Wood anatomy of Polygonaceae: analysis of a family with exceptional wood diversity

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Quantitative and qualitative data are presented for woods of 30 species of woody Polygonaceae. Wood features that ally Polygonaceae with Plumbaginaceae include nonbordered perforation plates, storage in narrow vessels and axial parenchyma, septate or nuclear fibres, vasicentric parenchyma, pith bundles that undergo secondary growth, silica bodies, and ability to form successive cambia. These features are consistent with pairing of Plumbaginaceae and Polygonaceae as sister families. Wood features that ally Polygonaceae with Rhabdodendraceae include nonbordered perforation plates, presence of vestured pits in vessels, presence of silica bodies and dark-staining compounds in ray cells, and ability to form successive cambia. Of the features listed above, nonbordered perforation plates and ability to form successive cambia may be symplesiomorphies basic to Caryophyllales sensu lato. The other features are more likely to be synapomorphies. Wood data thus support molecular cladograms that show the three families near the base of Caryophyllales sensu lato. Chambered crystals are common to three genera of the family and may indicate relationship. Ray histology suggests secondary woodiness in Antigonon, Atraphaxis, Bilderechyia, Dedeckera, Eriogonum, Harfordia, Muehlenbeckia, Polygonum, and Rumex. Other genera of the family show little or no evidence of secondary woodiness. Molecular data are needed to confirm this interpretation and to clarify the controversial systematic groupings within the family proposed by various authors. Vessel features of Polygonaceae (lumen diameter, element length, density, degree of grouping) show an extraordinary range from xeromorphy to mesomorphy, indicating that wood has played a key role in ecological and habitat shifts within the family; the diversity in ecology and habit are correlated with quantitative wood data. © 2003 The Linnean Society of London, Botanical Journal of the Linnean Society, 2003, 141, 25–51.

ADDITIONAL KEYWORDS: Caryophyllales sensu lato — chambered crystals — ecological wood anatomy — helical thickenings — Plumbaginaceae — silica bodies — Rhabdodendraceae — successive cambia — systematic anatomy — vestured pits.

INTRODUCTION

In Caryophyllales: evolution and systematics (Behnke & Mabry, 1994), Polygonaceae (together with a sister family, Plumbaginaceae) were considered an outgroup of Caryophyllales (Rodman, 1994). The order Caryophyllales, as defined by Cronquist & Thorne (1994) in the book, and accepted by the other authors, is termed 'core Caryophyllales' or Caryophyllales sensu stricto here. Caryophyllales in this sense was a modification of the traditional Centrospermae (Eichler, 1876). A much altered definition of Caryophyllales has been expressed in DNA-based cladograms (e.g. Soltis et al., 2000), in which Dilleniaceae is the basal branch from which the branches of which (preceding the core Caryophyllales) include Rhabdodendraceae, Polygonaceae, Plumbaginaceae, Tamaricaceae, Frankeniaceae, Droseraceae, Nepenthaceae, Ancistrocladaceae, Dioncophyllaceae, Simmondsiaceae, and Asteropeaceae. This expanded Caryophyllales is termed 'Caryophyllales sensu lato' here. This notably expanded definition invites comparison of data sets, such as wood anatomy, within the newly defined order. Wood anatomy, which frequently contains characters indicative of systematic relationship, is one of these data sets, and the present paper represents one in a series in which woods of families of Caryophyllales sensu lato are compared.

Although woods of a number of genera and species of Polygonaceae have been described, these are chiefly in surveys of woods of geographical regions (see Gregory, 1994). The only previous overview of wood
anatomy of the family is in Metcalfe & Chalk's (1950) *Anatomy of the dicotyledons*. That presentation, although very useful, is necessarily very condensed. Therefore, an extended treatment of the woods of the family is desirable. Very probably, the predominantly herbaceous nature of Polygonaceae has delayed production of extended treatments. The family contains 49 genera and 1095 species according to Thorne (2000), but a large proportion of these species is herbaceous. A notable exception is the subfamily Coccoloboideae (8 genera, 230 species; more than half of these species belong to the genus *Coccoloba*). The worldwide distribution of Polygonaceae has also deterred a survey of the woody species. Aside from *Coccoloba* and *Triplaris*, only a few species in the family are genuinely arboreal, and nonarboreal species are rarely included in wood collections. Thus, wood samples of most genera of the family are not readily obtainable from xylaria, and the specimens used for the present study were assembled over a period of more than a decade. The samples from secured xylaria represent virtually all those available except for *Coccoloba*, which is relatively large (about 165 spp.) and which, on the basis of the present survey, is relatively uniform with respect to wood anatomy.

Growth forms are diverse; among these are true trees, lianas, shrubs of various sizes, perennials with woody roots, and 'woody herbs' in which cane-like stems of several years' duration are innovated from the base. The genus *Eriogonum* alone has remarkable diversity, ranging from mat-like alpine shrubs with contorted stems (*E. kennedyi*) to shrubs that reach tree-like size on island areas (*E. giganteum*). The range of wood anatomy relates to the diverse growth forms within the family as a whole and parallels habit and habitat in genera such as *Eriogonum*. Some Polygonaceae are probably primarily woody; others are likely secondarily woody (for criteria, see discussion on paedomorphosis in Carlquist, 2001a). The two woody species of *Rumex* studied here, *R. giganteus* (Hawaii) and *R. lunaria* (Canary Islands) are likely examples of secondary woodiness.

The range of wood anatomy within Polygonaceae also relates to ecology. I know of no other family in which quantitative data on vessel features, data which relate to mesomorphy and xeromorphy, have such an extreme range.

In addition to habit and ecology, systematic distinctions play a role in the great diversity of polygonaceous woods. The presence of silica bodies in some genera, calcium oxalate crystals in others, and the diverse modes of occurrence of calcium oxalate crystals exemplify such systematic distinctions.

Thus, examination of wood anatomy of Polygonaceae offers the opportunity to: (1) systematically compare wood anatomy within genera and within the family; (2) delineate systematic relationships; (3) describe relationships of wood anatomy to habit and to ecology.

**MATERIAL AND METHODS**

The Appendix presents a list of the specimens studied. If no institutional xylarium is indicated (w), the wood studied came from a herbarium specimen. A large set of duplicate wood specimens from the U. S. National Natural History Museum xylarium (USw) was incorporated into that of the Rancho Santa Ana Botanic Garden (RSAw), and are designated with the dual xylarium citation because the USw numbers or collector's numbers were retained. In Table 1 and in the Appendix, no infrafamilial classification has been employed. Although this may inconvenience the reader, the fullest systematic treatments of the family (Dammer, 1893; Roberty & Vautier, 1964) are markedly different, and interpret the phylogenetic sequence differently (based on whether cyclic or helically arranged tepals are primitive). Less detailed systematic treatments of the family (e.g. Maekawa, 1964; Thorne, 2000) offer additional possibilities rather than consensus. Molecular data on the family, when available, will probably provide a more reliable infrafamilial classification. Nevertheless, unusual wood anatomical features that may reflect relationships among genera are cited and discussed. To synthesize these data in a cladistic form would be premature and misleading, because the inframilial classification of the family is so controversial.

Most wood samples were available in dried form. The specimens of *Antigonon leptopus*, *Eriogonum kennedyi*, and *Polygonum lapathifolium* were preserved in 50% aqueous ethanal, which helps demonstrate the presence of starch. Dried specimens were boiled in water, stored in 50% ethanol, and sectioned on a sliding microtome. Because of the intermixture of hard and soft tissues (the result of the action of successive cambia), rotary microtoming, using the method of Carlquist (1982), was necessary for *Antigonon leptopus* stems. Sections were stained with a safranin-fast green combination. Additional sections of some of the species sectioned on a sliding microtome for SEM examination were left unstained, dried between clean slides, mounted on aluminium stubs, and sputter coated. An ISI WB-6 SEM located at the Rancho Santa Ana Botanic Garden was used for examination of vested pits, crystals, and silica bodies. The specimen of *Coccoloba cerifera* was a twig 4 mm in diameter; other samples are of mature woody stems. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

The data in Table 1 pertain to the specimens and collections listed in the Appendix. Terminology follows...
Table 1. Wood characteristics of Polygonaceae. Abbreviations: Ant. = Antigonon; Atr. = Atrophasia; Bil. = Bilderdykia; Cal. = Calligonum; Coc. = Coccobloa; Ded. = Dedekera; Eri. = Eriogonum; Gym. = Gymnopodium; Har. = Harfordia; Mue. = Muehlenbeckia; Neo. = Neomillspaughia; Pol. = Polygonum; Sym. = Symmeria; Tri. = Triplaris.

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<td>Tri. erinaceus</td>
<td>2.4</td>
<td>91</td>
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that of the IAWA Committee on Nomenclature (1964) except where modified or augmented by Carlquist (2001a); the IAWA glossary offers careful descriptions that correlate well with wood physiology, although a more recent one exists (IAWA Committee, 1989). Vessel lumen diameter is used rather than outside vessel diameter because lumen diameter more accurately reflects hydrologic functioning of a vessel. Where vessels are oval in transsection, the diameter is based on a average of long and short chords. Estimation of vessel diameter and number of vessels mm\(^2\) is difficult in those species in which vasicentric or vascular tracheids are present, because the imperforate nature of these tracheids is not evident in transsections. Absence of a perforation plate from an element the pitting of which is like that of a vessel can be determined accurately only from macerations. Estimated mean vessel diameters and vessel element lengths, indicated by parentheses in Table 1, are presented because marked dimorphism in vessels (as indicated by diameter) occurs, and data were collected separately for wide and narrow vessels. An arbitrary designation for wide vs. narrow vessels is necessary in such woods, and highlighting the presence of this phenomenon, rather than obtaining precise quantitative data relative to it, seems the important concern. Means are based on 25 observations per feature (note that in a species with dimorphic vessels, a much larger sampling would be necessary to obtain an accurate mean for vessel diameter).

The phylogenetic sequences and systematic groupings within the family have been quite diverse (e.g. Dammer, 1893; Maekawa, 1964; Roberty & Vautier, 1964). Therefore, the data of Table 1 and the Appendix are arranged in alphabetical order. Although the number of species studied may seem small for a family estimated to contain 1095 species, most of the larger genera are too herbaceous to offer any secondary xylem that would have a pattern mature enough to compare with that of true woody stems.

**RESULTS**

**SUCCESSIVE CAMBIA AND OTHER CAMBIAL VARIANTS**

One species of Polygonaceae, *Antigonon leptopus*, is an excellent example of successive cambia (Pfeiffer, 1926) and their products (Figs 1–4; figures are grouped at the end of the Results). The relatively old stem studied here shows vascular bands that in transsection are irregular in contour and subdivided by wide rays. Portions of two concentric rings of vascular tissue are shown in Figure 1. The secondary xylem (Fig. 2) is like that produced by species of Polygonaceae with single cambia. Inside the ring of cortical sclereids (Fig. 3), one can find periclinal divisions (arrows) that constitute a lateral meristem ("pericyclic meristem" of Pfeiffer, 1926). *Antigonon leptopus* is cited by Pfeiffer (1926) as an example of successive cambia, but the 'pericyclic meristems' (lateral meristems in my earlier papers on Caryophyllales with successive cambia) of a less conspicuous sort are mentioned by him in *Rheum* and *Rumex*. Perhaps in *Rheum* and *Rumex*, these meristems contribute to cortical expansion, since they evidently do not lead to successive cambia.

Apparently previously unreported are the strands of intraxylary phloem at the inner edges of fascicular zones adjacent to the pith in *Antigonon leptopus* (Fig. 4, arrowed). Pfeiffer did report fibrovascular bundles with secondary growth in the cortex of *Coccoloba*. He also reports phloem strands in "interfascicular areas" of *Polygonum*. Neither of these phenomena were observed in the material of *Coccoloba* and *Polygonum* in the present study. Pith bundles in which cambia form, producing secondary xylem centrifugally and secondary phloem centripetally, are figured by Dammer (1893) in *Rheum*.

**GROWTH RINGS**

Changes in vessel diameter can be seen within the vascular bands of *Antigonon leptopus* (Fig. 1). Narrow vessels succeeded by wider vessels occur in each of the two vascular bands. This counters a widely held but erroneous idea that initiation of a vascular band coincides with earlywood formation in dicotyledons with successive cambia.

In Polygonaceae with single cambia, growth rings vary from clearly diffuse porous to strongly demarcated changes with season in wood histology. Few Polygonaceae lack growth rings, with absence recorded only in *Coccoloba longifolia*, *C. rugosa*, *C. uiswena* (Fig. 20) and *Rumex lunaria* (Fig. 45). Growth rings with earlywood vessels perceptibly wider than latewood vessels, but with no other appreciable seasonal differences, were observed in *Bilderdykia multiflora* (Fig. 11), *Coccoloba laurifolia*, *C. polystachya*, *C. rotundifolia*, *Eriogonum arborescens*, *Gymnopusium argonoides*, *Harfordia macroptera*, *Muehlenbeckia astonii* (Fig. 34), *Polygonum lapathifolium*, and *Triplaris melanodendron*. In *Polygonum lapathifolium*, earlywood (Fig. 43, top), is characterized by wider vessels, but the wide vessels are surrounded by narrower vessels.

Growth rings with vessels wider in earlywood and narrower in latewood, but also with vessels more numerous in latewood were observed in *Atraphaxis pungens*, *Calitogonum comosum*, and *Eriogonum giganteum* (Fig. 24). These features, plus occurrence of vascular tracheids in latewood were recorded for *Antigonon leptopus* (Figs 1, 3), *Dedecera eurekensis,*

**WOOD ANATOMY OF POLYGONACEAE**

**Eriogonum deserticola** (Fig. 33), **E. fasciculata** (Fig. 32) and **E. giganteum** (Fig. 24). Growth rings with the above features, but without lateward vascular tracheids and with lateward libriform fibres narrower and thicker-walled than those of earlywood, were observed in **Calligonum arborescens** (Fig. 16), **Neomillspaughia emarginata** (Figs 39, 41), **Ruprechtia sp.**, **Triplaris americana** (Fig. 51), **T. pavonii**, and **T. surinamensis**.

**VESSELS**

Mean number of vessels per group (Table 1, column 1) shows an exceptional range in Polygonaceae. Means of 2.0 vessels per group or less occur in **Coccoloba longifolia**, **C. rugosa**, **Harfordia macroptera**, **Rumex giganteus** (Fig. 47), **R. lunaria** (Fig. 45). **Ruprechtia sp.**, **Symmeria paniculata**, and all species of **Triplaris** except **T. surinamensis**. At the other extreme, vessel groupings so large that accurate counts and means are impossible to calculate occur in some Polygonaceae; the extensiveness of these groupings may not be evident from some photomicrographs because very narrow vessels resemble libriform fibres. Illustrations that show extensive vessel groupings are offered here for **Antigonon leptopus** (Fig. 1), **Bilderdykia multiflora** (Fig. 11), **Muehlenbeckia astonii** (Fig. 34), and **Polygonum lapathifolium**. The mean number of vessels per group for a species such as **Calligonum arborescens** (Fig. 18) is difficult to obtain because patches of very narrow lateward vessels (which may include some vascular tracheids) may be large while earlywood vessels can be solitary or in small groups.

Mean vessel lumen diameter (Table 1, column 2) shows an amazing range from 18 \( \mu \text{m} \) (**Harfordia macroptera**, **Muehlenbeckia astonii**: Fig. 34) to over 100 \( \mu \text{m} \) in the tropical trees **Coccoloba polystachya**, **C. rugosa**, and **Triplaris americana** (Fig. 51).

Vessel dimorphism, in which vessel diameter tends to fall into a bimodal pattern (although never exactly so), occurs in the 'woody herb' **Polygonum lapathifolium** (Fig. 43). More marked vessel diameter dimorphism occurs in the lianas **Antigonon leptopus** (Fig. 1) and **Bilderdykia multiflora** (Fig. 11). The narrow vessels in **Antigonon leptopus** (Figs 1, 3) average 10 \( \mu \text{m} \) in lumen diameter, whereas the wider vessels average 145 \( \mu \text{m} \).

Vessel density (Table 1, column 2) is often thought to be approximately inversely proportion to vessel diameter. In Fouquieriaceae, the vessel density to vessel lumen diameter ratio is close to 2.0 for most species (Carlquist, 2001b), but in Polygonaceae, one finds a much wider range, because tropical trees have few, wide vessels and thus have low density/diameter ratios: **Coccoloba polystachya** (0.05), **C. uvifera** (0.06), **Triplaris americana** (0.1), and **T. melanodendron** (0.06) are representative of this tendency. Relatively high vessel density/diameter ratios occur in dryland polygonaceous shrubs with narrow vessels, many per unit transection (**Dedeckera**, **Eriogonum**, **Harfordia**, **Muehlenbeckia**). Although not a dryland shrub, such a ratio is found in the wood of the canelike stems of **Polygonum lapathifolium**.

Mean vessel element length in Polygonaceae (Table 1, column 3) shows a wide numerical range, from 105 \( \mu \text{m} \) in the sand dune shrublet **Dedeckera eurekensis** to 549 \( \mu \text{m} \) in the tropical tree **Coccoloba polystachya**. This range, however, is lower than one would expect, considering that the mean vessel element length for dicotyledons as a whole is 649 \( \mu \text{m} \) (Metcalfe & Chalk, 1950: 1360).

Vessel element length was computed separately for the short and long vessel elements in two species of Polygonaceae with vessel dimorphism. In **Antigonon leptopus**, wide vessel elements have a mean length of 83 \( \mu \text{m} \) (and are thus mostly wider than they are long – see above), whereas narrow vessel elements have a mean length of 140 \( \mu \text{m} \). In **Bilderdykia multiflora**, the wide vessel elements have a mean length of 90 \( \mu \text{m} \), the narrow ones a mean length of 173 \( \mu \text{m} \).

Vessel wall thickness (Table 1, column 3) mostly falls between 2 and 4 \( \mu \text{m} \) in Polygonaceae. Wider vessels tend to have thicker walls. Thus, the tropical tree genera **Coccoloba**, **Neomillspaughia**, and **Triplaris** have mean wall thickness greater than 3.0 \( \mu \text{m} \) (the twig specimen of **Coccoloba cereifera** falls below that, and has narrower vessels). For species with a wide range of vessel diameter, a range of mean thicknesses is shown in Table 1. A range in vessel wall thickness is particularly characteristic of the genera with vessel dimorphism, **Antigonon** and **Bilderdykia**.

Pit cavity diameter (measured parallel to long axis of vessel) is relatively uniform (3–5 \( \mu \text{m} \)) for most of the family (Table 1, column 6). Pits with somewhat greater diameter occur in **Coccoloba**, **Gymnopodium**, **Rumex**, and **Triplaris** (Table 1, column 6). This applies to pit cavities of both vessel-to-vessel and vessel-to-ray and vessel-to-axial parenchyma pitting. Vessel pitting is alternate, and generally circular, with some tendency toward oval shapes. More elongate shapes, corresponding to the term pseudoscalariform, were observed in vessel-to-vessel pitting in **Antigonon leptopus**, **Dedeckera eurekensis**, **Eriogonum fasciculatum**, and, to a modest extent, in **Ruprechtia sp.**, **Triplaris americana**, **T. melanodendron**, and **T. surinamensis**. Pit aperture shape is narrowly elliptical on vessel to vessel pits, but more widely elliptical in vessel to axial parenchyma or vessel to ray parenchyma.

Vestured pits have been reported in Polygonaceae for the genera **Brunnichia**, **Muehlenbeckia**, and
Triplaris, and have been reported to be absent in Coccoloba (Jansen et al., 1998). In the present study, vestured pits are figured for Atraphaxis frutescens (Figs 5, 6), A. pungens (Figs 7, 8), Gymnopodium antigonoides (Fig. 9), Muehlenbeckia astonii (Fig. 36), Ruprechtia sp. (Fig. 59), Rumex giganteus (Fig. 40), Triplaris pavonii (Figs 56, 57) and T. surinamensis (Fig. 58). Vestured pits were also observed and photographed with SEM but not figured in the present paper for Bilderdykia aubertii, Coccoloba longifolia (both vessel-to-vessel and vessel side of vessel-to-ray pitting), C. polystachya, C. uifera, Eriogonum giganteum, Polygonum lapathifolium, Triplaris americana, and T. melanodendron. In view of the presence of vested pits in Coccoloba, in contrast with the absence reported earlier, and in view of the numerous new reports for the family offered here, many more instances of vested pit occurrence are likely to be found in the family.

The vesturing in pits of Rumex, Ruprechtia, and Triplaris is unusually dense and extensive, spreading onto the vessel wall facing the lumen. Vesturing on simple perforation plates of Muehlenbeckia was reported by Kucera et al. (1977). Observation by means of SEM is the obvious technique for rendering vesturing clearly. However, in some families reported vestures are probably droplets of secondary compounds, and thus cross-checking with light microscopy, as done here, should be employed.

Grooves interconnecting pit apertures on vessel walls have not previously been reported in vessels of Polygonaceae (Carlquist, 2001a: 96). In the present study, such grooves were observed in Antigonon leptopus, Bilderdykia aubertii, Calligonum arborescens, Coccoloba laurifolia, Eriogonum fasciculatum, E. kennedyi, and Polygonum lapathifolium. In the present study, helical thickenings in vessels are reported for Atraphaxis pungens (Figs 7, 8), Bilderdykia multiflora (narrow vessels), Eriogonum giganteum (Figs 26–29), E. heermannii (thickenings slender and well spaced from each other), and Muehlenbeckia astonii (Fig. 36). Helical thickenings in vessels have been reported in latewood of Polygonaceae for vessels of Eriogonum fasciculatum and E. giganteum (Carlquist & Hoekman, 1985). Earlier, Solereder (1908) listed helical thickenings in the polygonaceous genera Calligonum, Chorizanthe, and Triplaris; Record (1936) observed helical thickenings in vessels of Coccoloba, Eriogonum, and Ruprechtia.

Nonbordered perforation plates were recorded on vessels in the present study on wood longitudinal sections of Antigonon leptopus, Atraphaxis pungens, Bilderdykia multiflora, Calligonum arborescens, C. comosum, Coccoloba laurifolia, C. uifera, Dedekeria eurekensis, Eriogonum giganteum (Fig. 28), Gymnopodium antigonoides, Harfordia macropera, Muehlenbeckia astonii, Neomillspaughia emarginata, Polygonum lapathifolium, Rumex giganteus, Ruprechtia sp., Symmeria paniculata, Triplaris americana, and T. melanodendron. These are all new records for the family and include all of the genera studied. Nonbordered perforation plates probably characterize the family. However, an occasional bordered perforation plate can be found in a few of the species examined, as shown for Eriogonum giganteum (Fig. 29).

Vessel restriction patterns occur in Muehlenbeckia astonii (Fig. 34) and Polygonum lapathifolium (Fig. 43). In these examples, vessels are restricted to the central portions of fascicular areas, forming strips down the centres of fascicular areas. Thus, vessels are not, with few exceptions, in contact with ray cells. Vessel restriction patterns of this sort are probably much more common in dicotyledonous woods than has at present been noted. The phenomenon has been recorded in seven families, which are not closely related to each other (Carlquist, 2001a: 53).

IMPERFORATE TRACHEARY ELEMENTS

Libriform fibres with simple pits characterize all of the Polygonaceae studied. Mean length (Table 1, column 7) ranges from 210 to 1378 μm. The genera with the lowest mean fibre length are the shrubs Dedeckera and Eriogonum; those with the longest are the trees Coccoloba, Gymnopodium, Neomillspaughia, Symmeria, and Triplaris. Fibre wall thickness is relatively uniform in the family (Table 1, column 8), and no fibres indicative of reaction wood were observed in the species studied.

Judging from the presence of starch (see below) and septa in fibres of Polygonaceae, the family is probably characterized by living fibres (Carlquist, 2001a: 136). Species in which fibres were not observed to have septa include Atraphaxis pungens, Bilderdykia multiflora, Calligonum arborescens, Dedeckera eurekensis, Eriogonum arborescens, E. deserticola, E. fasciculata, E. giganteum, E. heermannii, E. kennedyi, Rumex giganteus, and R. lunaria. A single septum per libriform fibre was observed in Antigonon leptopus, Coccoloba laurifolia, C. uifera, Harfordia macropera, and Polygonum lapathifolium; more than one recorded in Coccoloba longifolia, C. polystachya, C. rotundifolia, C. rugosa, Gymnopodium antigonoides, Muehlenbeckia astonii, Neomillspaughia emarginata, Ruprechtia sp., Symmeria paniculata, Triplaris americana, T. melanodendron, T. pavonii, and T. surinamensis (about four per fibre in T. surinamensis). The above data do not include the septa in crystal-bearing fibres, which are described below in connection with crystal occurrence.

Another type of imperforate tracheary element is common in some species. Imperforate fusiform cells
pitted like vessels and formed at the termini of growth rings, and termed vascular tracheids (Carlquist, 2001a) are common. These are not to be confused with vasicentric tracheids, which surround vessels and are best known in *Quercus*, although they occur in many other dicotyledons (Carlquist, 2001a). Vascular tracheids must be identified in macerations, because in sections, perforation plates are often missing from what are probably very narrow vessels. Vascular tracheids were observed in *Antigonon leptopus*, *Dedeckera eurekensis*, *Eriogonum arborescens*, *E. deserticola*, *E. fasciculatum*, *E. giganteum*, *E. heermannii*, and *E. kennedyi*. Helical thickenings were observed in the vascular tracheids of *E. kennedyi*.

**AXIAL PARENCHYMA**

Throughout Polygonaceae, axial parenchyma occurs as scanty paratracheal or vasicentric. In wood transverse sections, axial parenchyma occurs in the form of a few cells in contact with vessels, or scattered among larger groups of vessels in contact with each other; no apotracheal parenchyma was observed. Axial parenchyma is scarce in some species, such as *Atraphaxis pungens*. A nonsubdivided axial parenchyma cell can be mistaken for a libriform fibre unless one notices the larger pits characteristic of axial parenchyma; also, axial parenchyma cells tend to have thinner walls than libriform fibres in any given species.

Strands of axial parenchyma (Table 1, column 9) consist of one, occasionally two cells in *Atraphaxis pungens*, *Bilderdykia multiflora*, *Dedeckera eurekensis*, *Eriogonum arborescens*, *Muehlenbeckia astonii*, and both species of *Rumex*. Strands of two cells were recorded in *Calligonum* (both species) and in *Harfordia macropera*. Strands of two to four cells characterize *Antigonon leptopus*, *Coccoloba* (all species), and *Eriogonum arborescens*. Strands of five cells were observed in *Symmeria paniculata* and *Eriogonum* (all species except *F. arborescens*), *Coccoloba species* (such as *C. uvifera*, *Gymnopodium antigonoides*, and *Harfordia macropera* (Table 1, column 10). Multiseriate rays (including biseriate rays) are about as common as uniseriate rays in *Atraphaxis pungens*, *Calligonum arborescens* (Figs 17, 19), *Eriogonum deserticola* (Fig. 30), *E. giganteum* (Fig. 25) and other species of *Eriogonum*, and *Rumex lunaria* (Fig. 46). Multiseriate rays were observed to be more common than uniseriate rays in *Bilderdykia multiflora* (Fig. 12), *Calligonum comosum*, *Coccoloba rugosa*, *Dedeckera eurekensis*, *Eriogonum arborescens*, *Muehlenbeckia astonii* (Fig. 35), *Neomillospaughia emarginata* (Fig. 40), *Polygonum lapathifolium* (Fig. 44), *Rumex giganteus* (Fig. 48), *Ruprechtia sp.*., *Triplaris americana* (Fig. 52), and the other species of *Triplaris*. *Symmeria paniculata* is the only species observed in which uniseriate rays are absent or nearly so (Table 1, column 10).

Ray histology in Polygonaceae is diverse. Using the ray types of Kribs (1935) and Carlquist (2001a) and the data on wood histology (Table 1, columns 10 and 11), the following types can be designated for species in the family. Homogeneous Type I occurs in *Antigonon leptopus* (Fig. 2), *Calligonum comosum*, most *Coccoloba species* (such as *C. uvifera*, Fig. 21), *Eriogonum arborescens*, *Muehlenbeckia astonii* (Fig. 35), *Neomillospaughia emarginata* (Fig. 40), *Ruprechtia sp.* and all species of *Triplaris* (see Fig. 52). Homogeneous Type 2 occurs in *Symmeria paniculata*. Homogeneous Type III characterizes *Coccoloba longifolia*, *C. polystachya*, and *C. rugosa*. Heterogeneous ray types are less common. Heterogeneous Type IIB occurs in *Calligonum arborescens* (Fig. 17), *Coccoloba rotundifolia*, and *Eriogonum spp.* (e.g. *E. giganteum*, Fig. 25). Paedomorphic Type I characterizes *Atraphaxis pungens*, *Bilderdykia multiflora* (Fig. 12), *Coccoloba cereifera*, *Dedeckera eurekensis*, *Eriogonum fasciculatum*, *H. heermannii*, *Muehlenbeckia astonii* (Fig. 35), *Polygonum lapathifolium* (Fig. 44), *Rumex giganteus* (Figs 48), and *R. lunaria* (Fig. 46). The rare Paedomorphic Type III occurs in *Harfordia macropera*. The stems studied for *E. kennedyi*, although mature, proved entirely rayless, which is a new family record for this condition.

The height of multiseriate rays (Table 1, column 12) is greatest in the two lianoid species studies, *Antigonon leptopus* (Fig. 2, extreme left) and *Bilderdykia multiflora* (Fig. 12). The nonlianoid species *Polygonum lapathifolium* (Fig. 44) also has tall rays. In the majority of Polygonaceae, multiseriate ray height averages
Width of multiserrate rays (Table 1, column 13) is close to two cells for most Polygonaceae (Figs 21, 51, 52). Significantly wider rays occur in Antigonon leptopus (Fig. 2), Bilderdykia multiflora (Figs 12, 14), Calligonum arborescens (Figs 17, 19), Muehlenbeckia astonii (Fig. 35), Polygonum lapathifolium (Fig. 44), Rumex giganteus (Fig. 48), R. lunaria (Fig. 46), and Symmeria paniculata.

The height of uniseriate rays (Table 1, column 14) ranges from 41 μm in Antigonon leptopus to 257 μm in R. lunaria. Although this range seems considerable, 13 of the 32 species studied are notably short in uniseriate ray height, with means between 95 and 105 μm.

Ray cell wall thickness of more than 2 μm was recorded for Atrophaxis pungens, Bilderdykia multiflora (Fig. 14), Calligonum arborescens (Fig. 19), Eriogonum deserticola, E. fasciculatum, E. heermannii, Muehlenbeckia astonii (Figs 37, 38), Neomillspaughia emarginata (Fig. 42), and Polygonum lapathifolium. Ray cell wall thickness between 1 and 2 μm characterizes the remaining species. Ray cells were observed to have lignified secondary walls, with few exceptions. The druse-containing cells in rays of Bilderdykia multiflora (Fig. 14) have thin nonlignified walls.

Tangentially orientated walls in procumbent ray cells bear numerous pits, at least some of which are bordered, as seen in sectional view (Fig. 22). At least a few bordered pits on tangential walls of ray cells were observed in Atrophaxis pungens, Calligonum arborescens, Coccoloba laurifolia, C. polystachya, C. rotundifolia, Dedekera eurekensis, Eriogonum arborescens, E. deserticola, E. fasciculatum, Gymnopodium antigonoides, Harfordia macropera, Muehlenbeckia astonii, Neomillspaughia emarginata, Polygonum lapathifolium, Rumex giganteus, and Symmeria paniculata. Borderer pits on ray cells of dicotylyledonous woods are common (see Carlquist, 2001a: 213, 221–223). Such bordered pits have been reported infrequently because most workers view the pits in face view, when the borders are difficult to see, whereas in sectional views of pits, the borders are clearly evident.

**STOREYED STRUCTURES**

Storeyed structures are relatively common in Polygonaceae (Table 1, column 15), but not as conspicuously as in woods of some dicotylyledonous families. Many workers look for storeyed libriform fibres and rays; a few instances of storeyed libriform fibres can be cited in Polygonaceae: Bilderdykia multiflora (inconspicuous storeyed structure in Fig. 12), Polygonum lapathifolium (Fig. 44, especially at right), and Rumex lunaria (Fig. 46, throughout). More commonly, narrow vessels and axial parenchyma strands associated with vessels are storeyed, as shown for Calligonum arborescens (Fig. 19). Storeyed narrow vessels and associated axial parenchyma strands were recorded for Antigonon leptopus, Dedekera eurekensis, Eriogonum deserticola, E. heermannii, Gymnopodium antigonoides, and Polygonum lapathifolium. Where vascular tracheids are present, they occur with narrow vessels and conform to the same storeying patterns as narrow vessels. Probably, storeyed cambia and storeyed sieve-tube elements are more widespread in Polygonaceae than are storeyed secondary xylem cells. In Coccoloba, lack of narrow vessels, combined with elongation of fibres (F/V ratio about 2.0 in this genus) would minimize storeyed structure in wood.

**TYLOSES**

Tyloses were observed in Triplaris americana (Fig. 51) and T. surinamensis. These tyloses have thin but lignified walls.

**SILICA BODIES AND CRYSTALS**

Polygonaceae are unusual in having both silica bodies and calcium oxalate crystals in wood cells, but in no species, except for Gymnopodium antigonoides, do these two occur together (Table 1, column 16). Silica bodies were observed only in ray cells in Calligonum arborescens, C. comosum, Eriogonum arborescens, E. deserticola (Fig. 31), E. heermannii, Gymnopodium antigonoides (Fig. 10), Muehlenbeckia astonii (Fig. 38), and Ruprechtia sp. The silica bodies of most species, as seen with SEM, tend to have the form of spheroids with irregular surfaces (Figs 10, 31), whereas those of Muehlenbeckia astonii bear prominent protuberances (Fig. 38). Silica bodies may be more common than the listing in Table 1 indicates because ray cells in many species of the family are filled, or nearly so, with dark-staining amorphous deposits that tend to obscure silica bodies.

Calcium oxalate druses were observed in the secondary phloem of Atrophaxis pungens, although they are absent in the wood (Table 1, column 16). In dicotyledons at large, calcium oxalate crystals tend to occur more commonly in pith, phloem, and cortex than in secondary xylem. In rays of secondary xylem, druses were seen in Bilderdykia multiflora (Figs 14, 15) and Rumex giganteus (Fig. 50). In Bilderdykia multiflora, druses and rhomboidal crystals occur in thin-walled idioblastic cells larger than ray cells lacking crystals, whereas in Rumex giganteus, druses occur in cells identical with crystal-free ray cells.

Rhomboidal crystals occur in three modes: in ray cells (usually singly); in nonseptate libriform fibres (numerous crystals of various sizes per fibre); and as...
bands that are reminiscent of axial parenchyma. The observed in C. rotundifolia (Fig. 22: note the occurrence in other idioblastic ray cells.

Rhombooidal crystals of various sizes (grading into crystal sand) occur in nonseptate fibres of Harfordia macroptera.

Chambered crystals exhibit a range of forms. The strands of chambered crystals in Polygonaceae seem to be variations of septate fibres. This is suggested most clearly in the radial sections of Coccoloba rotundifolia (Fig. 22) and C. rugosa (Fig. 23). In C. rotundifolia, the fibres are nearly as long as crystals-free fibres, but septa are composed of primary wall material only. This is also true in the SEM view of Triplaris americana (Fig. 53; some septa probably lost in sectioning). Crystalliferous fibres are also seen for this species with light microscopy in a radial section (Fig. 54) and in a transsection (Fig. 55). In C. rugosa (Fig. 23), the septa between the crystals are thicker, with lignified walls, more like those of a strand of axial parenchyma (note mirror-image crystal pairs at top of Fig. 3). In some crystalliferous fibres of Triplaris, chambered crystals may occur in part of a given fibre, whereas the remainder of the fibre may have one or two septa and lack crystals (Fig. 54).

All species of Coccoloba have crystals except for C. cereifera, in which a relatively thin stem from a herbarium specimen was studied. Crystalliferous fibres may therefore not occur in the earliest secondary xylem of a stem of Coccoloba. All species of Triplaris studied have chambered crystals in fibres.

The crystals of Neomillspaughia emarginata have been regarded as present in axial parenchyma by Metcalfe & Chalk (1950), but I regard these strands as homologous to the fibres containing chambered crystals in Coccoloba and Triplaris. The strands of rhombooidal crystals in Neomillspaughia are very similar in morphological details to those of Coccoloba and Triplaris, differing only in that the strands end in cells that are somewhat rounded rather than pointed. Moreover, no diffuse parenchyma has been reported for Polygonaceae, so the origin of the crystalliferous strands seems more likely from fibres than from interpolation of diffuse strands of crystal-bearing parenchyma.

Metcalfe & Chalk (1950) note that the crystalliferous fibres of Triplaris surinamensis tend to occur in bands that are reminiscent of axial parenchyma. The crystalliferous fibres of Triplaris are clearly not axial parenchyma, but there is a nonrandom distribution of the crystalliferous fibres in some species. This was observed in C. rotundifolia (Fig. 22: note the occurrence of a group of crystalliferous fibres) and in all four of the species of Triplaris studied. These crystalliferous fibres occur in concentric bands that alternate with bands of noncrystalliferous fibres. The bands are not precisely defined: there are some scattered crystalliferous fibres within the bands of noncrystalliferous fibres.

AMORPHOUS DEPOSITS

Woods of Polygonaceae characteristically bear deposits of dark-staining materials. These are not common in ray cells, and are evident here in Figures 1, 12, 17, 19, 20, 21, 24, 25, 30, 35, 40, 44—48, 52 and 54. The characteristic mode of deposition of these compounds is seen in Figure 22 (bottom). In Neomillspaughia, the axial crystal-bearing strands (modified crystalliferous fibres?) bear some crystal-free cells that contain dark-staining deposits (Fig. 42). Dark-staining deposits were observed in at least some libriform fibres in Caligonom arborescens, C. laurifolia, C. rotundifolia, C. rugosa, C. uvifera (Figs 20, 21), Eriogonum fasciculatum, E. giganteum, Gymnopodium antigenoides, Harfordia macroptera, Muehlenbeckia astonii, Rumex giganteus, and R. lunaria.

Dark-staining deposits were seen in axial parenchyma in Coccoloba uvifera, Dedeckera eurekensis, Gymnopodium antigenoides, and Symmeria paniculata; these deposits are to be expected in axial parenchyma of other Polygonaceae.

STARCH

Because libriform fibres are septate in many species of Polygonaceae, one can use the term 'living fibres' for them: septate fibres are indicative of prolonged fibre longevity. This designation is underlined by the presence of starch, which was observed in libriform fibres of Antigonon leptopus, Eriogonum arborescens, and E. kennedyi. The wood samples studied for these three species were taken from living specimens and were preserved in 50% aqueous ethanol, a method that tends to preserve starch. Very likely, starch occurs in libriform fibres of many other Polygonaceae, and is to be expected in axial parenchyma of at least some Polygonaceae.

DISCUSSION AND CONCLUSIONS

SYSTEMATIC AND PHYLOGENETIC RELATIONSHIPS

In a series of recent molecular-based phylogenies that include or are restricted to Caryophyllales, Polygonaceae and Plumbaginaceae appear as sister families (Downie & Palmer, 1994; Manhart & Rettig, 1994; Williams et al., 1994; Downie et al., 1997; Soltis et al., 2003 The Linnean Society of London, Botanical Journal of the Linnean Society, 2003, 141, 25-51
Figures 1–4. Stem sections of *Antigonon leptopus* including wood. Fig. 1. Transection of stem, cortex above; two vascular bands shown. Fig. 2. Tangential longitudinal section; wide, tall rays at extreme right and left. Fig. 3. Portion of stem section showing cortical sclereids (top), secondary xylem and phloem (below), and tangential lateral meristem divisions in cortex (arrows). Fig. 4. Transection of pith of old stem, showing intraxylary phloem. Scale bars: Figs 1, 2 = 50 μm; 3, 4 = 20 μm.
Figures 5–10. SEMs of details from wood of Polygonaceae. Figs 5, 6. *Atraphaxis frutescens*, vestured pits from tangential section. Fig. 5. Inside surface of vessel. Fig. 6 External surface of vessel. Figs 7, 8. *Atraphaxis pungens*, inside surface of vessels. Fig. 7. Prominent helical thickenings on latewood vessel. Fig. 8. Vestured pits and helical thickenings from vessel. Figs 9, 10. *Gymnopodium antigonoides*, portions of tangential sections. Fig. 9. Pits as seen from external side of vessel, showing vestigial vesturing. Fig. 10. Silica bodies in ray cell. Scale bars = 5 μm.
Figures 11–15. Wood sections of Bilderdyka multiforma. Fig. 11. Transection; earlywood in upper half of photograph. Fig. 12. Tangential section, showing tall rays. Fig. 13. SEM of vessel wall (vertical axis horizontal), showing grooves interconnecting many pairs of pit apertures. Fig. 14. Tangential section; a ray at left and another at right contain thin-walled druse-containing idioblasts. Fig. 15. SEM of druse from ray cell of tangential section; druse fractured by sectioning. Scale bars: Figs 11, 12 = 50 μm; 13, 15 = 5 μm; 14 = 20 μm.

Figures 16–19. Wood sections of *Calligonum arborescens*. Fig. 16. Transection, ring porous, showing growth ring; earlywood in top 2/5 of photograph. Fig. 17. Tangential section; rays are relatively short and wide. Fig. 18. Transection to show margin between latewood and earlywood. Fig. 19. Tangential section; narrow vessels are storied (centre, top to bottom). Scale bars: Figs 16, 17 = 50 μm; 18, 19 = 20 μm.
Figures 20–23. Wood sections of Coccoloba. Figs 20, 21. *C. uvifera*. Fig. 20. Transection; diffuse porous; dark-staining compounds fill many cells. Fig. 21. Tangential section; most rays are uniseriate or biseriate. Fig. 22. *C. rotundifolia*. Radial section to show crystalliferous fibres (more than one crystal between some septa); below, ray cells containing dark-staining compounds. Fig. 23. *C. rugosa*. Radial section to show septate fibre (centre) and, to left of centre, a crystalliferous fibre in which relatively thick, lignified walls separate the chambered crystals. Scale bars: Figs 20, 21 = 50 μm; 22 = 20 μm; 23 = 10 μm.
Figures 24-29. Wood sections of *Eriogonum giganteum*. Fig. 24. Transection; fluctuation in vessel diameter is not typical ring porous, but is related to differences in moisture availability within and between years. Fig. 25. Tangential section; most rays are short, biseriate or uniseriate. Figs 26-29. SEMs of interior of vessel wall from radial section. Fig. 26. Sparse helical thickenings from earlywood vessel. Fig. 27. Densely placed helical thickenings from latewood. Fig. 28. Portion of nonbordered perforation plate. Fig. 29. Portion of bordered perforation plate; helical thickenings on vessel wall below the paired rims of the perforation plate. Scale bars: Figs 24, 25, scale bars = 50 µm; Figs 26-29, scale bars = 5 µm.
Figures 30–33. Wood sections of *Eriogonum*. Figs 30, 31. *E. deserticola*. Fig. 30. Tangential section. Dark-staining material present in most ray cells. Fig. 31. Silica bodies in two ray cells from tangential section. Fig. 32. *E. fasciculatum*. Tangential section; earlywood in upper half of photograph. Fig. 33. *E. heermannii*. Transection, to show strongly marked fluctuation in vessel diameter, corresponding to seasonal moisture availability. Scale bars: Figs 30, 33 = 50 μm; 31 = 5 μm; 32 = 20 μm.
Figures 34–38. Wood sections of *Muehlenbeckia astonii*. Fig. 34. Transection; vessels restricted to central portions of fascicular areas. Fig. 35. Tangential section; irregular storeying evident. Fig. 36. SEM photograph of inner surface of vessel from tangential section showing helical thickenings and vested pits. Figs 37, 38. SEM photographs of ray cells from tangential section, to show silica bodies. Fig. 37. Portion of silica body; protuberances present on silica body surface. Fig. 38. Small silica bodies and deposits. Scale bars: Figs 34, 35 = 50 μm; 36–38 = 5 μm.
Figures 39–42. Wood sections of *Neomillspaughia emarginata*. Fig. 39. Transection; many vessels in radial multiples. Fig. 40. Tangential section; rays are uniseriate to triseriate. Fig. 41. Transection. Scattered among the empty libriform fibres are fibres containing chambered crystals. Fig. 42. Radial section, showing longisection of file of chambered crystals (right of centre; portions of other files at top); all ray cells are procumbent. Scale bars: Figs 39, 40 = 50 μm; 41, 42 = 20 μm.
Figures 43–46. Wood sections of Polygonaceae. Figs 43, 44. Polygonum lapathifolium. Fig. 43. Transection; vessel restriction pattern clearly evident. Fig. 44. Tangential section; storying of fibres and vessels common. Figs 45, 46. Rumex lunaria. Fig. 45. Transection. Most vessels are solitary. Fig. 46. Tangential section; storeying evident in narrow vessels and libriform fibres. Scale bars = 50 µm.
Figures 47-50. Wood sections of *Rumex giganteus*. Fig. 47. Transection; vessel density is low. Fig. 48. Tangential section; rays are very tall, multiseriate. Fig. 49. SEM of inner vessel surface (long vessel axis orientated horizontally) to show elongate nature of pits; vesturing evident in pits. Fig. 50. SEM of druse in ray cell, from tangential section. Scale bars: Figs 47, 48 = 50 μm; 49, 50 = 5 μm.
Figures 51–55. Wood sections of Triplaris. Figs 51, 52. *T. americana*. Fig. 51. Transection; growth rings present; vessels in radial multiples; tyloses in vessels at bottom. Fig. 52. Tangential section; most rays are biseriate. Fig. 53. *T. melanodendron*. SEM of radial section; chambered rhomboidal crystals in fibre at left, a single septum and pits visible in fibre at right. Figs 54, 55. *T. surinamensis*. Fig. 54. Radial section, showing septate fibres; some fibres are septate without crystals, some are septate and have parts with crystals, parts without them; procumbent ray cells at bottom. Fig. 55. Transection; near centre, crystals in septate fibres (grey areas surrounding crystals are septa behind crystals). Scale bars: Figs 51, 52 = 50 µm; 53 = 5 µm; 54 = 20 µm; 55 = 10 µm.

Figures 56–59. SEMs of vested pits of Polygonaceae from tangential wood sections. Figs 56, 57. *Triplaris pavonii*. Fig. 56. Vestured pits seen from inside of vessel. Fig. 57. Vestured pits seen from outside of vessel. Fig. 58. *Triplaris surinamensis*; vesturing extends extensively from pit aperture onto inner surface of vessel. Fig. 59. *Ruprechtia* sp.; vesturing extends to moderate degree from pit apertures to inside surface of vessel; band of vesturing near perforation plate, bottom. Long axis of vessel is horizontal in Figs 56–67, but vertical in Figs 58 and 59. Scale bars = 5 μm.
In the cladogram of Soltis et al. (2000), Rhabdodendraceae were placed basal to the branch of Caryophyllales s.l. that includes Polygonaceae and Plumbaginaceae. [Note: in the last sentence of Carquist (2001c), the wording indicating that Rhabdodendraceae should be included in Caryophyllaceae is an error; inclusion in Caryophyllales was intended.]

Features that are shared by Rhabdodendraceae and Polygonaceae include ability to form successive cambia (some species only), presence of silica bodies, presence of vestured pits in vessels, and presence of massive deposits of dark-staining compounds, especially in rays (Carquist, 2001c). Silica bodies occur in Plumbaginaceae as well as in Caryophyllales s.l. (Ancistrocladaceae and Dioncophyllaceae) and might be a synapomorphy. The presence of vestured pits in Polygonaceae in Polygonaceae and Rhabdodendraceae, on the contrary, seems better interpreted as a synapomorphy, because the feature is absent elsewhere in Caryophyllales (either s.s. or s.l.).

The presence of successive cambia in one or more species of a family characterizes Caryophyllales s.s. (except for Achatocarpaceae, Cactaceae, Didieriaceae, and Portulacaceae). The absence of successive cambia in some Phytolaccaceae (Carquist, 2000), most Plumbaginaceae, and some Rhabdodendraceae is curious. However, the successive cambia of *Stegnosperma* (Carquist, 1999a) may provide an explanation. As shown in that genus by Horak (1981a, 1981b), the onset of successive cambial activity may be delayed considerably; this is also true in Basellaceae (Carquist, 1999c). Thus, presence of successive cambia could be a synapomorphy in Caryophyllales (at least Caryophyllales s.s.), and in the genera or species of that group in which successive cambia have never been observed, onset of successive cambia might be delayed indefinitely or the genetic information for their formation may be lost. This explanation would be more parsimonious than a hypothesis that successive cambia originated independently in each of the caryophyllaceous clades in which both normal and successive cambia, or only successive cambia, are present. This may appeal to some as counterintuitive, because some large families of Caryophyllales lack successive cambia (Cactaceae, Portulacaceae), and successive cambia do not occur in most clades of dicotyledons. The retention of successive cambia in roots of Caryophyllaceae (Pfeiffer, 1926; Carquist, 1995) is also suggestive, because Caryophyllaceae is commonly placed basally within Caryophyllales s.l. (e.g. Soltis et al., 2000).

The presence of nonbordered perforation plates in Caryophyllales is pervasive (see Carquist, 1999b, 2000). Although the entirety of Caryophyllales has not been surveyed with respect to this feature, only a few nonbordered perforation plates have been observed (some Cactaceae, Carquist, unpublished; *Eriogonum* _giganteum_, Fig. 29, this paper; *Stegnosperma*, Horak, 1981a but not Carquist, 1999a). In addition to the widespread occurrence of nonbordered perforation plates in Caryophyllales, their occurrence in genera placed more basally in Caryophyllales s.l. by Rodman (1994) and Soltis et al. (2000) is suggestive that they are a synapomorphy in Caryophyllales s.l. They occur in numerous families of Caryophyllales (see Carquist, 2000; they are also present in Tamaricaceae and Plumbaginaceae: Carquist, unpublished), and are omitted from the cladograms of Soltis et al. (2000).

At the intrafamilial level within Polygonaceae, some features parallel taxonomic distribution and relationships proposed by earlier authors. Dammer (1893) includes *Coccoloba* and *Triplaris* in the same subfamily (admittedly in different tribes). Closeness of these two genera (along with *Neomillspaughia*) is suggested by the presence of chambered crystals in septate fibres (Table 1, column 16). Other genera without chambered crystals (*Antigonon*, *Muehlenbeckia*, *Ruprechtia*, and *Symmeria*) are also placed by Dammer (1893) in the subfamily Coccoloboideae. Maekawa (1964) stresses closeness of cocoloboids and triplaroids.

The occurrence of silica in ray cells and the occurrence of calcium oxalate crystals is almost mutually exclusive in the species studied: only one genus (*Gymnopodium*) was observed to have both. The genera with silica bodies — *Calligonum*, *Eriogonum*, *Muehlenbeckia*, *Ruprechtia*, and *Symmeria* — are assigned to a...
number of distinct subfamilies and tribes both by Dammer (1893) and by Robert & Vautier (1964). Silica presence is therefore unlikely to parallel taxonomic distinctions unless it is discovered in more genera and species that form well-supported systematic groupings within the family.

Eriogonum appears to be a distinctive group on the basis of silica bodies, narrow multiseriate rays (nearly all biseriate), lack of septa in fibres, and presence of few cells (often only one) per strand in axial parenchyma. There are, however, distinctive wood features within Eriogonum (pervasive parenchyma in E. alata and E. latifolium; raylessness in E. kennedyi; helical thickenings in vessels of E. giganteum and E. heermannii and in vasicentric tracheids of E. kennedyi). The sampling of woody species of Eriogonum from western North America studied here represents only a small portion of this group. Further study of these would probably reveal many differences in wood, mostly related to habit and ecology. Amazingly, this large group of distinctive species of Eriogonum were nearly all reduced to a single species of the south-eastern U. S., E. tomentosum Mich., by Robert & Vautier (1964).

Other distinctions in wood anatomy that may prove to parallel generic taxonomic distinctions include occurrence of successive cambia (Antigonon), vessel dimorphism (Bilderdykia), Homogeneous Type II rays (Symmeria), co-occurrence of silica bodies and calcium oxalate crystals (Gymnopodium), and occurrence of numerous calcium oxalate crystals within nonseptate fibres (Harfordia). With these genera, as well as with other groupings that seem at present to correlate with taxonomy, much more study is needed, because Polygonaceae is a family with 49 genera and 1095 species (Thorne, 2000).

More extensive systematic conclusions will be possible when the series of papers on Caryophyllales, which includes the present paper, is concluded.

HABIT

Polygonaceae are relatively uniform with respect to the F/V ratio (Table 1, column 17). One might have expected great elongation of libriform fibres in trees such as Triplaris. The significance of the F/V ratio (which admittedly has a limited range) appears to represent, in a very general way, the degree of phylectic advancement (Carlquist, 1975). Imperforate tracheary elements are only a little longer than the vessel elements with which they are associated in dicotyledons widely regarded as primitive (Bailey & Tupper, 1918).

Ray cells are a very sensitive indication of habit and of ontogenetic and phylectic change in habit. There is an assumption (Krubs, 1935) that cells seen as square in radial section are morphologically equivalent to upright cells. Multiseriate rays in which upright and/or square cells are more common than procumbent cells can be considered as paedomorphic rays (Carlquist, 2001a, fig. 6.2). Species with paedomorphic rays include Antigonon leptopus, Atropaclus pungens, Bilderdykia multiflora, Coccoloba cereifera, Dedeckera eurekensis, Eriogonum spp., Harfdoria macroptera, Muehlenbeckia axonii, Polygonum lapathifolium, Rumex giganteus, and R. lunaria. Because these have paedomorphic rays, they probably represent derivation from herbaceous or less woody ancestors, rather than from clearly woody ancestors, according to concepts of paedomorphism in wood (Carlquist, 2001a). The sole exception is Coccoloba cereifera, for which a twig from an herbarium specimen was used. Such a twig would be expected to have juvenile wood; in the other species listed above, juvenility in rays is extended for the life of the plant. Aside from the ray histology, the species in the above list do not suggest true woodiness in aspect (e.g. Polygonum, Rumex). A detailed molecular phylogeny of Polygonaceae is needed to confirm this interpretation. As a whole, Polygonaceae appear to be derived from woody ancestors. Maekawa (1964) places the arborescent tribes (subfamilies of other authors) Coccobelae and Triplaridae at the base of his phylogenetic series for the family. This interpretation agrees with the data from rays. The phylogenetic arrangement of Dammer (1893) places Coccoloba and Triplaris (and allied genera) near the end of his treatment, whereas the location of these woody genera by Robert & Vautier (1964) is intermediate within the family.

Dimorphism in vessel element diameter (and length: narrower vessel elements are appreciably longer) occurs in Antigonon and Bilderdykia, both of which are lianas. Antigonon is the only genus of Polygonaceae known to have successive cambia. Both of these features are found in a much higher proportion of lianas than in nonscandent woody dicotyledons (Carlquist, 1985).

ECOLOGY

The arbitrary ratio termed Mesomorphy (Table 1, column 18) has proved useful when comparing families, genera, and species of dicotyledons (Carlquist & Hoekman, 1985). For most dicotyledon families of medium size, such as Pittosporaceae, the values range mostly between 50 and 150. The total range in Pittosporaceae is 23–165 (Carlquist, 1981). In Polygonaceae, the total range is from 0.49 to 34 173 (Table 1, column 18). In view of the mean Mesomorphy figures for Californian desert shrubs (20.9), riparian trees (253) and woodland trees (1950), the range of values in Polygonaceae is extreme. Ten of the 32 species studied here had values lower than the mean for southern Cal-
Woods of Polygonaceae

Wood Anatomy of Polygonaceae

Ifornian desert shrubs, the most xeric category in the southern Californian flora. Nine of the 32 had values higher than the means for southern Californian woodland shrubs, the most mesic category in the Californian flora. Thus, Polygonaceae show exceptional radiation into very wet as well as very dry areas as well as many habitats in between, and to suit these habitats with the formulation of their wood. Plumbaginae, sister family to Polygonaceae, has extremely xeromorphic wood. The average mesomorphy ratio figure for Plumbaginae as a whole is 4.1, and the range is from 0.5 (Armeria maritima L.) to 30 (Plumbago capensis Thunb.) The lowest figure in Polygonaceae (0.49 in Antigonon leptopus) is not really comparable to other values, since transverse section areas viewed for this analysis included conjunctive tissue as well as secondary xylem; however, most species with successive cambia do not have markedly xeromorphic wood (Carlquist, 1975).

In dicotyledons that have fibre-tracheids or libriform fibres rather than tracheids (sensu I. W. Bailey, IAWA Committee on Nomenclature (1964); Carlquist, 2001a, and others), degree of vessel grouping correlates with other xeromorphic wood features and reflects the xeric nature of habitats (Carlquist, 1984). In Polygonaceae, this correlation is evident. The species with exceptionally large groupings of vessels either: (1) grow in notably dry habitats (Araphaxis pungens, Dedeckera eurekensis, Muehlenbeckia asto-nii); (2) are lianas, with attendant vessel dimorphism (Antigonon leptopus, Bilderdykia multiflora), or (3) are ‘woody herbs’ in which stems flower as soil moisture decreases markedly (Polygonum). The low mean number of vessels per group for Coccloba, Ruprechtia, Symmeria, and Triplaris correlates with the status of these genera as elements of moist tropical forest (with freshwater readily available from a water table if not at the soil surface). The vessels per group figures for Eriogonum spp. may not seem very elevated, but they are certainly higher than those of the genera with more mesomorphic woods. In Eriogonum and Calli-gonum, the mean number of vessels per group and vessel density may not be spectacularly large (compare to Cassiope with about 2000 vessels mm\(^{-2}\); Wallace, 1986), but there are large latwood vessel groupings, where resistance to embolism through narrow conduit diameter (Hargrave et al., 1994) is most important. Thus, both large vessel groups and very narrow vessels occur conjunctively in latwood and probably serve to maintain water columns to foliage during dry seasons.

The presence of vestured pits, probably very common in Polygonaceae, might be another feature that aids survival under conditions of low moisture availability. If one looks at the systematic distribution (Jansen et al., 1998), there is no clear interpretation on comparative grounds. Certainly some groups with vestured pits have succeeded well in xeric habitats (Eucalyptus). Vestured pits may persist in some basically xeric groups that have shifted into mesic ecological niches; presence of vestured pits is probably not a nonadaptive feature, although it may have originated in a limited number of phylads for genetic and morphogenetic reasons. Experimental work on the functioning of vestured pits in comparison to that of nonvestured pits is very much needed.

Another indication of the wide range of adaptation of Polygonaceae can be seen in the high proportion of species with growth rings. Only Symmeria and two species of Coccloba are reported to lack any perceivable growth ring formation. The presence of vascular tracheids and extremely narrow vessels characterizes the latwood of many species (see Fig. 18, for example).

Although foliar characteristics in many dryland Polygonaceae are xeromorphic (drought-deciduous leaves, linear leaves with inrolled margins, small leaf area, thick cuticularization of leaf epidermis), wood is obviously related to the adaptation of so many species to exceptionally dry areas. The occurrence in the same family of both highly xeromorphic and mesomorphic woods (Triplaris is typical of the latter) is perhaps unexpected because woody representatives of several other families of Caryophyllales favour drier habitats and have been unable to enter mesic habitats like tropical rain forests: Caryophyllaceae (Carlquist, 1995) and Plumbaginaceae (Carlquist & Boggs, 1996) are exemplary in this regard. Polygonaceae thus is a family in which ecological shifts have been numerous and extreme, and wood has played a decisive role in these shifts.

REFERENCES


Carquist S. 1999a. Wood and stem anatomy of Stegnosperma (Caryophyllaceae); phylogenetic relationships; nature of lateral meristems and successive cambial activity. IAWA Journal 20: 149–163.


APPENDIX

SPECIMENS STUDIED

Bilderdykia multiflora Roberty & Vautier, SFCw-R1213-40

Calligonum arborescens Litv., Arabia, Aw-22928.
C. comosum L’Her., Turkستان, Podgorski 801 (RSA).
Coccoloba cereifera Schwant., Brazil, Eiten 6786 (RSA).
C. longifolia Fisch., Jamaica, USw-5918 (in RSAw).
C. polystachya Wedd., Brazil, Krukoff 6114, USw (in RSAw).
C. rotundifolia Meissn in DC., Haiti, USw-4334 (in RSAw).
C. rugosa Desf., Jamaica, USw-5943 (in RSAw).
Dedeckera eurekensis Reveal & J. T. Howell, Eureka Dunes, California, D. Wiens, s. n.
Eriogonum arborescens Greene, Santa Cruz Is., California, Raven 15832 (RSAw).
E. deserticola S. Wats., Imperial Co, California & Wolf 1868 (RSAw).
E. fasciculata Bent., Claremont, California, Carlquist, s. n.
E. giganteum S. Wats., Santa Catalina Is. & Carlquist 1820 (RSAw).
E. heermanii Dur. & Hilg., southern California, Davidson 4258 (RSAw).
E. kennedyi Porter ex Wats., Mt. San Antonio, California, Carlquist, s. n.
Gymnopusium antigonoides S. F. Blake, Belize, USw-13555.
Harfordia macroptera (Benth.) Greene & Parry, N. Baja California, Mexico, Davidson 5487 (RSAw).
Muehlenbeckia astonii Petrie, cult. University of Auckland, Carlquist 3092 (RSAw).
Neomillspaughia emarginata (Donn.-Sm.) S. F. Blake, Mexico, USw-13565 (in RSAw).
Polygonum lapathifolium Aiton, Peru, Carlquist 7161 (RSAw).
Rumex giganteus Aiton, Maui, Hawaii, Carlquist 2060 (RSAw).
R. lunaria L., Tenerife, Canary Islands, Carlquist 2429 (RSAw).
Ruprechtia sp., Misiones, Argentina, BAw-52595.
Symmeria paniculata Benth., Brazil, Krukoff 6749 (RSAw).
Triplaris americana L., Venezuela, ZTw, s. n. (in RSAw).
T. melanodendron Standl. & Steyerm., Panama, USw-103 (in RSAw).
T. pavonii Meisn., Brazil, Krukoff 6249 (USw in RSAw).
T. surinamensis Cham., Surinam, Stahel 50 (RSAw).
