Wood anatomy of Plumbaginaceae

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CARLQUIST, SHERWIN, AND COLBY J. BOGGS (Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105). Wood anatomy of Plumbaginaceae. Bull. Torrey Bot. Club 123:135—147. 1996.—Although few of the following wood characteristics may be synapomorphic, at least some species of Plumbaginaceae share the with Polygonaceae simple perforation plates, small pits on lateral vessel walls, libriform fibers as imperforate tracheary elements, paratracheal axial parenchyma, storying, silica bodies, and dark-staining amorphous deposits. These features suggest close relationship between the two families. A similar roster of features is cited as supporting placement of the two families close to Caryophyllales, a placement suggested recently on the basis of macromorphology and rbcL evidence. The latter evidence also links the two families with Nepenthaceae and Droseraceae. These latter families resemble each other in wood anatomy, although their wood features are significantly more primitive than those of Plumbaginaceae. Raylessness and paedomorphic rays in Plumbaginaceae suggest an herbaceous-or near-herbaceous ancestry for the family. Wood of Plumbaginaceae is markedly xeromorphic. Large fusiform silical bodies in axial xylem idioblasts and conjunctive tissue astrosclereids are newly reported for dicotyledons. Newly reported for Plumbaginaceae are vessel restriction patterns, pervasive axial parenchyma, abaxial axial parenchyma, raylessness, storying, and centripetal successive cambia.

Key words: Aegialitis, Caryophyllales, Centrospermae, Droseraceae, ecological wood anatomy, Limonium, Nepenthaceae, Plumbaginaceae, Polygonaceae, systematic wood anatomy.

Wood anatomy of Plumbaginaceae has previously been little studied, despite the potential interest of this topic. The summary of wood of Plumbaginaceae offered by Metcalfe and Chalk (1950) is based on only one species, Plumbago capensis. In terms of structural types in wood, Plumbaginaceae is diverse (e.g., rays present or absent, cambium simple or multiple and successive). The family is relatively large (19 genera, 775 species: Thorne 1992), but few species develop very much secondary xylem; lack of woodiness may account for neglect of the family. Although Plumbago reaches about 1.5 m, its stems are innovated from the shrub base and they do not exceed about 1 cm in diameter. The only shrubs in the family reported to attain 2 m or more are Limonium arborescens and L. dendroides (Svent.) Kunkel & Sund. (Bramwell and Bramwell 1974), the woodiest products of an adaptive radiation in that genus on the Canary Islands (Carlquist 1974). The presence of a few woody species in a family that is predominantly composed of herbaceous perennials leads one to ask whether woodiness is primitive or has evolved secondarily in the family. Wood anatomy is worthy of study with respect to this question, as well as with respect to the divergent growth forms in the family.

Wood anatomy is often of interest with respect to systematic affinities. Concepts on affinities of Plumbaginaceae have changed in recent years. Earlier, the family was placed in or close to orders such as Primulales or Ericales (Pax 1891, Nowicke and Skvarla 1977, Thorne 1992). Cronquist (1984) placed Plumbaginales, Polygonales, and Caryophyllales together in subclass Caryophyllidae, a treatment doubtless inspired by the study of Rodman et al. (1984), who chose Plumbaginaceae and Polygonaceae as outgroups for cladistic and phenetic analysis of Caryophyllales, but who also demonstrated the closeness of the two families to Caryophyllales in their studies. A close relationship among Plumbaginaceae, Polygonaceae, and Caryophyllales was supported by the rbcL analysis of Williams et al. (1994). However, in the cladograms of that study, Plumbaginaceae and Polygonaceae are on a branch that represents a sister group to Caryophyllales and also a sister group to a branch that includes Droseraceae and Nepenthaceae. Williams et al. (1994) also cite secondary compounds in support of this placement and wonder whether the salt glands of Plumbaginaceae may be close homologs of the glandular trichomes of Droseraceae and Nepenthaceae, an intriguing possibility in view of the divergent functions of glandular trichomes in the two families. Comparison of wood anatomy of Plumbaginaceae to that of Polygonaceae, Caryophyllales, Droseraceae, and Nepenthaceae is warranted in view of the results of these recent studies.

Plumbaginaceae often occupy saline soils, the latter varying from brackish marshes (Limonium

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Table 1. Quantitative wood features of Plumbaginaceae. Key to columns: 1 (VG), mean number of vessels per group; 2 (VD), mean radial lumen diameter of vessels, µm; 3 (VM), mean number of vessels per mm²; 4 (VL), mean length of vessel elements, µm; 5 (VV), mean thickness of vessel walls, µm; 6 (TL), mean length of imperforate tracheary elements, µm; 7 (TW), mean thickness of imperforate tracheary elements, µm; 8 (FV), F/V ratio (imperforate tracheary element length divided by vessel element length); 9 (MH), mean height of multiseriater rays, no. of cells; 10 (MW), mean width of multiseriater rays, no. of cells; 11 (ME), Mesomorphy ratio (vessel diameter times vessel element length divided by no. of vessels per mm²). Collections and measurement conventions given in Materials and Methods.

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spp.) to marine bluffs (Armeria) to marine flats (the mangrove Aegialitis). Other Plumbaginaceae occupy habitats that are relatively dry, but not notably salty (Plumbago). All of these habitats may be considered xeric, and thus examination of wood anatomy with respect to xeromorphy is appropriate.

Materials and Methods. The wood samples studied here were all available in dried form. Woods of Aegialitis annulata, Limonium peregrinum, and L. rubicicifolium were collected from wild-occurring plants (Table 1). Samples of Ceratostigma griffithii, L. arborescens and Plumago capensis were derived from cultivated specimens. The remaining wood samples were derived from herbarium specimens listed (Table 1). Wood samples were boiled in water and stored in 50% ethanol. The harder wood samples (Limonium arborescens, L. peregrinum, L. perezii, L. rubicicifolium, and Plumago capensis) were sectioned on a sliding microtome. Woods of the remaining Plumbaginaceae were sectioned in paraffin after softening in ethylene diamine, a procedure devised to deal with soft wood samples (Carlquist 1982). Sections were stained with a safranin-fast green combination. Some sections of Limonium peregrinum and L. rubicicifolium were dried between clean slides, mounted on aluminum stubs, and studied with an ISI WB-6 scanning electron microscope (SEM). This procedure proved valuable in examining the unusual silica bodies of L. rubicicifolium and the vessel sculpturing of L. peregrinum. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Collection data for the specimens is as follows. Acantholimon caryophyllaceum Boiss., rocks at bottom of agglomerate cliffs, river valley W of Yukari Narlca to Bargessaray, 2200 m, Turkey, J. C. Archibald 8007 (RSA); Aegialitis annulata R. Brown, shrubs to 2 m with widened bases, intertidal zone on rocky sublimate, Lamaroo Beach, Darwin, Northern Territory, Australia, S. Carlquist 15207 (RSA); Armeria maritima L., marine bluffs near Cambria, San Luis Obispo Co., California, Tucker 211 (SBG); Ceratostigma griffithii Clarke, cultivated in the Huntington Gardens, San Marino, California; Limonium arborescens (Brouss.) O. Kunze, cultivated in gardens surrounding greenhouse, University of California at Santa Barbara, S. Carlquist 8176 (SBG); L. californicum (Boiss.) Heller, erect perennial from heavy caudex, salt marsh with Scirpus spp., upper Newport Bay, Orange Co., California, R. F. Thorne 45583 (RSA); L. commune S. F. Gray, moist sand on bay side of Silver Strand, San Diego Co., California, E. A. Purer 5573 (RSA); L. cretaceum Tscherkassova, Akshagtau, Vil Dist., Aktubinsk Prov., Kazakstan, I. Tscherkassova 5842 (RSA); L. peregrinum (Bergius) R. A. Dyer, shrub to 1 m, branched from near base, vicinity of Geelbek, Cape Prov., South Africa,
S. Carlquist 4550 (RSA); L. perezi Hubbard, cultivated in Santa Barbara, California; L. rumicifolium (Svent.) Kunkel & Sund., perennial with short woody caudex, on cliffs well into canyon from highway, Barranco de Angostura near Era del Cardon, Tenerife, Canary Islands, Spain, S. Carlquist 2604 (RSA); Plumbago capensis Thunb., cultivated in Claremont, California.

Quantitative data are given in Table 1. Vessel diameter is measured as the widest radial lumen diameter. The mean number of vessels per group is based on a single vessel = 1, two vessels in contact = 2, etc. Figures for vessel density (no. of vessels per mm²) are derived from survey only of secondary xylem; conjunctive tissue (Aegialitis) is not included. Terminology follows the IAWA Committee on Nomenclature (1964).

**Results.** **ANATOMICAL DESCRIPTIONS.** Growth rings are present or absent in Plumbaginaceae. Strictly diffuse porous species include Plumbago capensis (Figs. 1, 2) and Limonium peregrinum (Fig. 6). No growth rings were observed either within or between successive secondary xylem strands of Aegialitis annulata (Fig. 21). In the remaining species, there is a slight to marked differentiation in vessel diameter or abundance with respect to season. At the center of the transection photograph of Limonium arborescens (Fig. 10), vessels are somewhat more abundant. In a section of a root of this species (Fig. 12), a parenchyma band (top) includes both latewood and some earlywood, with noticeable difference in vessel diameter within the parenchyma band. Noticeable change in vessel diameter is also present in L. californicum (Fig. 18). Strongly marked growth rings are present in L. cretaceum (Fig. 19). In this species, growth rings begin with relatively wide (for this species) vessels, but then vessels are followed by a band of thick walled libriform fibers, after which more wide vessels, then narrow latewood vessels are formed. Growth rings in Acantholimon caryophyllaceum are like those of L. cretaceum, but no libriform fibers are present. In L. peregrinum, the transition from latewood to earlywood (not shown in Fig. 6) is evident in formation of wider and fewer vessels in earlywood, followed by narrower and more numerous vessels in latewood.

Mean number of vessels per group (Table 1, column 1) shows a range from 1.3 to 6.2. The mean, 3.7, is well above the mean one would find in most families of dicotyledons Comparative figures for this feature are available only for a scattering of families (but see Carlquist and Hoekman 1985). A high degree of vessel grouping is shown by Limonium cretaceum (Fig. 19), but appreciable vessel grouping can also be seen in other transections (Figs. 1, 2, 6, 10, 12, 14, 18, 20, 21). Vessels occur in radial chains in earlier-formed secondary xylem of Plumbago capensis (Fig. 1), but this pattern disappears in later-formed secondary xylem (Fig. 2). Radial chains are also evident in Aegialitis annulata (Fig. 21). In the remaining Plumbaginaceae, vessel grouping is in the form of pore multiples.

Vessel lumen diameter (Table 1, column 2) shows a range from 9 to 32 µm, with a mean of 19 µm. The narrowness of vessels in Plumbaginaceae can be placed in proportion by mentioning that Metcalfe and Chalk (1950) found a mean vessel diameter of 94 µm for the world flora (probably mostly tree species), and Carlquist and Hoekman (1985) reported a mean vessel diameter of 35.2 µm for the woody southern California flora. Admittedly, both of those means are based on external vessel diameter, but that usually adds 6 µm or less to the diameter. Vessel diameter is a sensitive indicator of wood xeromorphy, and will be discussed in connection with the ecological conclusions later.

Vessel density (Table 1, column 3) is expressed in mean number of vessels per mm². Vessel density for the family as a whole (515) is relatively high compared with other families. In the woody southern Californian flora as a whole (Carlquist and Hoekman 1985), the mean figure is 100, and that figure is much higher than what one finds in trees of wet forests. Relatively low vessel density for the family occurs in Plumbago capensis (Figs. 1, 2) and Aegialitis annulata (Fig. 21). Both of these species have what has been termed vessel restriction patterns (Carlquist 1988). In Plumbago capensis, vessels tend to occupy the central portions of fascicular xylem in earlier-formed secondary xylem (Fig. 1), with no vessels in contact with rays. In later-formed secondary xylem (Fig. 2), this pattern vanishes. In Aegialitis annulata, vessels also tend to occur in radial chains in the centers of xylem areas (Fig. 21) and are not distributed randomly within these areas of libriform fibers. Limonium cretaceum also has a type of vessel restriction: vessels are absent midway into the growth ring, where they are replaced by thick-walled libriform fibers (Fig. 19).

Vessel element length (Table 1, column 4) in Plumbaginaceae is notably low, 100 µm. The
Figs. 1-5. Wood sections of *Plumbago capensis*. 1. Transection of earlier-formed secondary xylem; vessels in radial chains, restricted to central portions of fascicular areas. 2. Transection of later-formed secondary xylem; vessels not in radial chains. 3. Tangential section; rays are very tall. 4-5. Sections of vessel walls from tangential section. 4. Section showing outer part of wall shaved by sectioning so as to show grooves interconnecting pit apertures. 5. Section showing grooves (above) and pits as they appear when wall is not shaved (below). Figs. 1-3, scale above Fig. 1 (divisions = 10 μm); Figs. 4-5, scale above Fig. 4 (divisions = 10 μm).
Figs. 6–9. Wood sections of *Limonium peregrinum*. 6. Transection, no growth ring activity evident. 7. Tangential section; rays absent. 8–9. SEM photographs of vessels from tangential section. 8. Wider vessel; helical thickenings less prominent. 9. Narrower vessel; helical thickenings more prominent. Figs. 6–7, scale above Fig. 1; Figs. 8, 9, scales in upper left = 5 μm.
Figs. 10–13. Wood sections of *Limonium*. 10–12. *L. arborescens*. 10. Transection of stem; rays contain dark-staining compound. 11. Tangential section of stem; rays contain procumbent cells in central portions. 12. Transection of root; band of axial parenchyma, above. 13. *L. rumicifolium*, tangential section; rays are composed of upright cells. Figs. 10, 11, 13, scale above Fig. 1. Fig. 12, scale above Fig. 12 (divisions = 10 µm).
Figs. 14–17. Wood sections of *Limonium rumicifolium*. 14. Transection; arrows indicate idioblasts that bear a single silica body each. 15. Tangential section; dark fusiform objects are silica bodies; arrows indicate stories in pairs of vessel elements. 16–17. SEM photographs of silica bodies from tangential section. 16. Portion of silica body; surface shaved by sectioning (upper 2/3 of photograph) shows pores in silica. 17. Tip of a silica body (left), showing rough surface; portion of silica body exposed by sectioning, extreme right. Figs. 14, 15, scale above Fig. 12; Figs. 16, 17, scales at upper left = 5 μm.
Figs. 18–21. Wood sections of *Limonium* and *Aegialitis*. 18. *L. californicum* transection of wood, portion near pith below; libriform fibers are only present in earlier-formed secondary xylem. 19. *L. cretaceum*, transection showing sequence of cell types formed in fascicular xylem; the libriform fibers are formed amid the earlywood. 20. *L. commune*, transection of wedges of secondary xylem (with associated secondary phloem) produced by cambia in pith. 21. Transection of a strand of vascular tissue surrounded on all sides by conjunctive tissue (which contains dark-staining deposits); vessels form a radial chain in the secondary xylem. Figs. 18, 20, scale above Fig. 1; Figs. 19, 21, scale above Fig. 12.
mean length for the woody southern Californian flora is 233 µm (Carlquist and Hoekman 1985), and the figure for the world flora is given as 649 µm by Metcalfe and Chalk (1950). Vessel element length is closely related to wood xeromorphy or mesomorphy (Carlquist 1988) and will be discussed below with respect to ecological conclusions.

Mean vessel wall thickness (Table 1, column 5) for the family is relatively great (3.3 µm) considering the narrowness of vessels (in dicotyledons at large, wider vessels tend to have thicker walls). The vessels of Aegialitis annulata (Fig. 21) are typical for the family. Vessels of Limonium rumicifolium (Fig. 14) are relatively thicker than the average for the family. In L. cretaceum (Fig. 19), there is a marked fluctuation in vessel wall thickness: narrower vessels have thinner walls.

All vessels in Plumbaginaceae have simple perforation plates. Lateral wall pits of vessels in Plumbaginaceae are relatively small. Lateral wall pits circular in outline with a pit cavity diameter of about 3 µm were observed in Limonium arborescens, L. peregrinum, and L. rumicifolium. Circular pits about 4 µm in diameter occur in Acantholimon caryophyllaceum, Plumbago capensis, and L. arborescens; 2—4 septa per libriform fiber are present in Limonium arborescens (Figs. 1, 2) and Ceratostigma griffithii, whereas relatively thick-walled libriform fibers are present in Limonium arborescens (Fig. 12), L. perezii, L. rumicifolium (Fig. 14), and L. cretaceum (Fig. 19).

One can compute a ratio between imperforate tracheary element length and vessel element length (Table 1, column 8). This ratio, sometimes called the “F/V ratio,” is, within limits, an indicator of phyletic advancement: ratios between 1.0 and 1.5 indicate primitiveness; higher ratios (ratios above 4.0 are infrequent) indicate a greater degree of division of labor between the conductive (vessels) and the mechanical systems (fibers) in woods (Carlquist 1975). The F/V values for Plumbaginaceae are relatively high compared to those found in families commonly thought to have primitive wood (e.g., Iliciaceae).

Axial parenchyma in Plumbaginaceae consists of undivided cells except for Ceratostigma griffithii, in which axial parenchyma is subdivided into strands of two cells, and Plumbago capensis, in which strands consist of 1—6 (mostly 3—4) cells. As seen in wood transections, axial parenchyma consists of occasional paratracheal cells. These can be seen as relatively thin-walled (and therefore wide-lumened) cells adjacent to vessels in Fig. 21. In Limonium arborescens (Figs. 10, 12), L. peregrinum (Fig. 6), L. peregrinum, and L. rumicifolium (Fig. 14), axial parenchyma is scanty but almost always abaxial to the vessel in position. Axial parenchyma is both paratracheal scanty and abaxial in Ceratostigma griffithii and Plumbago capensis (Figs. 1, 2).

Toward the periphery of the root of Limonium arborescens, there are bands of marginal axial parenchyma (one such band, Fig. 12, top). Acantholimon caryophyllaceum has, in addition to scanty paratracheal parenchyma, diffuse-in-aggregates and terminal bands. Limonium cretaceum (Fig. 19) has axial parenchyma throughout fascicular areas except for the middle portions
of growth rings, which consists of thick-walled libriform fibers.

Axial parenchyma is so abundant in some species that it replaces all imperforate tracheary elements. *Armeria maritima* has axial parenchyma of this type, a type that has been termed pervasive (Carlquist 1995a). Pervasive axial parenchyma also characterizes *Limonium californicum* (Fig. 18; patches of libriform fibers formed earlier in secondary growth, bottom half of photograph). In *L. commune*, parenchyma is intermediate between pervasive and paratracheal, because libriform fibers are only partly replaced by axial parenchyma.

Rays are absent in *Armeria maritima* and *Limonium peregrinum* (Fig. 7). Only extensions of primary rays are present in wood of *Acantholimon caryophyllaceum*; the cambium in fascicular areas adds no rays, so a partial form of raylessness is present. Rays are relatively infrequent in most other Plumbaginaceae, suggesting that the cambium initiates relatively few rays, and that most rays are extensions of primary rays (e.g., Figs. 1–3). All rays are multiserate in Plumbaginaceae, no uniseriate rays were observed. If these rays consisted of procumbent cells, they could be referred to Kribs's Homogeneous Type II. However, there are procumbent cells in the centers of rays in some species (e.g., *Limonium arborescens*, Fig. 11), but in that species more than half of the ray cells are upright. This situation occurs in *L. perezii*, *L. rumicifolium*, and *Plumbago capensis* (Fig. 3) as well. Only upright ray cells were observed in *Aegialitis annulata*, *Ceratostigma griffithii*, *L. californicum*, *L. commune*, and *L. cretaceum*. Rays that are multiserate only and that consist mostly of upright cells correspond to Paedomorphic Type II (Carlquist 1988), and thus all rays of the Plumbaginaceae studied are referable to that type. Rays in the family are relatively short (Table 1, column 9) and narrow (Table 1, column 9). Rays of *Plumbago capensis* (Fig. 3) are unusually tall for the family. Conditions more typical for the family are illustrated by *L. arborescens* (Fig. 11) and *L. rumicifolium* (Fig. 13).

Silica bodies have not hitherto been reported in Plumbaginaceae. A very unusual type of silica body with an unusual mode of occurrence is present in *L. perezii* and *L. rumicifolium* (also, rarely, in *L. arborescens*). These silica bodies occur in idioblasts distributed diffusely in the fibrous portion of the wood (Fig. 14, arrows). A few occur as tip cells of rays. The silica bodies are fusiform in shape (Fig. 17) and much larger than silica bodies elsewhere in dicotyledons (ter Welle 1976). In most dicotyledons, silica bodies are spherical to ovoid and do not exceed 50 μm in diameter, whereas the silica bodies of *L. perezii* and *L. rumicifolium* are more than 100 μm long. Because of their size and brittleness, most of the silica bodies in sections are broken (note break in silica body at left in Fig. 17). The silica bodies when studied with SEM show characteristics seen in silica bodies elsewhere (see Carlquist 1988); porous structure (Fig. 16, pores revealed in shaven surface) and rough, almost warty surface (Fig. 17).

As seen in gross aspect, woods of *Limonium* have a red-brown color, perhaps suggesting deposition of a tanninlike substance. Massive deposits of compounds that stain prominently can be seen in ray cells of *L. arborescens* (Fig. 10) as well as in vessels (Fig. 12). These compounds often appear yellowish in unstained material. Dark-staining compounds occur prominently in conjunctive tissue of *Aegialitis annulata* (Fig. 21, blackish spots).

Storying can be seen in some, but by no means all, of the vessels and axial parenchyma cells of *Limonium rumicifolium* (Fig. 15, arrows). Storying of this sort was also seen in *L. arborescens* and *L. perezii*. In *Ceratostigma griffithii* and *Plumbago capensis*, storying can be seen in many libriform fibers if one examines tangential sections carefully. Very likely, storied cambia are not uncommon in Plumbaginaceae, but in most species, storying may not be evident in wood cells because of cell elongation. In Plumbaginaceae, imperforate tracheary elements elongate considerably (see F/V ratio, Table 1, column 8), and each element elongates differently, thereby obscuring the storied pattern. Vessel elements and axial parenchyma cells or strands elongate little as they mature from fusiform cambial initial derivatives. Storying has not previously been reported in Plumbaginaceae (Carlquist 1988).

Wood produced from successive cambia was reported by Record (1936) in *Acantholimon, Aegialitis*, and *Limoniastrum*. Our material of *Acantholimon* has prominent bands of terminal parenchyma, but these bands do not contain phloem, and therefore we regard Record's (1936) report of wood of this type for *Acantholimon* as doubtful. *Aegialitis annulata* does have secondary xylem and secondary phloem produced by successive cambia. The vascular tissue takes the form of strands, circular to oval in transsectional outline, in a background of con-
junctive tissue (Fig. 21). Some strands of vascular tissue that are tangentially wider in this species may contain one or two rays that have been derived from cambial action, and these rays consist of upright cells. Conjunctive tissue between the strands of vascular tissue does not qualify as ray tissue.

The conjunctive tissue of Aegialitis annulata (Fig. 21) is composed of thin-walled parenchyma cells with dark-staining contents. In addition, there are numerous idioblastic astrosclereids in the conjunctive tissue. These sclereids take the form of cells with cuboidal shapes from which slender arms radiate.

Successive cambia are commonly found in the cortex of stems or roots of dicotyledons, but in a few instances, successive cambia form in the pith (Carlquist 1988). These latter cambia have been termed centripetal cambia, and have been reported for only a few families of dicotyledons (see Carlquist 1988: 262). There is secondary xylem and secondary growth produced by the action of centripetal cambia in the pith of Limonium californicum and L. commune (Fig. 20). Each of these cambia produce considerable secondary growth, which can be accommodated as growth proceeds because of the large diameter of the pith and the ability of the thin-walled pith cells to collapse.

Conclusions and Discussion. HABITAL CONCLUSIONS. Raylessness has been associated with herbaceous groups in which a transition to (or sometimes possibly from) a woody habit is occurring (Barghoorn 1941, Carlquist 1970, Gibson 1978). Raylessness in Armeria maritima and Limonium peregrinum may therefore indicate secondary woodiness in those species. Acantholimon caryophyllaceum does not initiate rays from fascicular cambium areas, and thus is, in a sense, rayless. The occurrence of paedomorphic rays in the remainder of Plumbaginaceae may also be an indication of secondary woodiness. The woodiest species of Plumbaginaceae are Limonium arborescens and L. dendroides on the Canary Islands. These likely are woody derivatives of more nearly herbaceous ancestors. An alternative hypothesis would have to say that these restricted insular species are relics from which the remainder of this worldwide genus have been derived—such a hypothesis that seems quite unlikely. The habitual diversification of Limonium on the Canary Islands seems much like what has happened on other islands where diverse woody growth forms have been derived autochthonously from herbaceous or minimally woody ancestors (Carlquist 1974). The woodiness of the two shrubby Canarian Limonium species relates to minimal frost in the habitats where those species occur.

ECOLOGICAL CONCLUSIONS. Wood xeromorphy can be measured by means of a formula termed the Mesomorphy Ratio (vessel diameter times vessel element length divided by number of vessels per mm²: see Carlquist and Hoekman 1985). The Mesomorphy Ratio value for desert shrubs of southern California is 20.9; the value for alpine southern Californian shrubs is 27.1 (Carlquist and Hoekman 1985). These values are not only low compared with those of woods from more mesic regions, but they are higher than the Mesomorphy Ratio values of Plumbaginaceae (Table 1, column 11). The mean Mesomorphy Ratio value for the family is 4.1. This accords with the concept that Plumbaginaceae characteristically grow in dry and/or saline habitats. Not surprisingly, Plumbago capensis, which has broad thin leaves and grows in moderately moist scrub, has the highest value for the family (30). Limonium arborescens also has a value relatively high for the family (23); it occurs in moderately moist scrub on the north side of Tenerife (Bramwell and Bramwell 1974). The next highest value for the family is represented by the mangrove Aegialitis annulata. One can make a case that a mangrove is not in a dry situation, since the water supply is unlimited, although a mangrove must counter the osmotic pressure of saltwater. However, Aegialitis annulata is an intertidal mangrove, and its roots are occasionally exposed. The lowest Mesomorphy Ratio values for the family occur in species characteristic of localities that are both dry and salty: Acantholimon caryophyllaceum (0.6) and Armeria maritima (0.5). One can view wood xeromorphy in terms of any of the three quantitative vessel element features that make up the Mesomorphy Ratio, but these three measures tend to run parallel to each other.

Another quantitative vessel feature that tends to indicate wood xeromorphy is the mean number of vessels per group. Vessels tend to stay solitary in woods that have tracheids as the imperforate tracheary element type, regardless of ecology, but if a wood has fiber-tracheids or libriform fibers, greater degrees of vessel grouping indicate greater xeromorphy. This is shown by the fact that the two species with the lowest Mesomorphy Ratio values for the family, Acan-
tholimon caryophyllaceum and Armeria maritima, have the highest figures for number of vessels per group.

In addition to quantitative vessel features, there are qualitative wood features that indicate xeromorphy. Helical thickenings in vessels are indicative of greater degrees of physiological drought (Carlquist 1975). In the present study, Acantholimon caryophyllaceum and Limonium peregrinum have helical thickenings. Helical thickenings may be lacking in other species for various reasons; for example, the pseudoscalariform pitting may preclude the formation of helical thickenings.

Presence of parenchyma instead of imperfectate tracheary elements characterizes the two woods with the lowest Mesomorphy values, Acantholimon caryophyllaceum and Armeria maritima. A relatively high degree of parenchymatization characterizes other Plumbaginaceae: Limonium californicum and L. commune. One can hypothesize that parenchyma of conjunctive tissue in Aegillis is physiologically equivalent to parenchyma within the wood of other Plumbaginaceae. Parenchyma likely serves for water storage to some degree. In this connection, it expands and contracts with water availability. If parenchyma contracts and expands, adjacent vessels would be affected. The presence of pseudoscalariform pitting in vessels of Armeria maritima, Limonium californicum, L. commune, and L. cretaceum is notable may permit increase vessel flexibility, and certainly those species do have abundant axial parenchyma.

SYSTEMATIC CONCLUSIONS. Wood anatomy only infrequently is useful at the species level. However, the wood anatomy of Limonium peretii is virtually identical to that of L. rumicifolium. This supports the idea of Bramwell and Bramwell (1974) that L. rumicifolium represents an inland population very similar to L. peretii and the that two populations may be conspecific.

Plumbaginaceae are divided into two subfamilial groups, currently called Plumbaginoideae and Staticoideae (Pax 1891; Thorne 1992). Of the genera in the present study, Ceratostigma and Plumbago belong to Plumbaginoideae, whereas the remaining genera studied are placed in Staticoideae. Ceratostigma and Plumbago are alike in having nucleate sepalate fibers that tend to be clearly storied, and also agree in having strands of more than one cell in axial parenchyma. Alternative conditions occur in the Staticoideae. Although conclusions are premature on the basis of so few species, these distinctions may prove consistent for the two subfamilies.

With respect to affinity of Plumbaginaceae to other families, wood anatomy is of interest because new ideas have recently been been offered on relationships of the family. Rodman et al. (1984) hypothesized that Plumbaginaceae and Polygonaceae are close to each other and to Carpophyllales; Williams et al. (1994) agreed with this conclusion, but place Droseraceae and Nepenthaceae equally close to Plumbaginaceae. Nepenthes has xylem more primitive than that of Plumbaginaceae in several significant respects: scalariform as well as simple perforation plates; tracheids as imperfectate tracheary elements; diffuse-in-aggregates axial parenchyma; and presence of both multisierate and uniseriate rays (Carlquist 1981). The wood of Drosophyllum (Droseraceae) is very similar to that of Nepenthes, but has simple perforation plates exclusively. Wood anatomy thus validates the conclusion of Williams et al. (1994) that Droseraceae and Nepenthaceae are close to each other, but wood data, interpreted according to usual criteria, would place that pair of families at a lower level of specialization than Plumbaginaceae, Polygonaceae, or Carpophyllales.

Plumbaginaceae have simple perforation plates exclusively, minute pits on lateral walls of vessels, libriform fibers as the imperfectate tracheary element type (vestigial borders or pits in a few species), paratracheal axial parenchyma, multisierate rays or no rays. All of these features can be seen in Polygonaceae also, as can two features reported newly here for Plumbaginaceae: storied and presence of silica bodies (Carlquist 1988). To be sure, the mode of occurrence of silica bodies in Plumbaginaceae is different from that in Polygonaceae. Polygonaceae differ from Plumbaginaceae in ray type: Polygonaceae have both multisierate and uniseriate rays, and most species studied do not have paedomorphic rays like those of Plumbaginaceae. These differences between the two families could easily be due to different ancestry: Polygonaceae (at least the typically woody species) probably derive from a woody ancestry, whereas Plumbaginaceae likely have had an herbaceous or relatively less woody ancestry.

Rodman et al. (1984) chose Plumbaginaceae and Polygonaceae as outgroups for their cladistic and phenetic study of Carpophyllales, and the results of that study tend to support that choice. Williams et al. (1994) confirm such a relationship on the basis of rbcL sequence data. All of
the features listed in the preceding paragraph can be found in Caryophyllales. However, tracheids rather than fiber-tracheids or libriform fibers occur in Stegnospermataceae (Bedell 1980) and some Caryophyllaceae (Carlquist 1995b). If tracheids are a presumably more primitive wood expression, can Stegnospermataceae and Caryophyllaceae be derived from a group that only have libriform fibers or fiber-tracheids like libriform fibers? Currently accepted concepts of wood evolution would say this is unlikely. Another possibility is that now-vanished tracheid-bearing ancestors of Plumbaginaceae and Polygonaceae gave rise to the line that led to Caryophyllales. Except for this feature, wood of Caryophyllales is compatible with the possibility that order has been derived from an ancestor with wood like that of Plumbaginaceae or Polygonaceae. However, we need more information on wood of Caryophyllales, and we need more information on wood of Polygonaceae. When woods of these groups, currently under study, are better understood, more precise phylogenetic analyses will be possible.

Literature Cited


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