WOOD ANATOMY OF MARTYNIACEAE AND PEDALIACEAE

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ABSTRACT

Quantitative and qualitative features are reported for one species of *Martynia* (Martyniaceae) and for seven species of six genera of Pedaliaceae. The inclusion of woody annuals as well as of shrubs provides a broader picture of Pedaliaceae than hitherto available. The wood features of Martyniaceae and Pedaliaceae (listed in the Systematic Conclusions) are compatible with placement of these families in Scrophulariales (Bignoniales). If individual features of the two families are compared with those of other families of the order, however, no one family can be cited as more closely related to Martyniaceae and Pedaliaceae than any other. Martyniaceae is not necessarily the family closest to Pedaliaceae, but its wood is like that of herbaceous Pedaliaceae and may reflect not merely scrophularialean affinity but the similarity of its herbaceousness to that of Pedaliaceae as well. Wide vessels in Martyniaceae and Pedaliaceae very likely relate to high transpiration rates in the summer-wet areas where many of them grow. Low vessel density and apotracheal parenchyma bands that may store water and be related to semisucculence in *Sesamothamnus*. Thin-walled imperforate tracheary elements and predominance of upright ray cells in Martyniaceae and Pedaliaceae bear a relationship with the herbaceous nature of taxa.

Key words: Bignoniales, ecological wood anatomy, Martyniaceae, Pedaliaceae, Scrophulariales, wood anatomy.

INTRODUCTION

Martyniaceae and Pedaliaceae are small families usually placed near each other in Scrophulariales (Bignoniales of some authors). Pedaliaceae consist of 12 genera and 70 species (Ihlenfeldt 1967). Martyniaceae have three genera containing 12 species (Heywood 1978). The inherent interest of wood anatomy of these two families lies in examining the nature of wood in predominantly herbaceous families, studying the relationship between the two families and their ordinal placement, and comparing the nature of wood anatomy to the ecology of the species studied.

Although wood anatomy of Martyniaceae and Pedaliaceae has been little studied because of their herbaceous nature, the nature of wood in predominantly herbaceous families is insufficiently known and is worthy of investigation. *Martynia annua* L., sole species of *Martynia*, is a large annual: the stem studied here was 3.5 cm in diameter; the other species of the family are less woody to varying degrees. In Pedaliaceae, *Uncarina* consists of shrubs and small trees, and Outer and Veenendaal (1983) have studied wood of one species. The genera *Sesamothamnus* (seven species) and *Stigmatosiphon* (monotypic) are shrubs. The remaining genera are annuals or facultative perennials, but wood of some of these has been studied because there is no clear threshold below which studies in wood anatomy are less valuable. Consequently, some species with relatively little wood have been included. *Ceratotheca triloba* E. Mey. is a perennial or facultative

annual in which woody stems up to 1 cm in diameter can be formed. *Holubia saccata* Oliver, *Pedalium murex* L., *Rogeria longiflora* J. Gay, and *Sesamum indicum* L. are annuals. The bases of these plants, if not so woody as that of *Martynia annua,* offered wood sufficient for sectioning—the criterion by which species were selected for this study. To be sure, specimens of other annuals in the family could have been sought, but I believe that such a detailed survey would not have revealed additional diversity sufficient to justify the effort. Some kind of selection is always required in comparative studies. The diversity uncovered when the most distinctive taxa are studied is the indicator for further study usually used. The data on wood anatomy of the two families in Metcalfe and Chalk (1950), Pawar and Kulkarni (1971), and Outer and Veenendaal (1983), although definitely of value, need to be supplemented.

Outer and Veenendaal (1983) claimed a relationship between Pedaliaceae and Bignoniaceae on the basis of wood structure of *Uncarina leandrii* H. Humb. Although a large number of Bignoniaceae is used for comparison in that study, smaller numbers of Acanthaceae and only one genus of Scrophulariaceae (*Paulownia,* sometimes claimed to belong to Bignoniaceae) are taken into account because Outer and Veenendaal include only woodier taxa. The anatomical diversity uncovered in a study is often proportional to number of taxa studied, especially if the taxa are distinctive. Thus the greater range of features that Outer and Veenendaal (1983) found for comparison in Bignoniaceae may have tended to influence them to the conclusion that wood of *Uncarina* can be more closely matched by that of Bignoniaceae. A larger number of Pedaliaceae offers a safer basis for conclusions about systematic relationships, and consequently the present study was undertaken. Another question of phylogenetic interest is the degree of relationship between Martyniaceae and Pedaliaceae. Are Martyniaceae, a neotropical family, a sister group of Pedialiaceae, and Old World family, or are both independent derivatives of some ancestral stock? The present paper is part of a survey of wood anatomy of families of tubiflorous dicotyledons undertaken in an attempt to define orders and degrees of relationship among their component families.

The ecological nature of the habitat must be taken into account in assessing the systematic value of wood features. Outer and Veenendaal (1983) cite wider vessel diameter as a feature by which *Uncarina* resembles Bignoniaceae. Relatively wide vessels do characterize the Martyniaceae and some Pedaliaceae of the present study. However, most of the species studied here are from summer-wet areas, such as the Transvaal. The specimen of *Ceratotheca triloba* was collected in the Magaliesberg near Pretoria, Transvaal. The specimens of *Holubia saccata* and *Sesamothamnus lugardii* N. E. Brown are from the Soutpansberg, also in Transvaal. The specimen of *Rogeria longiflora* came from the Gordonia District of Cape Province, South Africa, also a summer-wet area; *Pedalium murex* grows in coastal sand areas of Ceylon, where tropical temperatures and a bimodal rainfall season prevail. *Martynia annua* also comes from a summer-wet portion of subtropical Mexico. Species from summer-wet or wet tropical areas are likely to transpire large volumes of water and have wide vessels to accommodate this. The specimen of *Sesamothamnus rivae* Engl. studied was collected on a rocky outcrop in the plateau lands of Kenya, and the specimen of *Sesamum indicum* is from a weedy population in the southern U.S.

MATERIALS AND METHODS

Wood of all species was available in dried condition. The sample of *Martynia annua* was provided by the New York Botanical Garden. I collected the wood specimen of *Ceratotheca triloba* in South Africa in 1973. The remaining wood samples were obtained from herbarium specimens. Specimens and herbaria are cited below in the headings of descriptions. Wood portions were boiled in water and stored in 50% ethyl alcohol. All samples were sectioned on a sliding microtome. Sections were stained in a safranin-fast green combination. Macerations were prepared with Jeffrey's Fluid and stained in safranin. Means were based on 25 measurements except for vessel wall thickness, libriform fiber wall thickness, and libriform fiber diameter, in which a typical condition was selected. Diameter of vessels is measured at the widest point (this is often a diameter taken in a radial direction in the stem) and includes the wall thickness. Vessels per mm² is based upon counting of each vessel rather than counting of vessel groups as has been done by some authors. Terminology agrees with that of the IAWA Committee on Nomenclature (1964). No borders were observed on pits of imperforate tracheary elements in any of the taxa studied. These elements are therefore termed libriform fibers. The present study was aided by a grant from the National Science Foundation, BSR 8419-169.

ANATOMICAL DESCRIPTIONS

Martyniaceae

MARTYNIA ANNUA (*Mori & Taylor 28807*, NY) (Fig. 1–4). — Growth rings absent (the entirety of wood of this sample, like that of the other annuals studied, could be said to constitute a single growth ring). Vessels in clusters (Fig. 1). Mean number of vessels per group, 1.73. Mean number of vessels per mm², 43. Mean vessel diameter at widest point, 74 μm (many vessels are radially widened, so that mean diameter does not give a reliable figure for the conductive area). Mean vessel element length, 305 μm. Mean vessel wall thickness, 2.0 μm. Perforation plates simple. Lateral wall pitting consists of alternate oval to circular pits (Fig. 4) mostly about 5 × 7 μm; pit apertures notably wide (Fig. 4); these data hold for vessel-ray and vessel-axial parenchyma pitting as well as for vessel-vessel pitting. Imperforate tracheary elements are all nonseptate libriform fibers. Mean libriform fiber diameter at widest point, 25 μm. Mean libriform fiber length, 660 μm. Mean libriform fiber wall thickness, 1.3 μm (Fig. 1). Pits of libriform fibers mostly on radial walls, slitlike, 2–2.5 μm long, sparse. Axial parenchyma vasicentric scanty (Fig. 4), in strands of three to seven (mostly five) cells. Sheaths of axial parenchyma mostly incomplete, but a few forming a sheath one to two cells wide around vessels or vessel groups. Rays both multiseriate and uniseriate, the former more common (Fig. 2). In both multiseriate and uniseriate rays, upright, square, and procumbent cells are all frequent. However, horizontal subdivisions following origin are common (Fig. 3); procumbent cells therefore appear much more common than they are when subdivisions are not counted. Ray cells with thin but lignified walls bearing simple pits. Mean multiseriate ray height, 1010 μm. Mean uniseriate ray height, 153 μm. Mean multiseriate ray width at widest point, 3.95 cells. Wood nonstoried (Fig. 2). Crystals absent in axial and ray parenchyma.
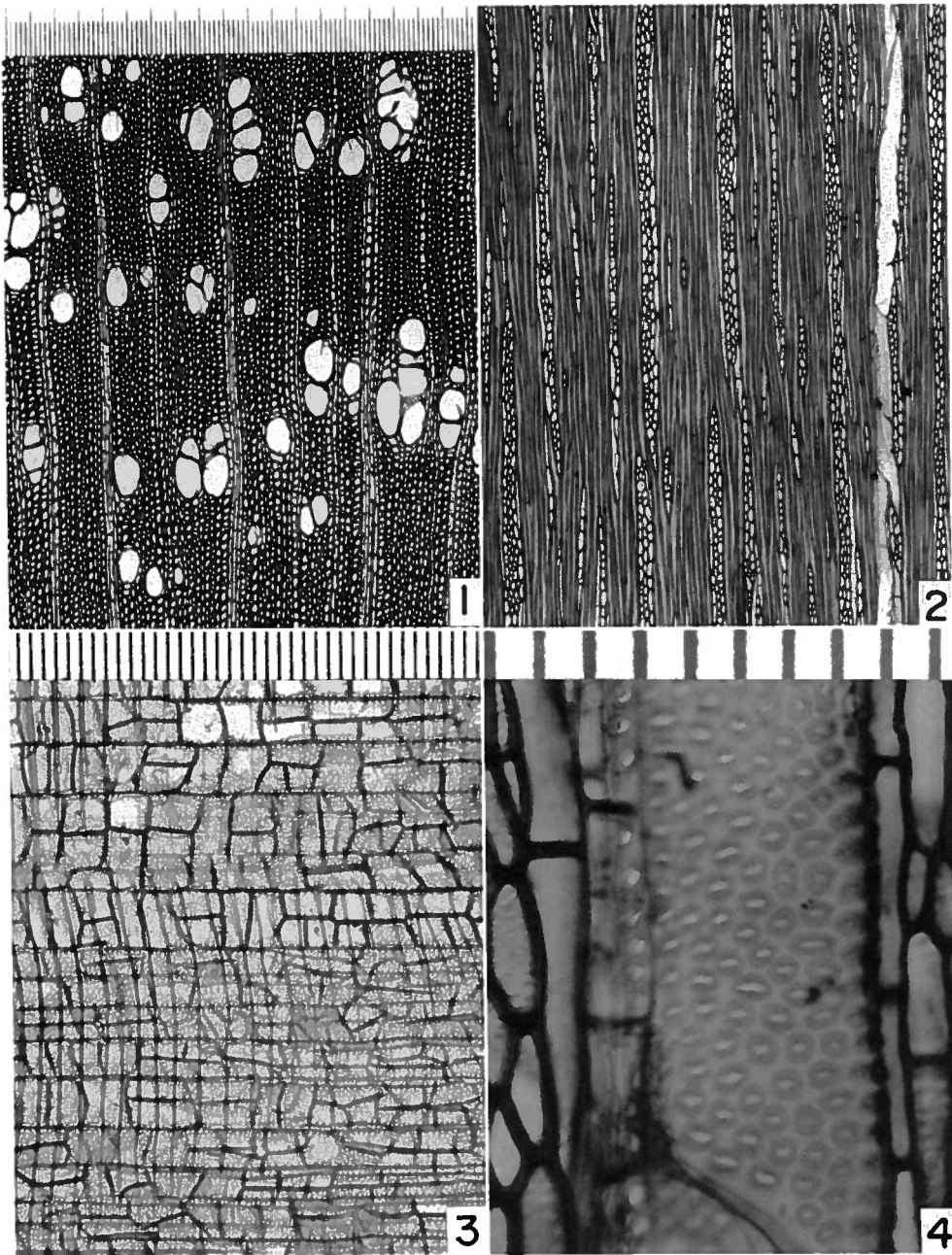
Fig. 1–4.   Wood sections of *Martynia annua* (*Nee & Mori 28807*).— 1. Transection; libriform fibers are relatively thin walled.—2. Tangential section; multiseriate rays are more common than uniseriate rays.—3. Radial section; upright, square, and procumbent cells are present, but many of these are horizontally subdivided following initiation.—4. Vessel from tangential section, with axial parenchyma strands to the left and right of it; pits in vessel walls have large apertures. (Fig. 1, 2, magnification scale above Fig. 1 [finest divisions = 10 μm]; Fig. 3, scale above Fig. 3 [divisions = 10 μm]; Fig. 4, scale above Fig. 4 [divisions = 10 μm].)

Pedaliaceae

CERATOTHECA TRILOBA (*Carlquist 5132,* RSA) (Fig. 5–6).—Growth rings present in stems more than one year old, latewood vessels narrower. Vessels often in clusters (Fig. 5). Mean number of vessels per group, 1.97. Mean number of vessels per mm², 39. Mean vessel diameter at widest point, 63 μm, many vessels wider radially than tangentially. Mean vessel element length, 196 μm. Mean vessel wall thickness, 2.3 μm. Perforation plates simple. Lateral wall pitting of vessels comprised mostly of oval pits about 4 × 5 μm, with narrowly elliptical pit apertures in vessel-vessel contacts; vessel-ray and vessel-axial parenchyma contacts consist of such pitting plus some more elongate pits. Imperforate tracheary elements are all nonseptate libriform fibers. Mean libriform fiber diameter at widest point, 32 μm. Mean libriform fiber length, 370 μm. Mean libriform fiber wall thickness, 2.3 μm. Pits of libriform fibers mostly on radial walls; pit apertures slitlike 1–2.5 μm long, pits sparse. Axial parenchyma all vasicentric scanty, composed of strands two to seven cells long. Most sheaths of axial parenchyma around vessels or vessel groups incomplete, a few completely surround vessels. Rays both multiseriate and uniseriate, the former much more common (Fig. 6). In both multiseriate and uniseriate rays, upright, square, and procumbent cells are common. Ray cells with thin but lignified walls bearing simple pits. Mean multiseriate ray height, 723 μm. Mean uniseriate ray height, 82 μm. Mean width of multiseriate rays at widest point, 3.4 cells. Wood nonstoried (Fig. 6). Crystals absent in ray and axial parenchyma.

HOLUBIA SACCATA (*Codd & Dyer 3893,* RSA).—Growth rings absent (plant annual). Vessels in clusters frequently. Mean number of vessels per group, 1.96. Mean number of vessels per mm², 88. Mean vessel diameter at widest point, 80 μm, many vessels wider radially than tangentially. Mean vessel element length, 412 μm. Mean vessel wall thickness, 2.3 μm. Perforation plates simple. Lateral vessel walls with oval or polygonal pits, typically about 6 × 7 μm, bearing narrowly elliptical apertures; the narrow axis of the pit apertures does not exceed 2 μm and is usually less. Imperforate tracheary elements are all nonseptate libriform fibers. Mean libriform fiber diameter at widest point, 37 μm. Mean libriform fiber length, 663 μm. Mean libriform fiber wall thickness, 2.0 μm. Pits of libriform fibers sparse, mostly on radial walls, slitlike, 1–2 μm in length. Axial parenchyma vasicentric scanty, very scarce, only a few cells seen. Rays both multiseriate and uniseriate, the former much more common. Upright and square cells common but procumbent cells infrequent in both multiseriate and uniseriate rays. Ray cells thin walled but lignified, with simple pits. Mean height multiseriate rays, 642 μm. Mean height uniseriate rays, 160 μm. Mean width of multiseriate rays at widest point, 3.1 cells. Wood nonstoried. Crystals not present in axial or ray parenchyma.

PEDALIUM MUREX (*Fosberg 51894,* RSA).—Growth rings absent (plants annual). Vessels clustered to a moderate degree. Mean number of vessels per group, 2.16. Mean number of vessels per mm², 88. Mean vessel diameter, 59 μm. Vessels only a little wider radially than tangentially as seen in transection. Mean vessel element length, 112 μm. Mean vessel wall thickness, 2.2 μm. Perforation plates simple. Lateral wall pitting of vessels consists of oval (or polygonal) pits, typically 6 × 6 μm, with slitlike to narrowly elliptical pit apertures on vessel-vessel contacts.
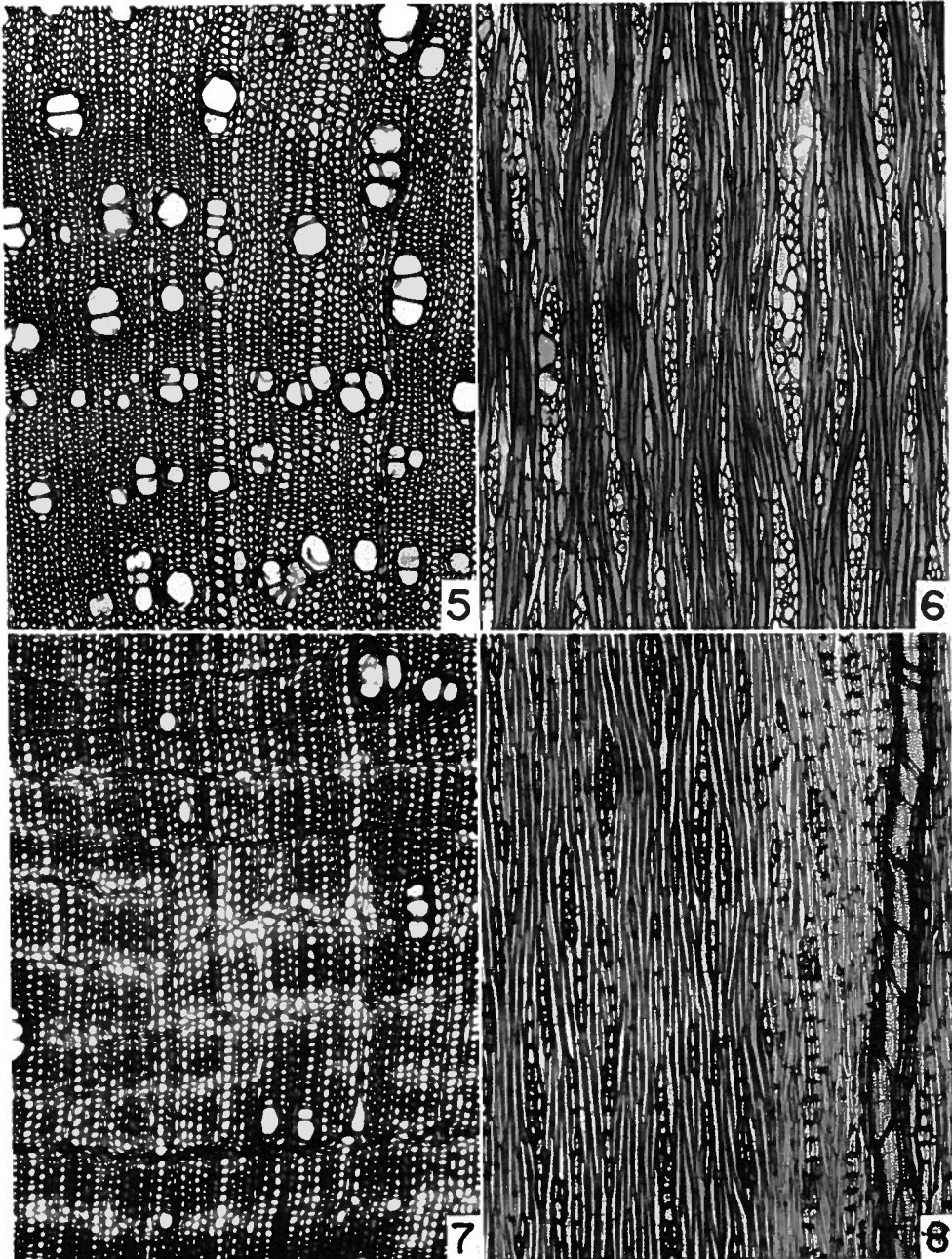
Fig. 5–8.   Wood sections of Pedaliaceae.—5–6. *Ceratotheca triloba* (*Carlquist 5132*).—5. Transection; vessels are mostly grouped.—6. Tangential section; no storying is evident.—7–8. *Sesamothamnus lugardii* (*Rodin 2725*).—7. Transection; vessels are relatively sparse, axial parenchyma bands are numerous.—8. Tangential section; parenchyma band is in right third of photograph; some libriform fibers conform to a storied pattern. (Fig. 5–8, magnification scale above Fig. 1.)

Vessel-ray and vessel-axial parenchyma pits are oval to elongate. Imperforate tracheary elements all nonseptate libriform fibers. Mean libriform fiber diameter, 25 μm. Mean libriform fiber length, 357 μm. Mean libriform fiber wall thickness, 2.0 μm. Libriform fiber pits sparse, slitlike, mostly on radial walls, 1–2 μm long. Axial parenchyma vasicentric scanty, strands composed of two cells. A band of thin walled apotracheal parenchyma like the bands of *Sesamothamnus* wood also observed. Rays both multiseriate and uniseriate, the former much more common. Upright and square cells common in both multiseriate and uniseriate rays. Ray cell walls thin but lignified, bearing simple pits. Mean multiseriate ray height, 514 μm. Mean uniseriate ray height, 77 μm. Mean multiseriate ray width at widest point, 4.2 cells. Wood nonstoried. Crystals not present in axial or ray parenchyma.

ROGERIA LONGIFLORA (*Wasserfall 1107,* RSA).—Growth rings absent (plants annual). Vessels commonly solitary but also in small clusters. Mean number of vessels per group, 2.12. Mean number of vessels per mm^2, 40. Mean vessel diameter, 57 μm. Mean vessel element length, 288 μm. Mean vessel wall thickness, 2.0 μm. Perforation plates simple. Lateral wall pitting of vessels composed of circular to oval pits 5–7 μm in diameter, with elliptical apertures (the narrow axis of which is up to 2 μm wide) on vessel-vessel contacts. Vessel-ray contacts with somewhat more laterally elongate pits. Imperforate tracheary elements all nonseptate libriform fibers. Mean libriform fiber diameter at widest point, 18 μm. Mean libriform fiber length, 542 μm. Mean libriform fiber wall thickness, 3.2 μm. Pits of libriform fibers sparse, slitlike, 2–3 μm long. Axial parenchyma vasicentric scanty, in strands of two to three cells, with walls as thick as those of libriform fibers. Rays both multiseriate and uniseriate, the former more numerous. Upright and square cells common but procumbent cells infrequent in both multiseriate and uniseriate rays. Ray cells thick walled like libriform fibers, pits simple. Mean multiseriate ray height, 435 μm. Mean uniseriate ray height, 184 μm. Mean multiseriate ray width at widest point, 3.0 cells. Wood nonstoried. Many ray cells contain a single rhomboidal crystal. Crystals are hexagonal, often with a central lacuna, and of various sizes but typically about half the length of the cell in which a crystal is located. Darkly staining resinlike globular deposits common in ray and axial parenchyma cells.

SESAMOTHAMNUS LUGARDII (*Rodin 2725,* UC) (Fig. 7–8).—Growth rings present but not easily discernible, some seasonal fluctuation in vessel diameter evident. Vessels often solitary (Fig. 7). Mean number of vessels per group, 1.92. Vessels relatively sparse (Fig. 7). Mean number of vessels per mm^2, 28. Mean vessel diameter, 54 μm. Mean vessel element length, 250 μm. Mean vessel wall thickness, 2.6 μm. Perforation plates simple. Lateral wall pitting of vessels composed of circular pits, 5–7 μm in diameter, apertures elliptical, on vessel-vessel contacts. Vessel-ray contacts have somewhat larger (narrow axis about 9 μm, long axis 10 μm or longer) pits with wide (gaping) apertures. Imperforate tracheary elements all libriform fibers; many septate. Mean libriform fiber diameter, 27 μm. Mean libriform fiber length, 403 μm. Mean libriform fiber wall thickness, 2.4 μm. Pits on libriform fibers sparse, slitlike, 1–2.5 μm long, sometimes longer because of splits in the apparently gelatinous walls. Axial parenchyma vasicentric scanty and apotracheal banded (Fig. 7). Vasicentric parenchyma occasionally forming complete sheaths around vessels or vessel groups, otherwise incomplete sheaths pres-

ent. Vasicentric parenchyma in strands of two (sometimes three) cells. Apotracheal parenchyma in tangential bands of indefinite extent, 1–3 cells in thickness. Apotracheal parenchyma mostly with nonlignified walls (Fig. 7), in strands of two cells typically, some cells undivided (Fig. 8). Rays both multiseriate and uniseriate, the former more common. Multiseriate rays composed mostly of upright and square cells, procumbent cells infrequent. Uniseriate rays composed of upright and square cells. Ray cells with thin but usually lignified walls bearing simple pits. Mean multiseriate ray height, 449 μm. Mean uniseriate ray height, 195 μm. Mean multiseriate ray width at widest point, 2.25 cells. Some libriform fibers storied (Fig. 8, right; storying obscure because of thickness of section). Apotracheal parenchyma also sometimes storied; rays not storied. Crystals not present in ray and axial parenchyma.

SESAMOTHAMNUS RIVAE (*Fosberg 49950,* POM).—Growth rings not apparent. Vessels almost exclusively solitary. Mean number of vessels per group, 1.08. Mean number of vessels per mm^2, 28. Mean vessel diameter, 44 μm. Mean vessel element length, 206 μm. Mean vessel wall thickness, 2.6 μm. Perforation plates simple. Lateral wall pitting of vessels composed of circular to oval pits 6–7 μm in diameter, apertures narrowly elliptical, on vessel-vessel contacts. Pits on vessel-ray and vessel-axial parenchyma contacts 8 × 10 μm (or larger), with notably wide (gaping) pit apertures. Imperforate tracheary elements all libriform fibers, some of them septate. Mean libriform fiber diameter, 28 μm. Mean libriform fiber length, 341 μm. Mean libriform fiber wall thickness, 2.2 μm. Pits on libriform fibers sparse, slitlike, 2–2.5 μm long. Axial parenchyma vasicentric scanty and apotracheal banded. Vasicentric parenchyma in the form of incomplete (rarely complete) sheaths around vessels and vessel groups, in strands of two to six (mostly two or three) cells. Apotracheal parenchyma in bands 1–3 cells thick, indefinite in tangential extent, in strands of two cells, with thin nonlignified walls chiefly. Rays are both multiseriate and uniseriate, the two types about equal in frequency. Both multiseriate and uniseriate rays are composed of upright and square cells commonly, only a few procumbent cells present. Ray cells thin-walled, mostly lignified, bearing simple pits. Mean multiseriate ray height, 750 μm. Mean uniseriate ray height, 193 μm. Mean multiseriate ray width at widest point, 2.20 cells. Some libriform fibers and some apotracheal parenchyma strands storied. Crystals not present in axial and ray parenchyma.

SESAMUM INDICUM (*Thorne & Davidson 16664,* RSA).—Growth rings absent (plants annual). Vessels mostly in clusters. Mean number of vessels per group, 2.88. Mean number of vessels per mm^2, 111. Mean vessel diameter, 49 μm. Mean vessel element length, 280 μm. Mean vessel wall thickness, 1.8 μm. Perforation plates simple. Lateral wall pitting of vessels composed of circular or polygonal pits 5–7 μm in diameter, apertures elliptical, on either vessel-vessel, vessel-axial parenchyma, or vessel-ray contacts. Imperforate tracheary elements all nonseptate libriform fibers. Mean libriform fiber diameter at widest point, 25 μm. Mean libriform fiber length, 590 μm. Mean libriform fiber wall thickness, 1.1 μm. Pits on libriform fibers very sparse, with slitlike apertures 1.5–2.5 μm long. Axial parenchyma vasicentric scanty, composed of strands two or three cells long. Rays both multiseriate and uniseriate, the two types about equal in frequency. Upright, square, and procumbent cells all common in both multiseriate and uniseriate rays.

Ray cells thin walled but lignified, walls bearing simple pits. Mean multiseriate ray height, 225 μm. Mean uniseriate ray height, 85 μm. Mean multiseriate ray width at widest point, 2.23 cells. Wood nonstoried. Crystals not present in axial and ray parenchyma.

SYSTEMATIC CONCLUSIONS

Martyniaceae and Pedaliaceae can be grouped together for the purpose of giving a summary of the features all species have in common. Vessels are solitary or grouped, with simple perforation plates. Lateral wall pitting of vessels consists of alternate circular (or polygonal where pits are crowded) to oval pits about 5–7 μm in diameter on vessel-vessel contacts; pits are sometimes longer (*Ceratotheca, Holubia, Pedalium, Rogeria*), occasionally wider as well (*Sesamothamnus*) on vessel-ray and vessel-axial parenchyma contacts. Vessel pits sometimes have wide (gaping) pit apertures (*Holubia, Martynia, Rogeria, Sesamothamnus*). Imperforate tracheary elements are libriform fibers with simple pits (vestigial borders on pits in *Uncarina,* which therefore has fiber-tracheids). Imperforate tracheary elements are mostly nonseptate, but septa are present in many libriform fibers of *Sesamothamnus.* Axial parenchyma is vasicentric scanty (very scarce in *Holubia*). In addition, bands of apotracheal parenchyma are present in *Pedalium, Sesamothamnus,* and *Uncarina.* Both multiseriate and uniseriate rays are present, the former more abundant to both equally abundant. Rays tend to have mostly upright and square cells and relatively few procumbent cells (procumbent cells fairly common in rays of *Ceratotheca, Martynia,* and *Sesamum*). Multiseriate rays often wider than two cells at widest point. Storied structure present in *Sesamothamnus* (libriform fibers, apotracheal parenchyma) and *Uncarina* (apotracheal parenchyma). Rhomboidal crystals are present singly in ray cells of *Rogeria* and *Uncarina.* Dark-staining droplets occur in parenchyma cells of *Rogeria.*

All of the features listed may be found in families of Scrophulariales (Bignoniales), an order that typically contains Acanthaceae, Buddlejaceae, Bignoniaceae, Gesneriaceae, Myoporaceae, Plantaginaceae, and Scrophulariaceae, among woody families, in addition to Martyniaceae and Pedaliaceae (Cronquist 1981; Dahlgren 1980; Takhtajan 1980; Thorne 1976). Herbaceous families of the order include Lentibulariaceae and Orobanchaceae. Retziaceae has been excluded from Scrophulariales (Dahlgren et al. 1979; Carlquist 1986); it belongs near or should be combined with Stilbaceae, a family of the order Lamiales.

Outer and Veenendaal (1983) do not report storied structure in *Uncarina,* but it clearly is present in the apotracheal parenchyma cells they figure in a tangential section. Other features reported here that they did not find on the basis of *Uncarina* include presence of septate fibers and presence of procumbent ray cells. For reasons given below, these features change the degree of affinity Pedaliaceae (along with Martyniaceae) have with particular scrophularialean families. Also, subsequent reports of particular features in recently studied families (Gesneriaceae, Myoporaceae) change the degree of closeness apparent on the basis of wood anatomy, as noted below. As mentioned in the introduction, presence of wide vessels does not so much ally Pedaliaceae to Bignoniaceae, as claimed by Outer and Veenendaal, as it demonstrates the transpiration regime in their environments. Storied structure can be found in some Bignoniaceae, but it can also be found in a number

of Myoporaceae (Carlquist and Hoekman 1986b). Septate fibers may commonly be found in Acanthaceae (Metcalfe and Chalk 1950) and Gesneriaceae (Carlquist and Hoekman 1986a), but they are rare in Bignoniaceae (Outer and Veenendaal 1983). The lack of procumbent cells in rays of *Uncarina,* thought to be a point of resemblance to Acanthaceae by Outer and Veenendaal, is rather an indication of paedomorphosis, which in turn is common in predominantly herbaceous groups (Carlquist 1962), such as Gesneriaceae (Carlquist and Hoekman 1986a) and Scrophulariaceae (Michener 1981, 1983). Crystals in ray cells occur in two families of Scrophulariales other than Pedaliaceae, namely, Gesneriaceae (Carlquist and Hoekman 1986a) and Myoporaceae (Carlquist and Hoekman 1986b). Bignoniaceae and Pedaliaceae are not alike on the basis of axial parenchyma, a feature not discussed by Outer and Veenendaal. Axial parenchyma is paratracheal in Bignoniaceae, but rather abundant and with tendencies toward aliform, aliform-confluent, and paratracheal banded arrangements (Metcalfe and Chalk 1950). In Pedaliaceae it is vasicentric scanty, but apotracheal banded parenchyma, not reported for Bignoniaceae, is present in *Pedalium, Sesamothamnus,* and *Uncarina.* Apotracheal bands of parenchyma may be found in Scrophulariaceae (Michener 1983), a few Myoporaceae (Carlquist and Hoekman, 1986b), and Acanthaceae (terminal parenchyma in *Anisacanthus,* Metcalfe and Chalk 1950).

Thus, if we take into account a wider range of data, Pedaliaceae do not appear decisively more closely related to Bignoniaceae than to any other family of Scrophulariales. If one looks at some other features, such as pollen, a similar situation is evident. The pollen of Pedaliaceae is polycolpate (that of Martyniaceae may represent a kind of derivation from a polycolpate condition). One can find polycolpate pollen in certain Bignoniaceae, but this condition is also characteristic of a number of Acanthaceae and Scrophulariaceae, and, to a lesser extent, a few Gesneriaceae (Erdtman 1952).

We can conclude that Pedaliaceae definitely do belong to Scrophulariales, but are not more closely allied to one family than to another on the basis of wood anatomy and probably pollen morphology. The wood of *Martynia annua* is comparable to that of herbaceous Pedaliaceae. This is not taken here to indicate a necessarily close relationship between Martyniaceae and Pedaliaceae, because some of the similarities could relate to herbaceous habit. The scent of herbage of Martyniaceae and Pedaliaceae does suggest closeness of the families. The present evidence does not rule out the possibility that Martyniaceae and Pedaliaceae represent independent but close derivatives of a common ancestral stock.

ECOLOGY AND HABIT

As mentioned above, the wide vessel diameter of most of the Pedaliaceae and of the *Martynia* sample studied very likely is indicative of a high transpiration regime, such as one might find in summer-wet areas of the Transvaal and other portions of southern Africa. Coastal Ceylon, habitat of *Pedalium murex,* is similar in being moist and hot most of the year. The wide vessels of Bignoniaceae can be related to the wet tropical areas in wich most of them grow; lianas are not only tropical but have notably wide vessels, so the lianoid Bignoniaceae do demonstrate elevated figures for vessel diameter. However, *Sesamothamnus* has relatively narrow vessels; its habitats are subject to prolonged drought. The bark and wood (apotracheal parenchyma bands) of *Sesamothamnus* suggest a degree of succulence, in turn related to slow but steady rates of transpiration which the narrowness

and lack of density of vessels would seem to indicate. The succulence and lack of probable strong fluctuation in transpiration in *Sesamothamnus* may also explain why vessel grouping in that genus is not pronounced. Vessel grouping tends to be found to a greater extent in woods from drier areas bearing libriform fibers or fiber-tracheids (Carlquist 1984). The conductive redundancy value increases as the growing season draws to an end, and this would explain why more than 1.9 vessels per group are found in all the Pedaliaceae other than *Sesamothamnus.* The apotracheal parenchyma bands of *Sesamothamnus* and *Uncarina,* which both occur in seasonally dry habitats, may be a water storage mechanism.

Presence of relatively thin-walled imperforate tracheary elements in Martyniaceae and Pedaliaceae may be related to herbaceous habit. The predominance of upright over procumbent cells is generally an indication of herbaceous habit, so occurrence of this feature in the annuals *Holubia saccata, Pedalium murex,* and *Rogeria longiflora* is not unexpected, although the correlation with habit is not a perfect one. One expects relatively short vessel elements in specialized taxa of dicotyledons unless paedomorphosis intervenes (Carlquist 1962). The relatively long vessel elements of *Holubia saccata, Martynia annua,* and *Sesamum indicum* may have this explanation.

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