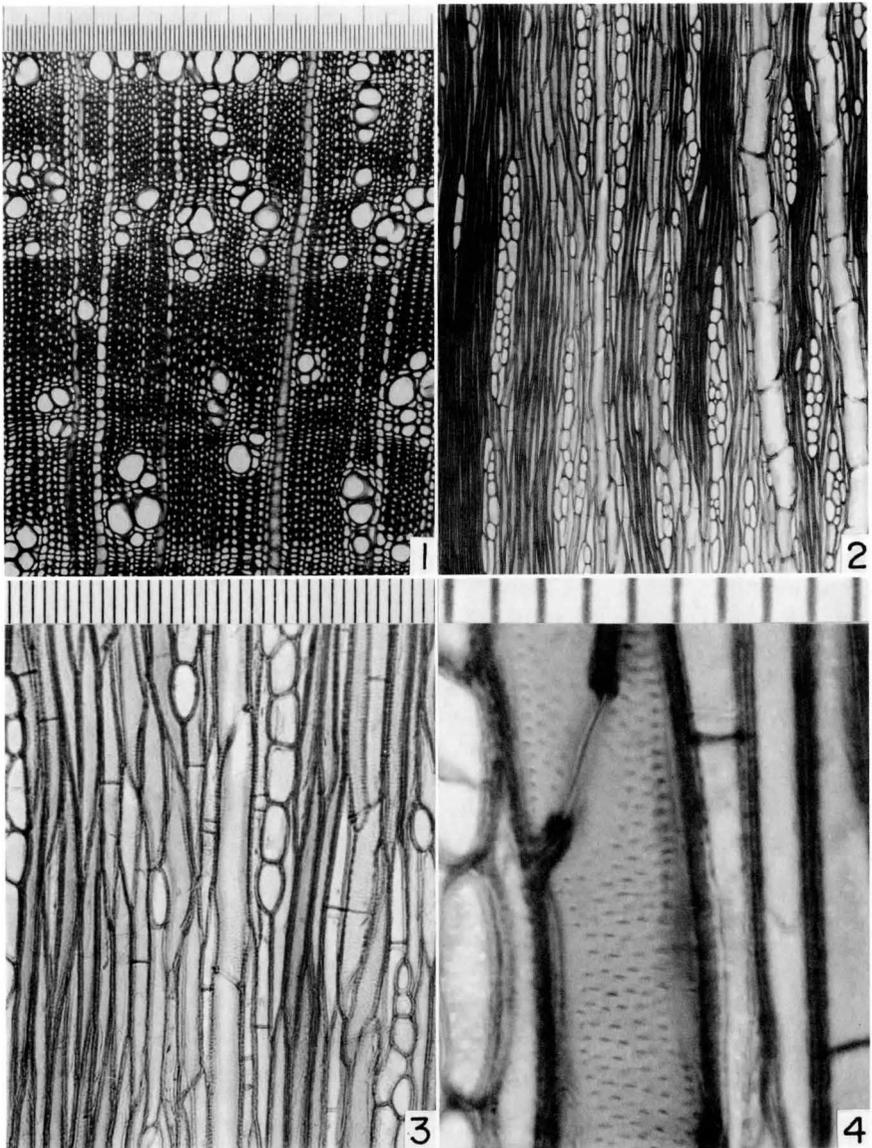
Figs. 1–4. Wood sections of *Darwiniothamnus tenuifolius* subsp. *tenuifolius (Eliasson 14)*.—
1. Transection; pale transverse bands are axial parenchyma.—2. Tangential section; banded axial parenchyma is storied.—3. Portion of tangential section to show fusiform and septate banded axial parenchyma cells.—4. Portion of tangential section to show oblique end wall, simple perforation plate, and minute pits on vessel wall. (Fig. 1, 2, magnification scale above Fig. 1 [finest divisions = 10 μm]; Fig. 3, scale above Fig. 3 [divisions = 10 μm]; Fig. 4, scale above Fig. 4 [divisions = 10 μm].)

chyma are wider and shorter than the libriform fibers, and may or may not be subdivided by at most a single wall (Fig. 3). Rays are both multiseriate and uniseriate; multiseriate rays are more common (Fig. 2). Mean multiseriate ray height is 438 μm, mean uniseriate ray height is 124 μm. Multiseriate rays average 2.5 cells wide at the widest point. Ray cells are mostly erect or square, with a few procumbent cells; some procumbent cells are the products of horizontal subdivisions of erect ray cells. Uniseriate wings are present on some multiseriate rays (Fig. 2). Banded parenchyma (which may be considered bands of short fibers) storied, the storied pattern conforming to that of vessel elements; ordinary libriform fibers nonstoried or only vaguely storied.

Lecocarpus pinnatifidus (Fig. 5–9).—Growth rings are absent, although some fluctuation in libriform wall thickness and in vessel diameter occurs (Fig. 5, 7). Vessels are often grouped in radial rows (Fig. 5, 7); the mean number of vessels per group is 3.2. Vessels are circular in transectional outline. Vessel diameter averages 42 μm; vessel wall thickness is 5 μm. The mean number of vessels per mm^2 is 125. All vessel elements have simple perforation plates; end walls are slightly oblique (Fig. 9). The mean vessel-element length is 162 μm. Lateral walls of vessels, whether facing other vessels, libriform fibers, or parenchyma cells, bear quite elongate pits which often appear perfectly scalariform in pattern (Fig. 8, 9). Libriform fibers average 497 μm in height, 30 μm in diameter at the widest point, and have an average wall thickness of 6 μm. Some libriform fibers are thinner-walled (Fig. 5, 7). Axial parenchyma is vasicentric only, most often with a single layer of cells around a vessel or vessel group. Axial parenchyma is subdivided into strands of two cells usually. Rays are almost exclusively multiseriate (Fig. 6). The multiseriate rays average 1741 μm in height; they average 7.5 cells wide at the widest point. Ray cells range from upright to square; a few procumbent cells occur scattered throughout the rays. Uniseriate wings are absent on the multiseriate rays. The thinner-walled fibers may be storied (Fig. 6, lower right), but the thicker-walled fibers are not.

Macraea laricifolia (Fig. 10–13).—Growth rings are absent in the material studied (Fig. 10). Vessels are in radial chains, especially near the pith (Fig. 10), or in pore multiples (Fig. 11), or solitary. The mean number of vessels per group is 1.5. Vessels are circular in transectional outline or radially widened, especially near the pith (Fig. 10). Vessel diameter averages 55 μm; vessel wall thickness averages 3.5 μm. The mean number of vessels per mm^2 is 57. Perforation plates are simple; end walls are rather oblique (Fig. 12). Vessel elements average 262 μm in length. Lateral wall pits on vessels are alternate on vessel-vessel, vessel-parenchyma and vessel-fiber contacts. Pits are circular, about 4 μm in diameter. Grooves on the vessel walls interconnect pit apertures adjacent in helices, and accompanying each groove
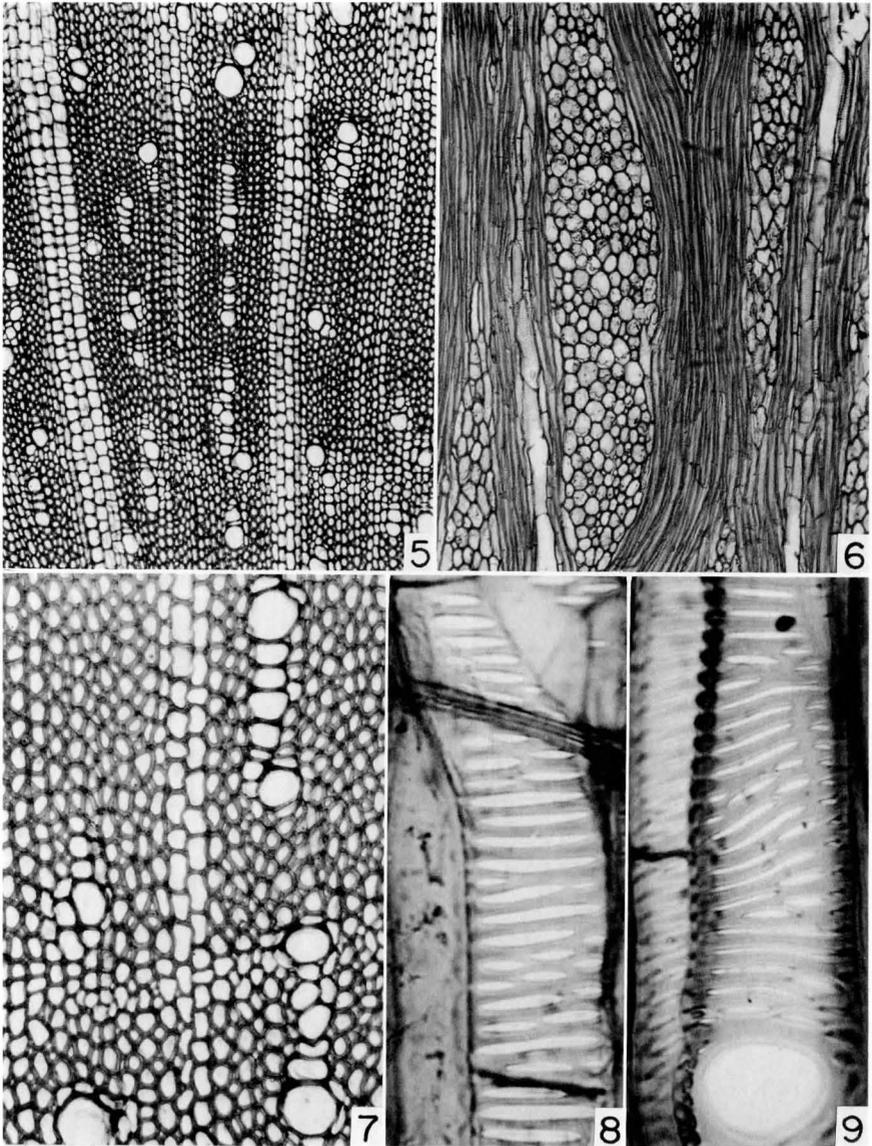
Figs. 5–9.   Wood sections of *Lecocarpus pinnatifidus (Eliasson 10)*.—5. Transection; paler zones above and below consist of wider, shorter fibers.—6. Tangential section; rays are wide, all multiseriate.—7. Transection; vessels arranged in radial chains.—8. Portion of vessel wall from tangential section showing intervascular pitting.—9. Portion of vessel wall from radial section, showing perforation plate and vessel-parenchyma pitting. (Fig. 5, 6, scale above Fig. 1; Fig. 7, scale above Fig. 3; Fig. 8, 9, scale above Fig. 4).
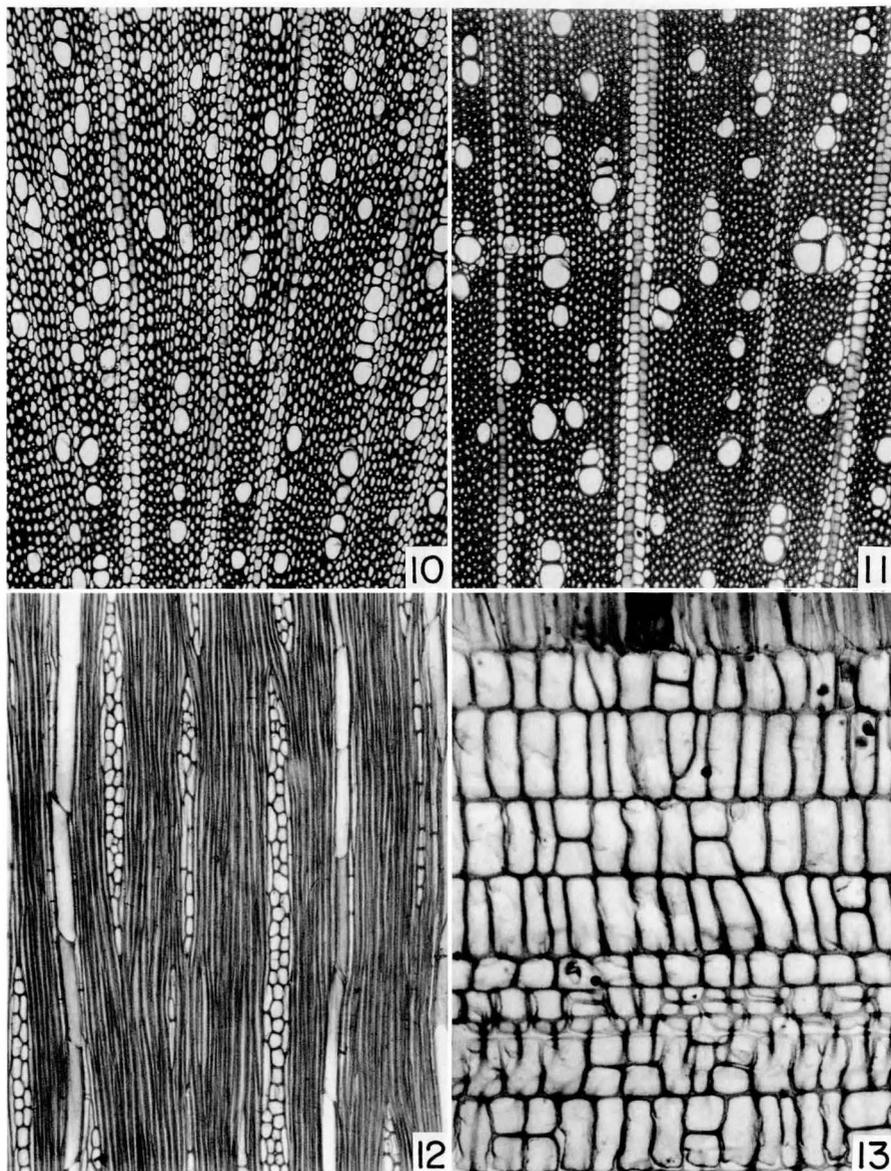
Figs. 10–13. Wood sections of *Macraea laricifolia (Eliasson 11)*.—10. Transection from near pith.—11. Transection from near periphery of stem; libriform fibers different in shape and size from those of Fig. 10.—12. Tangential section; vague storying evident.—13. Radial section, showing ray histology. (Fig. 10–12, scale above Fig. 1; Fig. 13, scale above Fig. 3.)

is a pair of helical thickenings. Libriform fibers average 545 μm in length. Libriform fibers average 23 μm in diameter. However, libriform fibers are wider in diameter and wider radially than tangentially near the pith (Fig. 10). In outer portions of the wood sample studied, libriform fibers are narrower in diameter and circular in outline (Fig. 11). Mean libriform fiber wall thickness is 3.5 μm. Axial parenchyma is scanty, with only a few cells forming a partial sheath, never more than one cell thick, around vessels or vessel groups. Axial parenchyma strands consist of two to four cells, two most commonly. Both multiseriate and uniseriate rays are present; multiseriate rays are much more common (Fig. 12). Multiseriate rays average 804 μm in height (uniseriate rays too few to produce a reliable mean). Multiseriate rays average 3.25 cells wide at the widest point. Ray cells range from square to markedly erect (Fig. 13); some square cells are formed by subdivision of erect cells (Fig. 13). The most markedly erect ray cells present occur on the sides, not in the central portions, of multiseriate rays (Fig. 12), and thus sheathing cells can be said to be present. Uniseriate wings are present on a few of the multiseriate rays. Storying is absent from the wood except in the form of a few patches of vaguely storied fibers (Fig. 12). Resinlike deposits are present, often as droplets, in a few of the ray cells (Fig. 13).

Conclusions

Anatomical distinctions.—Each of the three genera shows special anatomical features. Some of these seem related to habit or to ecology, and are discussed below.

Macraea is curious in having larger fibers, radially widened, near the pith, whereas more slender fibers, circular in transectional outline, occur in outer portions of the sample. *Darwiniothamnus* has banded parenchyma in addition to the vasicentric type. Vasicentric parenchyma is basic to wood in the entire family. However, the banded parenchyma is an innovation found in a scattering of asteraceous genera. It represents the phenomenon termed fiber dimorphism (Carlquist 1958), a concept applicable to an assortment of dicotyledon families (Carlquist 1980). Fiber dimorphism is incipient in *Lecocarpus* (Carlquist 1958) but is clearly present in *Darwiniothamnus*. Fiber dimorphism occurs in genera of the tribe Astereae other than *Darwiniothamnus*; it has been reported in *Baccharis angustifolia* Michaux, *Olearia furfuracea* (A. Rich.) Hook. f., and *Psiadia rotundifolia* Hook. f. (Carlquist 1960).

Anatomy with relation to habit.—Of the three genera in the present study, *Lecocarpus* forms the smallest shrubs (Eliasson 1971). These shrubs, which have the appearance of what one could call a woody herb (much like a

fruticose *Chrysanthemum* L. species), seem to show the greatest number of wood features referable to herbaceous modes of structure discussed under the rubric of paedomorphosis (Carlquist 1962). *Lecocarpus* is notable in this regard for lateral wall pits on vessels; the pits are much widened laterally, resembling metaxylem vessel pitting in this species (or in dicotyledons as a whole). Scalariformlike pitting in vessels of herblike plants with paedomorphic features has been attributed to lowered selection for mechanical strength (Carlquist 1975). The large rays of *Lecocarpus,* little altered between pith and outermost xylem compared to rays of typical woody plants, also betoken paedomorphosis. With respect to vessel pitting and rays, wood of *Lecocarpus* resembles wood of *Macropiper* Miq. (Piperaceae). Both genera seem to exemplify paedomorphosis clearly, although Patel's (1980) skepticism may reflect unfamiliarity with woods of herblike dicotyledons.

The predominance of erect ray cells in *Darwiniothamnus, Lecocarpus,* and *Macraea* is not unusual, for this tendency is common in woods of Asteraceae (Carlquist 1966). The tallness of ray cells is not correlated with long fusiform cambial initials in these genera. Tallness of ray cells seems likely to represent a juvenilism phenomenon in accord with earlier explanations (Carlquist 1962). Just as breakup in rays has been slowed, fewer subdivisions of ray initials result in fewer procumbent cells than one might find in rays of a typically woody dicotyledon.

Anatomy with relation to ecology.—Libriform fibers are about the same length throughout the genera studied here, but the genera differ with respect to mean vessel-element length: vessel elements average 221 μm long in *Darwiniothamnus,* 162 μm in *Lecocarpus,* and 262 μm in *Macraea.* The differences might be related not to differences among the genera with respect to habitat (all three can occur in a single site, as noted earlier), but with respect to the role of wood anatomy versus leaf characteristics in dealing with water relations. *Lecocarpus,* with the broadest leaves, has the shortest vessel elements; *Macraea,* with ericoid leaves, is intermediate in vessel length, while *Darwiniothamnus,* with needlelike leaves, has the longest vessel elements. If one accepts that shorter vessel elements connote greater xeromorphy of woods (Webber 1936; Carlquist 1966, 1975) there is an inverse relationship in the three genera between leaf area and vessel-element length. By restricting evaporation of water, smaller leaves may be a primary tool in dealing with dry conditions. Where leaves are longer and potentially might evaporate more water, wood of a more markedly xeromorphic pattern may be the primary tool in dealing with lowered water availability. The varying roles of wood anatomy and leaf anatomy or leaf physiology whereby different species deal differently with the same environment have been discussed earlier (Carlquist 1977a).

Vessel diameter and number of vessels per mm^2 are also indicators of ecology. Narrow vessels and high numbers of vessels per unit transection are independent indications of xeromorphy (Carlquist 1975). Therefore, they have been combined into a ratio called "vulnerability," vessel diameter divided by vessels per mm^2 (Carlquist 1977b). If one computes the vulnerability ratios for the three genera, they are as follows: *Darwiniothamnus*, 1.07; *Lecocarpus*, 0.33; *Macraea*, 0.96. These values, like the vessel-element lengths, show an inverse correlation between leaf surface and wood vulnerability: *Lecocarpus*, which has the broadest leaves, has the lowest vulnerability figure and thereby appears to be using wood rather than leaves as a primary tool for dealing with lowered water availability. *Darwiniothamnus* and *Macraea* are similar in having moderately high vulnerability values. In these two genera, somewhat less xeromorphic wood (as indicated also by vessel-element length) is coupled with leaves with minimal surface area and presumptively lower transpiration rates. A noteworthy feature of *Macraea* wood which does suggest moderate xeromorphy is the presence of helical sculpture (grooves plus bands) on vessel walls. Webber (1936) claimed correlation between presence of helical sculpture on vessel walls and drier habitat.

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