Wood anatomy of *Drosophyllum* (Droseraceae): Ecological and phylogenetic considerations

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CARLQUIST, SHERWIN AND ERIKA J. WILSON (Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105). Wood anatomy of *Drosophyllum*: ecological and phylogenetic considerations. Bull. Torrey Bot. Club 122:185–189.—*Drosophyllum lusitanicum*, the sole woody species of Droseraceae, has wood anatomical features very much like those of Dioncophyllaceae and Nepenthaceae. Features in common include vessel elements with simple perforation plates, fibriform vessel elements, tracheids with large fully bordered pits, diffuse (plus variously grouped) axial parenchyma, and paedomorphic rays 1–2 cells wide. Wood anatomy thus validates the close relationships claimed among *Drosophyllum*, Dioncophyllaceae, and Nepenthaceae on the basis of recent DNA studies. Wood anatomy of *Drosophyllum* is xeromorphic, in accord with the dry habitats of the species.

Key words: *Drosophyllum*, Droseraceae, Nepenthaceae, wood anatomy.

Drosophyllum lusitanicum (L.) Link, sole species of its genus, is a short lived subshrub or woody herb of Portugal, Spain, and Morocco (Diels 1906; Juniper et al. 1989). As reported by Penzig (1877), Diels (1906) and others, *Drosophyllum* differs from other Droseraceae in having secondary growth. Plants in open areas may be facultative biennials, but plants that grow (often in a prostrate fashion) through other shrubs may attain woody cylinders up to 1 cm in diameter (Juniper et al. 1989). The other genera of Droseraceae have centric bundles with few vessels and no perceptible cambial activity (Solereder 1908; Metcalfe and Chalk 1950). Solereder (1908) reported that vessels of *Drosophyllum* have simple perforation plates, but no other wood anatomical details have been reported for the genus. Presentation of a complete description of wood features is desirable primarily because of the ecology of the genus, unusual for Droseraceae, and new information about probable phyletic position of *Drosophyllum*.

The areas where *Drosophyllum* is or has been native are often described as dry (Lloyd, 1942; Juniper et al. 1989), although they occur on slopes near the western Mediterranean Sea and thus tend to have a winter rainy season. Some *Drosophyllum* habitats are rocky (quartzite is mentioned) or sandy (Diels 1906). The claim by Slack

(1979) that the *Drosophyllum* localities are "often alkaline," however, is questionable. Pines occur in some *Drosophyllum* localities (Diels 1906), and pines tend to be indicators of acid sands. Juniper et al. (1989) cite "acidic sands" as a *Drosophyllum* habitat, and Droseraceae other than *Drosophyllum* certainly show preferences for acid soils. The wood anatomy of *Drosophyllum* is worthy of examination with relation to dryness of habitat. Droseraceae are often considered plants of bogs, but the majority of species (Western Australia, South Africa) occur in summer-dry acid sands; in these species, survival of the dry season is achieved by tubers, scales covering the bud, annual habit, or other means (Diels 1906). These mechanisms are absent in *Drosophyllum*, and thus the nature of wood anatomy might be a prime tool in management of the water economy of the plant. The deep taproot reported for *Drosophyllum* (Juniper et al., 1989) may also be important to survival of the dry season, and the minimal surface provided by the linear leaf shape is doubtless also a factor.

The familial position of *D. lusitanicum* has been little doubted; it has universally been assigned to Droseraceae (Linnaeus described it as a species of *Drosera*). A recent study that integrates data from *rbc*L sequences and from macromorphology into a cladistic form (Williams et al. 1994) places *Drosophyllum* close to *Triphyophyllum* (Dioncophyllaceae) and *Nepenthes* (Nepenthaceae) in a clade terminating in other genera of Droseraceae (*Dionaea, Aldrovanda,* and *Drosera*). Lack of DNA for *Triphyophyllum* in the study of Williams et al. (1994) means that resolution of their cladogram among Drosera-

ceae, Dioncophyllaceae, and Nepenthaceae should be regarded as tentative. Their cladogram raises the possibility that Droseraceae might not be monophyletic, but the cladistic arrangement might have been somewhat different had DNA from Dioncophyllaceae been available. Wood anatomy thus may be of significance in assessing the phyletic position of *Drosophyllum*. Recent data on wood anatomy are available for Dioncophyllaceae (Gottwald and Parameswaran 1968) and Nepenthaceae (Carlquist 1981). Williams et al. (1994) consider Plumbaginaceae and Polygonaceae to be outgroups of the clade described above, with Caryophyllales somewhat more distant. Studies on wood anatomy of Plumbaginaceae and Polygonaceae are in progress (Carlquist, unpublished). A paper on wood anatomy of Caryophyllaceae (Carlquist 1995) adds significant data because most recent cladograms place Caryophyllaceae as basal or near-basal in Caryophyllales (see Carlquist 1995). These studies will widen the comparisons offered here. Williams et al. (1994) consider the glandular trichomes of Plumbaginaceae to be very similar to those of the *Drosophyllum*-Dioncophyllaceae-Nepenthaceae-Droseraceae clade, an interesting anatomical link because the functions of glands in Plumbaginaceae are markedly different from those of *Drosophyllum* clade.

Materials and Methods. Material of relatively mature cultivated plants of *D. lusitanicum* was provided by Joseph Mazrimas. Dried voucher specimens from these were prepared as Carlquist 8173 (SBBG). Stem and root portions were preserved in aqueous 50% ethanol. Because of small diameter of the woody cylinders and the hardness of the wood, sectioning them on a sliding microtome was not feasible. Instead, an alternative technique (Carlquist 1982) involving softening of wood with ethylene diamine, embedding in paraffin, and sectioning on a rotary microtome, was employed. Sections were stained with safranin and fast green; safranin was absorbed minimally, so the best staining was achieved by prolonged exposure to fast green. Macerations were prepared by means of Jeffrey's Fluid and stained with safranin.

Cell diameters and lengths are based on averages of 25 measurements; other quantitative data are based on conditions thought to be typical. Vessel diameters are measured as lumen diameter at widest point. Terms are in accordance with the IAWA Committee on Nomenclature (1964).

Results. The description below is based on both stems and roots, qualitative features of which were identical in the material examined. Quantitative data on stems are incorporated in the description, with data based on roots in a following paragraph. The illustrations (Figs. 1–4) are from root sections.

STEM ANATOMY. Growth rings absent or boundaries faint (Fig. 1). Vessels mostly solitary (Fig. 1), mean number of vessels per group, 1.16. Mean vessel lumen diameter, 23 μm. Mean number of vessels per mm², 248. Mean vessel element length, 301 μm. Mean vessel wall thickness, 2.3 μm. Perforation plates simple. About a third of the vessels fibriform, with fusiform cell shape and subterminal (sometimes lateral) perforation plates. Lateral wall pitting of vessels composed of alternate circular bordered pits, pit cavity diameter about 6 μm, pit aperture circular (Fig. 3). Imperforate tracheary elements all tracheids. Mean tracheid diameter at widest point, 18 μm. Mean tracheid length, 380 μm. Pits on tracheids fully bordered, about 5 μm in diameter (pit cavity diameter), both pit cavities and pit apertures circular in outline (Fig. 4). Axial parenchyma diffuse, scanty vasicentric, and (less frequently) diffuse-in-aggregates. Axial parenchyma present as undivided cells, less commonly as strands of two cells. Axial parenchyma walls about 1.2 μm thick. Rays mostly uniseriate, less commonly biseriate (wider multiseriate rays in stems are extensions of primary rays). Rays, as seen in tangential section (Fig. 2) most often composed of 1–3 cells, usually overlapping rather than superposed. Ray cells mostly upright, less commonly square. Ray cell walls about 1.2 μm thick. Pits interconnecting ray cells and ray-to-tracheid pits vestigially bordered. Helical thickenings observed on walls of a few ray cells in roots.

ROOT ANATOMY. Quantitative features of root secondary xylem are as follows. Mean number of vessels per group 1.19. Mean vessel diameter, 30 μm. Mean number of vessels per mm², 125. Mean vessel element length, 292 μm. Mean vessel wall thickness, 2.3 μm. Mean tracheid diameter, 19 μm. Mean tracheid length, 356 μm. Mean tracheid wall thickness, 2.4 μm. Other quantitative features as in stems.

The differences between root and stem wood are probably not statistically different except for vessel diameter. Vessels tend to be wider in roots than in stems of a given species (Patel 1965). The fusiform (rather than oval) shape of ray cells as
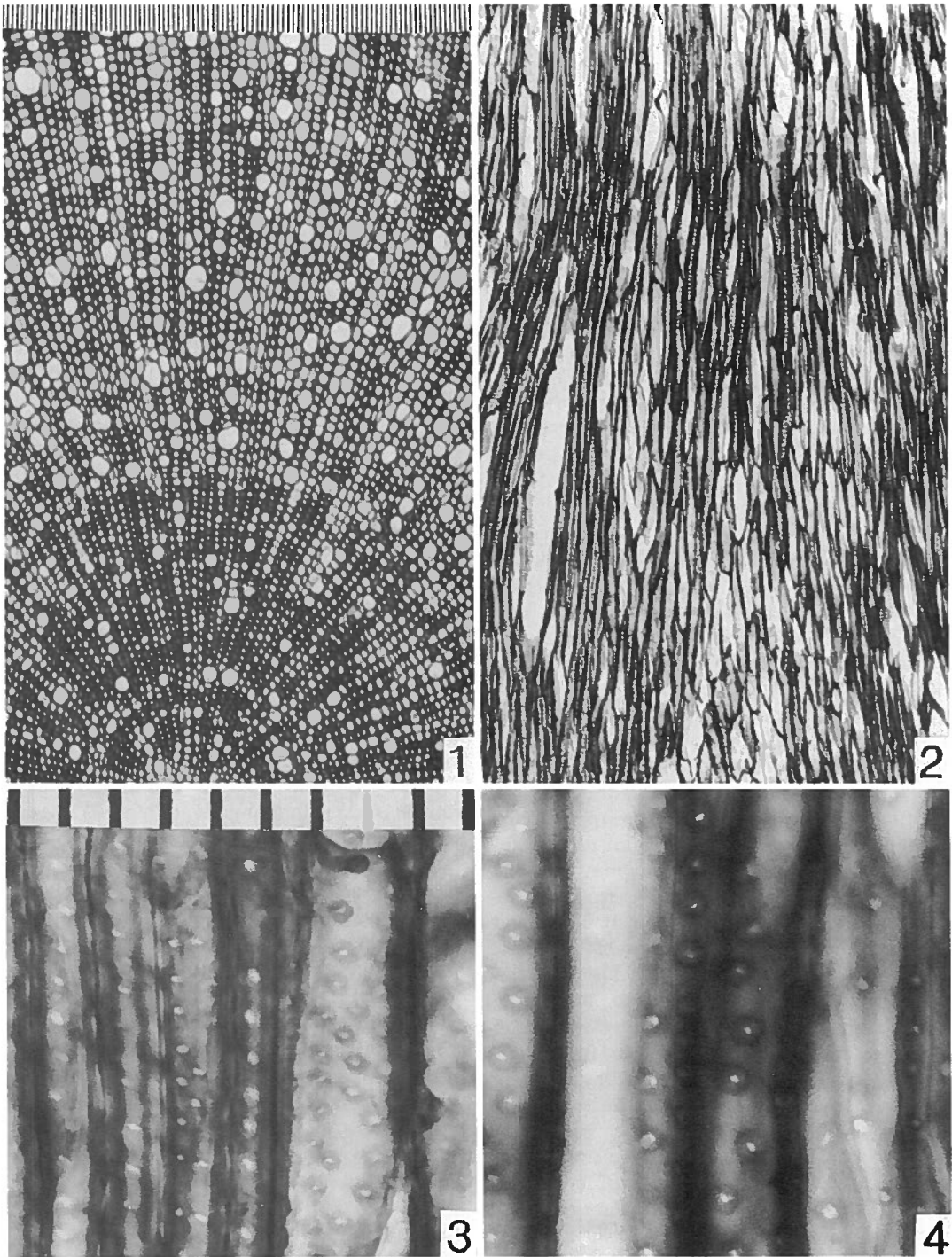
Figs. 1–4. Wood sections of root of *Drosophyllum lusitanicum, Carlquist 8173*. Fig. 1. Transection; vessels are narrow, mostly solitary. Fig. 2. Tangential section; rays are not readily visible because ray cells are fusiform in outline and overlap. Fig. 3. Radial section, showing fully bordered pits on narrow vessel (wide cell at right) and, to left of vessel, a tracheid. Fig. 4. Radial section, showing large circular bordered pits on vessels (left two-thirds of photograph) and vestigially bordered pits on axial parenchyma cells (right third of photograph). Figs. 1, 2, scale above Fig. 1 (divisions = 10 μm); Figs. 3, 4, scale above Fig. 3 (divisions = 10 μm).

seen in tangential section and their overlapping arrangement make ray cells difficult to distinguish from tracheids or fibriform vessel elements (Fig. 2).

Ecological Conclusions. Several features of the wood of *Drosophyllum* are xeromorphic. Although tracheids are often thought to be combined with primitive vessels (e.g., vessels with scalariform perforation plates), in a number of groups tracheids occur in combination with vessel elements with simple perforations plates. Most of these groups are cited in lists of true tracheids (as opposed to vasicentric tracheids) in a paper dealing with tracheid presence in woods of dry areas (Carlquist 1985). Cistaceae, Proteaceae, and Rosaceae are examples of families represented in dry areas in which tracheids may be found combined with vessel elements with simple perforation plates. The presence of tracheids in these groups is adaptive to dry conditions because tracheids resist embolism to a greater extent than vessel elements (review in Carlquist 1988: 322–325). The simple perforation plates in these woods can accommodate peak flows when brief periods of wet weather occur in typically dry areas.

Vessel grouping occurs proportionately to xeromorphy in woods with fiber-tracheids or libriform fibers, but it occurs minimally in woods in which tracheids are present (Carlquist 1984), and thus a low degree of vessel grouping occurs in wood of *Drosophyllum*. The marked overlapping of fibriform vessel elements may lead one to count the overlapping ends, as seen in a transection, as a pair of vessels rather than one, and an attempt was made to identify such instances. The vessel elements of *Drosophyllum* are relatively narrow compared with those of flowering plants at large. Narrow vessels have been cited as indicators of wood xeromorphy (e.g., Carlquist 1966). This correlates with a physiological finding, that narrow vessels embolize less readily than wide vessels in hot summer conditions (Hargrave et al. 1994). Short vessel elements also tend to characterize xeromorphic woods (Carlquist 1966, 1988). *Drosophyllum* does not exemplify this trend, perhaps because of the abundance of fibriform vessel elements in this species.

Systematic Correlations. The various cladograms provided by Williams et al. (1994) differ, depending on the bases of their construction. All,

however, show closeness of *Drosophyllum*, Dioncophyllaceae, and Nepenthaceae. Do these three groups share similar wood features?

Dioncophyllaceae have successive cambia (Gottwald and Parameswaran 1968), whereas *Drosophyllum* and *Nepenthes* do not, but this contrast does not extend to other features. All three have vessel elements with simple perforation plates. All three groups have fibriform vessel elements. Fibriform vessel elements have not been hitherto reported in Dioncophyllaceae, but are visible in a maceration prepared by the senior author from the specimen *Triphyophyllum peltatum* Airy Shaw, *Baldwin 14178* (US). All three groups have tracheids (sensu IAWA Committee on Nomenclature 1964) rather than fiber-tracheids and libriform fibers. All three have some diffuse axial parenchyma, but also some groupings of axial parenchyma: diffuse-in-aggregates in *Nepenthes,* scanty vasicentric in Dioncophyllaceae, both scanty vasicentric and diffuse-in-aggregates in *Drosophyllum*. The rays in all three groups are mostly uniseriate, less commonly biseriate, and rarely more than two cells wide. In all three groups, the ray cells are upright to square.

In contrast with this list of similarities, divergences among the three groups are relatively minor. In *Drosophyllum*, axial parenchyma is commonly not subdivided, in *Nepenthes*, strands of two are common, and in Dioncophyllaceae, strands of three to four cells are reported. Mean vessel diameter is much greater in Dioncophyllaceae and Nepenthaceae than in *Drosophyllum*. As mentioned above, vessel diameter is related to ecology, but it is also related to habit, and wide diameter correlates with scandent habit in Dioncophyllaceae and Nepenthaceae. Thus, vessel diameter is not a feature indicative of phyletic relationships.

Not only are the three groups virtually identical in features indicative of phyletic relationship, the three groups are at the same level of phyletic specialization—which one would not expect even if they were closely related (e.g., a wide range of specializations may be found within woods of Violaceae). The occurrence of paedomorphic rays in all three groups (rays would be classified as Paedomorphic Type I in the scheme of Carlquist 1988) suggests the possibility that a common ancestor of all might have been relatively nonwoody. This feature is worthy of consideration as studies proceed on the clade to which *Drosophyllum* belongs, as well as on clades close to that one.

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