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WOOD ANATOMY OF MYOPORACEAE: ECOLOGICAL AND  
SYSTEMATIC CONSIDERATIONS

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ABSTRACT

Quantitative and qualitative features are presented for 28 collections of three genera (*Bontia*, *Eremophila*, *Myoporum*); data on *Oftia* are also included since it is sometimes referred to Myoporaceae. Wood of all Myoporaceae represents variation on a basic plan: woods diffuse porous or semi-ring-porous; vessels with simple perforation plates; lateral wall pits of vessels alternate and circular, with grooves interconnecting some pit apertures; vessels grouped to various degrees into radial multiples; imperforate tracheary elements all fiber-tracheids with pit cavities 1-5  $\mu\text{m}$  in diameter (wider on contacts with ray cells), nonseptate; axial parenchyma vasicentric scanty plus, in some species, tangential paratracheal bands (sometimes terminal); rays multiseriate plus uniseriate (uniseriate almost exclusively in two species of *Eremophila*); ray cells procumbent exclusively, upright and square in uniseriate rays and in tips of multiseriate rays; rays storied in some species of *Eremophila*, axial parenchyma variously storied; crystals present in ray cells of some species of *Eremophila* and in fibers of *E. polyclada*; amorphous deposits and starch often present in parenchyma. *Oftia* differs from Myoporaceae by having: septate libriform fibers rather than fiber-tracheids; large pits on vessel walls; axial parenchyma nearly absent; and erect cells predominant in rays. *Oftia* may be placed in Scrophulariaceae. *Leucophyllum* differs from Myoporaceae by having: helical thickenings in vessels; vasicentric tracheids transitional from vascular tracheids; scarce axial parenchyma; and erect cells predominant in rays. *Leucophyllum* may be excluded from Myoporaceae. Wood anatomy of Myoporaceae shows relationship between Myoporaceae, Scrophulariaceae, and Gesneriaceae, and is also indicative of derivation from woody ancestors. Wood of Myoporaceae reflects xeromorphy, especially in *Eremophila*, but the foliar apparatus may partially preempt the role of wood in promoting safety, which is connoted by growth rings, narrow and numerous vessels, and grouped vessels.

Key words: *Bontia*, ecological wood anatomy, *Eremophila*, interconnected rays, Myoporaceae, *Myoporum*, Scrophulariales, wood anatomy.

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INTRODUCTION

Three genera have traditionally been assigned to Myoporaceae: *Bontia*, *Eremophila*, and *Myoporum*. *Bontia* is a monotypic shrub or small tree from the West Indies (and possibly tropical Mesoamerica: Willis 1980). *Eremophila* (including *Pholidia*, *Pholidiopsis*) occurs in Australia. Including recently described species (Dill 1975; Henderson 1978; Chinnock 1979, 1980, 1986), about 65 species of *Eremophila* are now known. Although *Eremophila* is not exclusively a desert genus as its name might suggest, it is indeed characteristic of dry habitats. *Myoporum* consists of about 30 species that range from eastern Asia to Australia, New Guinea, New Zealand, various Pacific islands (including the Hawaiian chain), and Mauritius (Willis 1980), a distribution that suggests infrequent events of seawater dispersal of the corky drupes. *Myoporum* can be found in dry lowland situations, but inland populations can enter moderately wet forest, as in the Kipuka Pualu (Hawaii) population referred to *M. sandwicense* var. *fauriei* by Webster

(1951). The ecological range of Myoporaceae is thus basically a narrow one, with some incursions into moderately moist conditions. The basically maritime nature of the family is evident if we imagine that the flora of dryland Australia (i.e., habitats of *Eremophila*) bears a relationship to seacoasts in its salinity and in its geological history: central and southern portions of the continent represent relatively recent embayments. One *Myoporum* is even a mangrove of sorts (Toyama and Itow 1975). The ecological range of the family is broad enough to deserve comparison with variations in wood anatomy, with due attention to the participation of other factors related to regulation of the water economy of the plant.

The generic composition of Myoporaceae has been questioned. *Oftia*, traditionally included in Myoporaceae, has been excluded on the basis of recent evidence from pollen (Niezgoda and Tomb 1975) and other features (Hallier 1905; Dahlgren and Rao 1971). Dahlgren and Rao believe *Oftia* should be transferred to Scrophulariaceae. Metcalfe and Chalk (1950) have reported, with uncertainty, the presence of intraxylary phloem in *Oftia*; this has needed reinvestigation, since intraxylary phloem (which is lacking in both Myoporaceae and Scrophulariaceae) would indicate other affinities for the genus. A Madagascan species first assigned to *Oftia* (Capuron 1972) has been segregated as a genus, *Ranopisoa* (Leroy 1977). Evidence from pollen morphology (Lobreau-Callen 1978) shows that *Ranopisoa* is like Myoporaceae in having three binorate ("endocolpar") colpae (furrows), whereas *Oftia* has four colpae and no appreciable transverse furrow formation (Niezgoda and Tomb 1975). The position of *Oftia* is considered in the present paper because of the availability of a relatively large wood sample collected by the senior author.

However, if *Oftia* (which consists of two species from South Africa if *Ranopisoa* is segregated) is transferred to Scrophulariaceae, other questions remain. The tribe Leucophylleae of Scrophulariaceae has pollen that closely matches that of Myoporaceae (Niezgoda and Tomb 1975), although other features of *Leucophyllum*, such as fruit morphology, show divergence from Myoporaceae. One notes, in this regard, Takhtajan's (1980) statement that Myoporaceae is a family with transitions to Scrophulariaceae, implying that some genera show intermediacy. The role of wood anatomy in such intermediacy is worthy of exploration. Wood anatomy of *Leucophyllum* is under study by Dr. David C. Michener, but observations based on wood of two species of *Leucophyllum* are included in the terminal section of this paper in an effort to help define Myoporaceae.

Conceding that Myoporaceae is closely allied to Scrophulariaceae, wood of Myoporaceae is of interest in defining the order and suborder to which these families belong. A survey of wood anatomy of tubiflorous dicotyledon families has been undertaken by the senior author. Although monographs of wood anatomy of several more families are contemplated, a summarization, in which Myoporaceae will be considered, should follow soon. Leading phylogenists place Myoporaceae close to Scrophulariaceae in the order Scrophulariales (or Bignoniales), as evidenced by the systems of Cronquist (1981), Dahlgren (1980), Takhtajan (1980), and Thorne (1976).

#### MATERIALS AND METHODS

Wood samples were available in dried condition only. The largest number of collections was contributed by the U.S. Forest Products Laboratory from their

Table 1. Wood characteristics of Myoporaceae.

Species	Collection	VD	V/MM	VL	V/G	VWT	TD	TL	TWT	MRH	MRW	URW	MESO
<i>Bontia daphnoides</i> L.	SJRw 35382	50.8	75.7	301	1.5	2.9	17.3	625	2.4	354	24.3	11.5	202.0
<i>B. daphnoides</i>	USw 36942	51.9	59.8	272	1.8	3.2	21.3	634	3.2	384	23.9	12.4	236.0
<i>B. daphnoides</i>	Leonard 11179 (USw)	47.7	89.2	241	1.7	3.2	19.1	602	3.1	299	19.9	10.1	129.0
<i>Eremophila alternifolia</i> R. Br.	SJRw 46308	27.1	253.0	218	3.1	3.3	15.6	511	2.3	160	17.5	9.4	23.4
<i>E. bigoniiflora</i> F. Muell.	SFCw-R 977.149	48.8	68.7	230	1.9	3.4	20.7	650	3.3	165	16.7	9.4	163.0
<i>E. duttonii</i> F. Muell.	SJRw 47213	30.4	125.0	190	3.5	3.1	18.7	440	3.1	204	33.9	13.1	46.2
<i>E. freelingii</i> F. Muell.	SJRw 47214	57.6	30.4	202	2.4	4.0	29.3	510	4.6	215	41.7	15.4	383.0
<i>E. latrobei</i> F. Muell.	Carlquist 5184 (RSAw)	23.7	270.0	165	2.6	3.4	16.9	406	3.1	156	18.3	8.3	14.5
<i>E. longifolia</i> F. Muell.	SJRw 47212	28.5	81.9	226	3.4	2.9	21.0	629	3.3	228	26.6	8.6	78.6
<i>E. longifolia</i>	Carlquist 5134 (RSAw)	40.9	72.3	253	1.9	4.0	16.8	659	2.8	155	20.1	10.6	143.0
<i>E. mitchelli</i> Benth.	SJRw 19379	47.0	141.0	212	2.5	3.1	15.9	597	2.8	226	24.4	12.6	70.7
<i>E. oppositifolia</i> R. Br.	MADw 39566	20.8	301.0	205	2.5	2.9	15.6	335	3.6	129	16.8	12.2	14.2
<i>E. polyclada</i> F. Muell.	SFCw-R 284.39	33.1	142.0	234	2.5	2.8	19.8	552	4.0	226	20.1	10.0	54.5
<i>E. scoparia</i> F. Muell.	SJRw 47250	25.5	149.0	192	2.0	3.2	17.8	446	3.4	262	16.8	8.7	32.9
<i>E. serrulata</i> Druce.	SJRw 47215	43.9	74.7	219	3.1	3.8	18.8	579	3.0	137	20.5	10.4	129.0
<i>Myoporum acuminatum</i> R. Br.	SJRw 14631	49.6	27.5	315	2.1	3.9	32.5	854	3.9	188	29.3	13.6	568.0
<i>M. acuminatum</i>	SJRw 46341	60.0	49.6	334	1.7	4.1	20.0	839	3.2	180	27.6	13.5	404.0
<i>M. laetum</i> Forst f.	SJRw 25470	56.0	35.2	336	2.5	3.0	30.1	1010	3.1	301	22.7	11.0	535.0
<i>M. laetum</i>	Carlquist 1552 (RSAw)	44.7	53.0	421	2.0	4.4	28.5	902	4.7	568	42.2	28.3	355.0
<i>M. montanum</i> R. Br.	SFCw-R 475.3	45.4	77.6	259	2.2	3.3	21.4	655	3.7	208	23.8	11.7	152.0
<i>M. platycarpum</i> R. Br.	SFCw-R 274.1	46.5	88.2	205	2.1	3.9	19.4	544	3.3	154	18.3	9.3	108.0
<i>M. platycarpum</i>	Carlquist 5143 (RSAw)	40.8	83.4	204	3.0	4.4	17.0	503	4.1	150	24.6	12.7	99.8
<i>M. rapense</i> F. Brown	SJRw 24304	17.6	454.0	292	3.7	2.5	18.7	896	2.4	161	22.8	9.9	11.3
<i>M. sandwicense</i> Gray var. <i>sandwicense</i>	SJRw 36336	42.8	48.2	354	1.7	4.0	21.7	1110	2.8	236	31.0	17.3	805.0
<i>M. sandwicense</i> var. <i>fauriei</i> Krn.	SJRw 24953	47.6	22.7	384	2.1	2.0	24.8	841	5.4	189	18.8	10.3	314.0
<i>M. sandwicense</i> var. <i>wilderi</i> (Sk.) Webster	SJRw 24785	36.5	99.4	304	2.5	3.0	19.9	803	2.6	253	28.4	13.6	112.0
<i>M. serratum</i> R. Br.	SJRw 46342	47.7	41.2	311	2.0	3.9	29.8	815	4.1	173	27.7	14.1	360.0
<i>M. stokesii</i> F. Brown	SJRw 37370	54.9	64.6	312	1.5	3.0	26.7	636	2.9	192	22.3	13.3	265.0
<i>Oftia africana</i> Bocq.	Carlquist 4632 (RSAw)	58.7	75.7	286	2.3	3.1	30.0	574	2.4	535	46.9	17.9	222.0
Family means		42.3	109.0	265	2.3	3.4	21.6	661	3.3	234	25.1	12.4	103.0

Legend for columns: VD = mean inside diameter of vessels at widest point,  $\mu\text{m}$ ; V/MM = mean number of vessels per  $\text{mm}^2$  of transection; VL = mean vessel element length,  $\mu\text{m}$ ; VWT = mean vessel wall thickness,  $\mu\text{m}$ ; TD = mean diameter of fiber-tracheids at widest point,  $\mu\text{m}$ ; TL = mean length of fiber-tracheids,  $\mu\text{m}$ ; TWT = mean wall thickness of fiber-tracheids,  $\mu\text{m}$ ; MRH = mean height of multiseriate rays,  $\mu\text{m}$ ; MRW = mean width of multiseriate rays at widest point,  $\mu\text{m}$ ; URH = mean height of uniseriate rays,  $\mu\text{m}$ ; MESO = Mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per  $\text{mm}^2$ ).

Samuel J. Record collection (*SJRw*) holdings, and by the Forestry Commission of New South Wales (*SFCw*). Field work by the senior author in Australia and South Africa yielded a few samples. Although *Myoporum laetum* is common in cultivation in southern California, both a sample from cultivation (*Carlquist 1552*) and one from a natural habitat near Wellington, New Zealand (*SJRw 25470*) were studied. The present study incorporates 20 species in three genera (Table 1). Thus, the surveys of *Eremophila* and *Myoporum* are not exhaustive, but they do cover wide ecological and taxonomic ranges within those genera. Polynesian Myoporaceae are identified in accordance with Webster (1951).

Wood samples were boiled in water, stored in 50% ethyl alcohol, and then sectioned on a sliding microtome. A few of the hardest samples benefited from an ethylene diamine treatment similar to that proposed by Kukachka (1977). Sections were stained with safranin; sections of many taxa were counterstained with fast green. Macerations of wood were prepared with Jeffrey's Fluid and stained with safranin. Means (Table 1) are based upon 20 measurements per feature except for vessel wall thickness and wall thickness and diameter of imperforate tracheary elements, in which means are based on an average of several measurements. Measurement of vessel diameter uses the widest diameter of each vessel and excludes the wall. Sections of most species were prepared by the junior author, who is also responsible for the data of Table 1 and for some qualitative observations. The senior author observed some qualitative features, prepared the photomicrographs, and constructed the text. This study was aided by a grant from the National Science Foundation, BSR 8419-169.

#### ANATOMICAL RESULTS

Table 1 summarizes quantitative data for the taxa studied. These are discussed below, but observations on qualitative features are also incorporated in the paragraphs below.

##### *Growth Rings*

Myoporaceae are characteristically evergreen; thus, despite the seasonal dryness of some of their localities, less prominent growth rings are to be expected in Myoporaceae than in families in which plants are deciduous because of drought or cold. A diffuse porous condition is illustrated here for *Bontia daphnoides* (Fig. 1) and *Myoporum laetum*. Other diffuse porous taxa include *M. acuminatum*, *M. montanum*, *M. sandwicense* (all varieties), *M. serratum*, and *M. stokesii*. Fluctuation of vessel diameter to a very limited extent, but with some change in thickness of imperforate tracheary elements, was observed in *Eremophila duttonii*, *Myoporum longifolia*, and *M. rapense* (Fig. 19). Other Myoporaceae could be regarded as semi-ring-porous because of various degrees of fluctuation of vessel diameter. Semi-ring-porous conditions are illustrated here for *Eremophila alternifolia* (Fig. 5), *E. bignoniiflora* (Fig. 7), *E. latrobei* (Fig. 20), *Myoporum platycarpum* (Fig. 17), and *Oftia africana* (Fig. 21). Apparent demarcation of growth rings by conspicuous parenchyma bands was observed in *Eremophila alternifolia* (Fig. 5), *E. bignoniiflora* (Fig. 7), *E. freelingii*, *E. scoparia*, and *Myoporum platycarpum* (Fig. 17). One should be cautioned, however, that parenchyma bands can occur at various points within growth rings as well as at the ends of growth

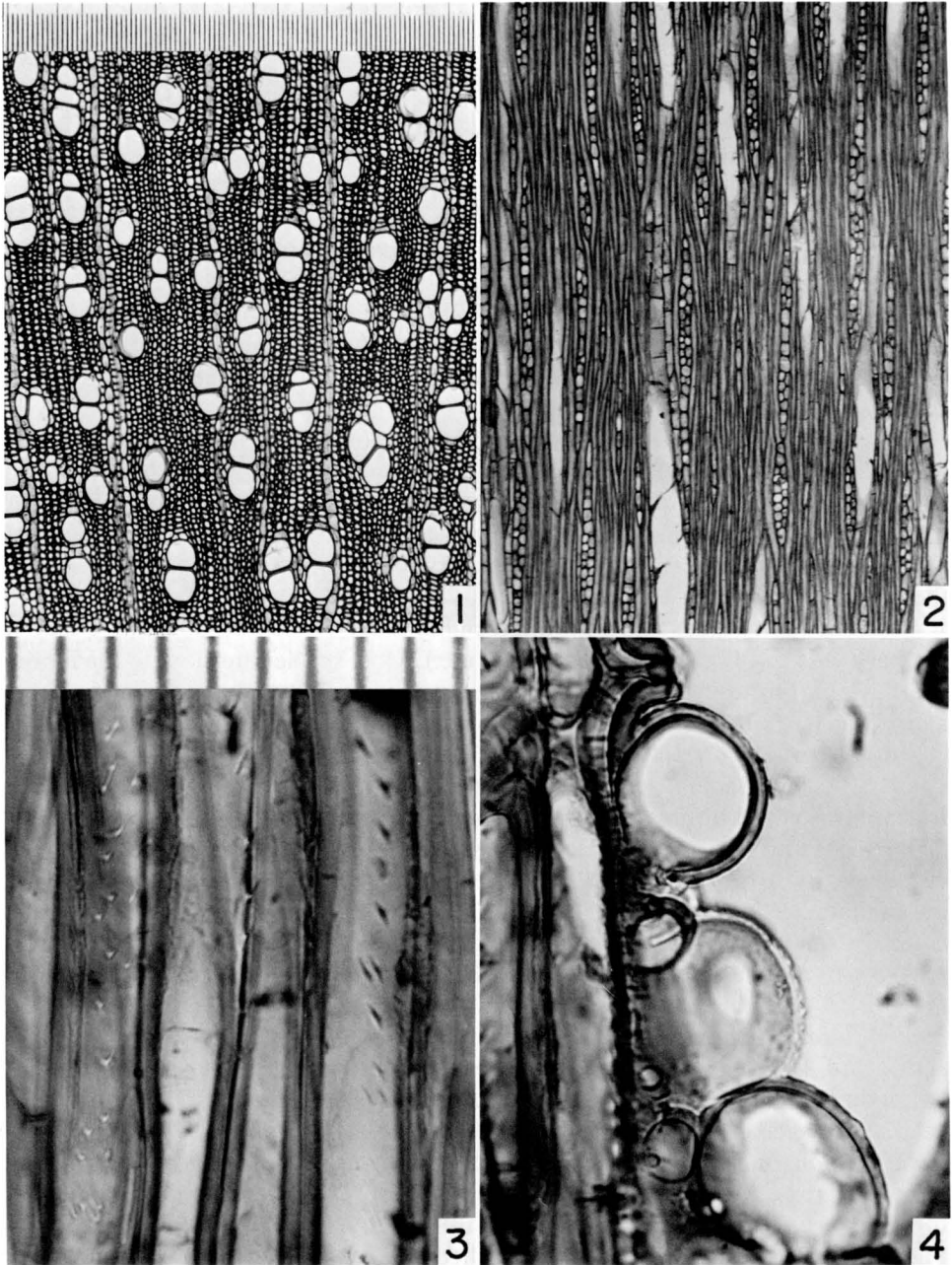


Fig. 1-4. Wood sections of Myoporaceae.—1-2. *Bontia daphnoides* (Leonard 11179).—1. Trans-section; growth rings absent.—2. Tangential section; some rays have multiseriate portions interconnected by a uniseriate portion.—3-4. *Eremophila freelingii* (SJRw 47214), radial sections.—3. Fiber-tracheids; slitlike pit apertures shown.—4. Tyloses, each covered by a thick film of a resinlike compound. (Magnification scale for Fig. 1-2 above Fig. 1 [finest divisions = 10  $\mu\text{m}$ ]; scale for Fig. 3-4 above Fig. 3 [divisions = 10  $\mu\text{m}$ ].)

rings. For example, in *Myoporum laetum* (Fig. 13) inconspicuous parenchyma bands are frequent within the growth rings.

### Vessel Elements

Vessel diameter is relatively narrow for the family as a whole, 42.3  $\mu\text{m}$  (Table 1). Wider vessels are represented in *Bontia* (Fig. 1), some species of *Eremophila*, such as *E. bignoniiflora* (Fig. 7), *E. freelingii*, and *E. mitchelli*, and are general in *Myoporum* (Fig. 13, 17) except for *M. rapense* (Fig. 19). Most species of *Eremophila* have narrow vessels (Fig. 5, 20).

Vessel density (number of vessels per  $\text{mm}^2$  transection) is close to being inversely proportional to vessel diameter in Myoporaceae, although not without deviation. The figures in Table 1 show this, and require no comment, except to note that the range in figures is wide (454 to 23).

Vessel elements are not notably short in Myoporaceae, although they fall well below the median for dicotyledons at large (approximately 600  $\mu\text{m}$ : Metcalfe and Chalk 1950:xxiv). One must concede that the Metcalfe and Chalk sampling tends to favor arboreal woody species over shrubs and woody herbs. The range in mean vessel element length (165 to 421  $\mu\text{m}$ ) in Myoporaceae is not great, and many of the species cluster near the family mean, 256  $\mu\text{m}$ .

Vessel grouping does show an appreciable range (1.46 to 3.69) in the family (solitary vessel = 1, a pair of vessels = 2, etc.). Most species are close to the family mean, 2.32. Grouping usually takes the form of radial multiples, ranging from short (Fig. 1, 7, 14, 17) to rather long (Fig. 5, 19, 20, 21).

Simple perforation plates exclusively were found in all of the Myoporaceae studied. A few double perforation plates (two perforations per end wall, not indicating a vessel bifurcation) were observed occasionally in *Oftia africana* (Fig. 23). Lateral wall pitting of vessels appears to consist of nearly circular to somewhat elliptical pits, arranged in alternate fashion. These pits were observed to be 2–3  $\mu\text{m}$  in diameter in *Eremophila duttonii*, *E. polyclada*, *E. scoparia*, and *Myoporum rapense*; 3.5–4.5 in *Bontia daphnoides*, *Eremophila alternifolia*, *E. freelingii*, *E. latrobei*, *E. longifolia*, *E. oppositifolia*, *E. serratum*, *Myoporum acuminatum*, *M. laetum*, *M. platycarpum*, and *M. sandwicense* var. *wilderi*; 4–5  $\mu\text{m}$  in *Eremophila bignoniiflora*, *Myoporum sandwicense* var. *fauriei*, *M. sandwicense* var. *sandwicense*, and *M. stokesii*; only in *Oftia africana* did pits range between 5 and 6.5  $\mu\text{m}$  in diameter (Fig. 24). Grooves interconnecting a few to numerous pit apertures in a helix were observed in *Bontia daphnoides*, *Eremophila bignoniiflora*, *E. latrobei*, *E. longifolia*, *E. serratum*, *Myoporum laetum*, *M. platycarpum*, *M. sandwicense* var. *sandwicense*, and *Oftia africana* (Fig. 24). Such grooves are figured for *Myoporum laetum* by Meylan and Butterfield (1978, Fig. 790 and especially Fig. 787). These grooves cannot be called "helical thickenings" because they represent indentations into, not thickenings of the vessel wall. Although stress has been laid on helical thickenings in the literature, helical grooves often occur without being accompanied by helical thickenings, as in some Asteraceae (Carlquist 1961, 1965). Vessel wall thickness in Myoporaceae is shown in Table 1. The range in thickness is not exceptional, but a loose correlation can be observed between vessel diameter and vessel wall thickness.

Tyloses were observed in vessel elements of a few Myoporaceae: *Bontia daphnoides*, *Eremophila bignoniiflora*, *E. freelingii* (Fig. 4), and *E. mitchelli*. In all of

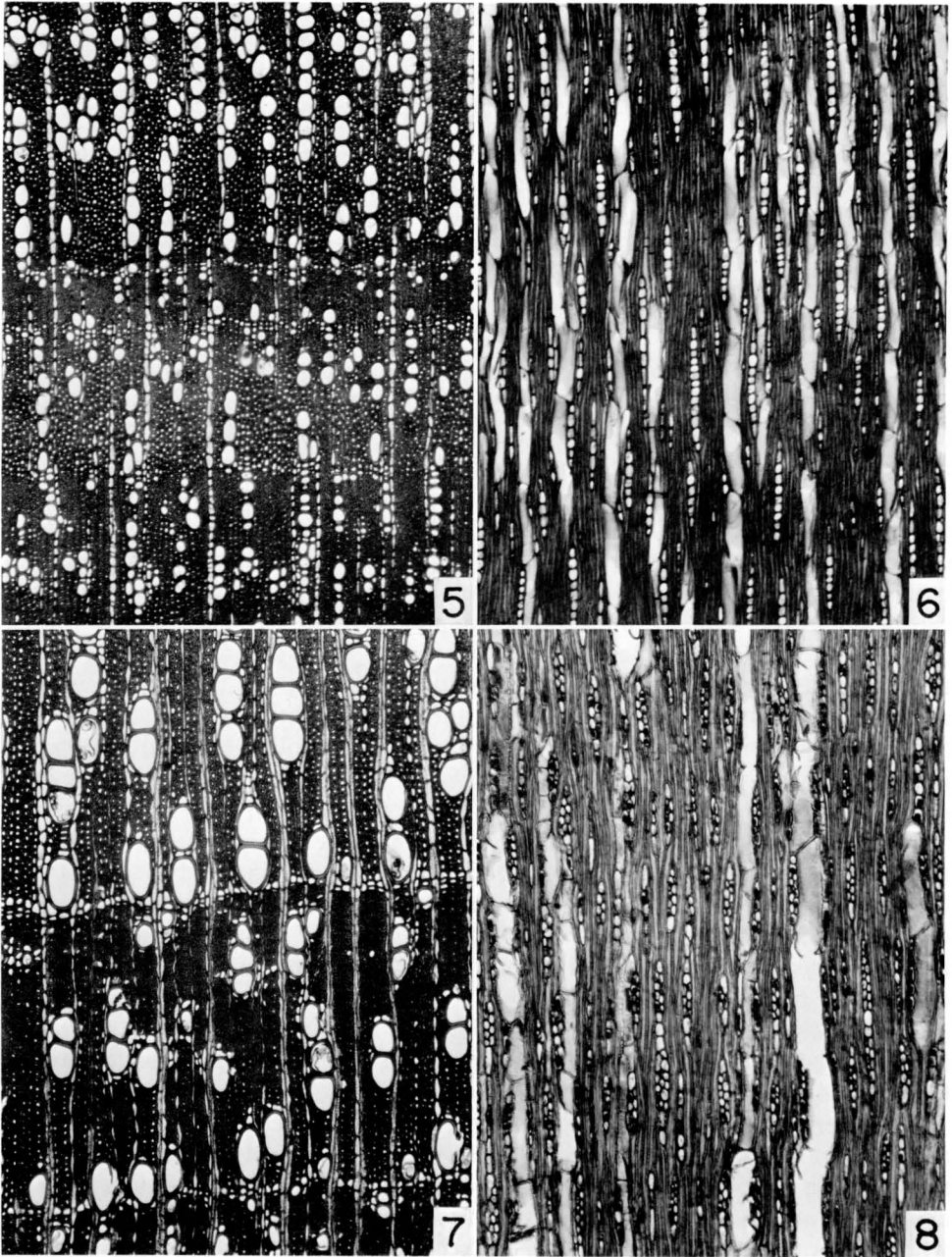


Fig. 5-8. Wood sections of *Eremophila*.—5-6. *E. alternifolia* (SJRw 47214).—5. Transection; semi-ring-porous condition and fluctuating fiber-tracheid wall thickness present.—6. Tangential section; rays are almost exclusively uniseriate.—7-8. *E. bignoniflora* (SFCw-R 977.149).—7. Transection. Two bands of terminal parenchyma are present.—8. Tangential section; many of the rays conform to a storied pattern. (Scale for Fig. 5-8 above Fig. 1.)



these, the tyloses are thin walled, spherical, and do not fill the lumina of vessels. Brown (1922) reports tyloses for *Myoporum sandwicense*.

### *Imperforate Tracheary Elements*

According to Bailey (1936) or the definitions of the IAWA Committee on Nomenclature (1933), the imperforate tracheary elements of Myoporaceae must be called fiber-tracheids because pits on them bear vestigial borders. Pits are also relatively sparse. Pit cavity diameters range between 1 and 2  $\mu\text{m}$  in *Eremophila bignoniiflora*, *E. latrobei*, *E. oppositifolia*, and *E. scoparia*; 2 and 3  $\mu\text{m}$  in *E. alternifolia*, *E. duttonii*, *E. mitchelli*, *E. polyclada*, *E. serrulata*, *Myoporum acuminatum*, *M. montanum*, *M. platycarpum*, and *E. sandwicense* var. *sandwicense*; 3 and 4  $\mu\text{m}$  in *Bontia daphnoides*, *Eremophila longifolia*, *Myoporum laetum*, *M. sandwicense* var. *fauriei*, and *M. serratum*; 4 and 5  $\mu\text{m}$  in *Eremophila freelingii* (Fig. 3) and *Myoporum stokesii*. However, note should be taken that these represent fiber-tracheid to fiber-tracheid pits within any given sample; fiber-tracheid to ray cell pits have pit cavities at least 1  $\mu\text{m}$  and often 2  $\mu\text{m}$  wider than those of fiber-tracheid to fiber-tracheid pits. This circumstance shows one should exercise caution in designating pit size in imperforate tracheary elements on the basis of a few observations. Length of apertures on the pits of the fiber-tracheids can be about the same as the pit cavity diameter, as in *Myoporum laetum* (Fig. 15; see also Meylan and Butterfield, 1978, Fig. 791). However, in most of the taxa studied, long slitlike pit apertures are common (Fig. 3). These apparent pit apertures probably are, to various degrees, the result of splitting due to dehydration (during microtechnical processing) of somewhat gelatinous walls. Notable gelatinous walls were observed in fiber-tracheids of *Eremophila oppositifolia* and *Myoporum sandwicense* var. *sandwicense*.

Metcalf and Chalk (1950) report imperforate tracheary elements in the family to have simple pits; this report is contradicted by the present study as well as by Meylan and Butterfield (1978). However, the pits of imperforate tracheary elements of *Oftia africana* are apparently simple (Fig. 25). Counterstaining produces a fringe of deeply stained area adjacent to the pit apertures, but no border can be detected by means of light microscopy.

Fiber-tracheids in Myoporaceae are about 2.5 times as long as vessel elements (figures based on family means, Table 1), although there are some minor deviations from that ratio in particular species.

Diameter of imperforate tracheary elements at the widest point (Table 1) parallels vessel element diameter rather closely, as can be seen by examining transections (Fig. 1, 5, 7, 13, 17, 19, 20, 21). Wall thickness of imperforate tracheary elements (Table 1) varies independently of cell diameter in Myoporaceae, although with narrow fiber-tracheid diameter, thicker appearance of walls is achieved with less wall thickness. Keeping that in mind, one can note relatively thin-walled fiber-tracheids in *Bontia daphnoides* (Fig. 2), *Myoporum laetum* (Fig. 13), and all varieties of *M. sandwicense*. The libriform fibers of *Oftia africana* (Fig. 21) are notably thin walled. Relatively thick-walled fiber-tracheids are characteristic of all species of *Eremophila* (Fig. 5, 7, 20); this accounts for the hardness of those woods. Wall thickness of fiber-tracheids can vary according to location within a growth ring, as in *Eremophila alternifolia* (Fig. 5) or *Myoporum rapense* (Fig. 19).

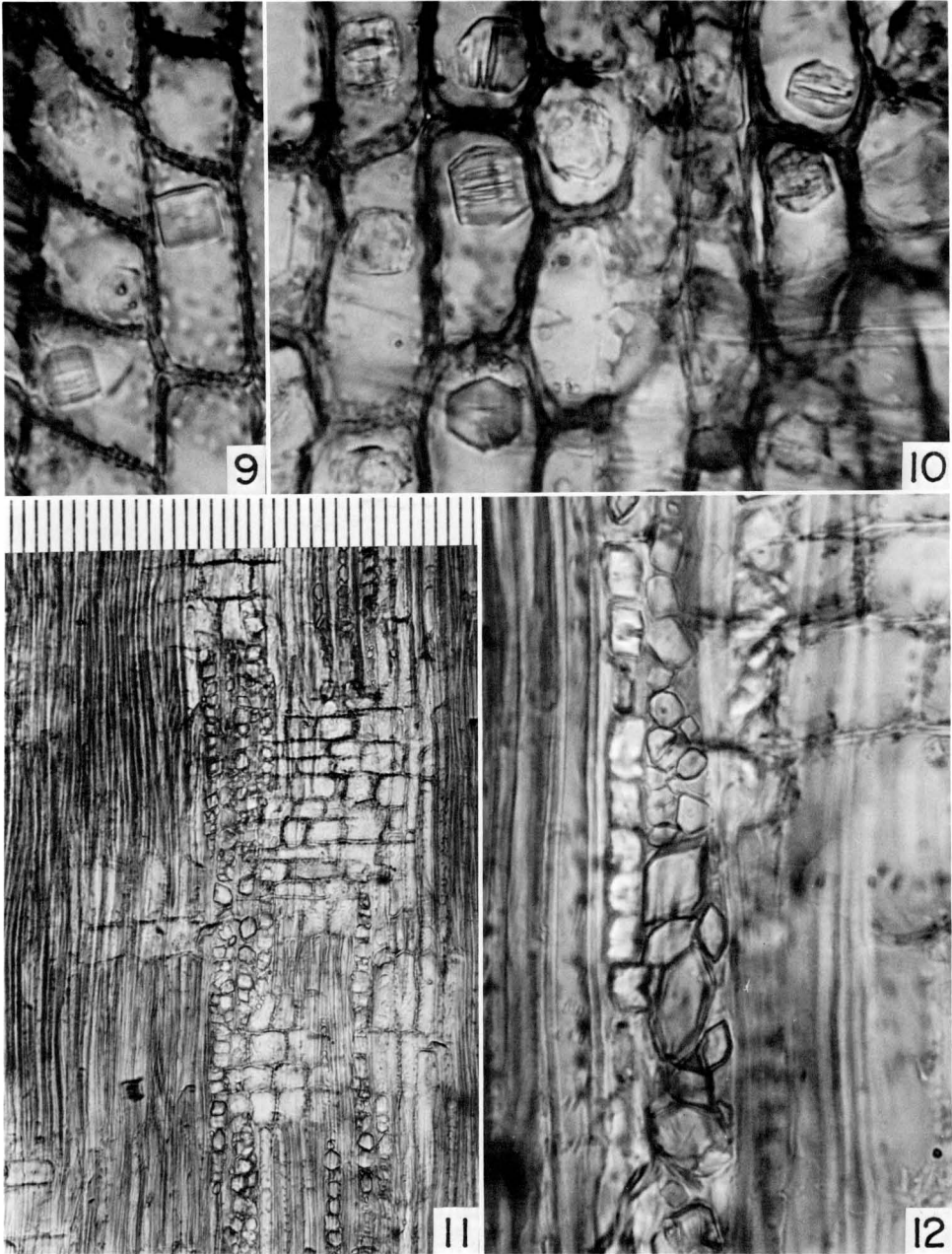


Fig. 9-12. Radial sections of *Eremophila* woods to show crystal occurrence.—9. *E. alternifolia* (SJRw 46308). Ray cells (radial axis oriented vertically).—10. *E. duttonii* (SJRw 47213). Ray cells (radial axis oriented vertically), note layering in crystals.—11-12. *E. polyclada* (SFCw-R 284.39).—11. Files of crystals representing contents of several crystal-containing fibers.—12. Characteristic sizes and shapes of crystals in crystal-containing fibers. (Scale for Fig. 9, 10, 12 above Fig. 3; scale for Fig. 11 above Fig. 11 [divisions = 10  $\mu$ m].)

No septa were observed in fiber-tracheids of Myoporaceae. However, septa do occur in a portion of the libriform fibers of *Oftia africana* (Fig. 25, left). No vasicentric tracheids or vascular tracheids were observed in either Myoporaceae or *Oftia*.

#### *Axial Parenchyma*

In all Myoporaceae, vasicentric scanty parenchyma is present. The sheathing of vessels may range from partial, only a few cells adjacent to a vessel, as in *Bontia daphnoides* (Fig. 1) or *Eremophila latrobei* (Fig. 20), to a complete sheath, as in *Myoporum platycarpum* (Fig. 17). Strands of axial parenchyma are composed mostly of two cells, but sometimes three or four, as in *Bontia daphnoides* (Fig. 2). In addition to vasicentric scanty parenchyma, various kinds of tangentially aggregated cells may be seen. In its least conspicuous form, where parenchyma cells look similar to fiber-tracheids in transection as in *Myoporum laetum* (Fig. 13), the bands are several cells wide and can be termed confluent, as was done by Metcalfe and Chalk (1950) and Meylan and Butterfield (1978). Some of the tangential bands are narrow and often occur in the terminal part of growth rings, as in *Eremophila alternifolia* (Fig. 5) or *E. bignoniflora* (Fig. 7). These bands are not always terminal, however. In addition to the two species just noted, tangential bands of axial parenchyma were observed in *Eremophila longifolia*, *E. polyclada*, *E. scoparia*, and *M. sandwicense* var. *sandwicense*. Axial parenchyma is very scarce in *Oftia africana*.

#### *Rays*

Myoporaceae characteristically have both multiseriate (including biseriate) and uniseriate rays, although multiseriate rays are nearly lacking in *Eremophila alternifolia* (Fig. 5) and *E. oppositifolia*. Multiseriate rays appear to be more common than uniseriate rays in *Bontia daphnoides* (Fig. 2), *Eremophila bignoniflora* (Fig. 8), *E. longifolia*, *Myoporum acuminatum*, *M. montanum*, *M. sandwicense* var. *fauriei*, *M. sandwicense* var. *wilderi*, *M. serratum*, and *M. stokesii*. In all species not named in this paragraph, multiseriate and uniseriate rays are about equally prevalent, as shown for *Myoporum laetum* (Fig. 14) and *M. platycarpum* (Fig. 18). In *Bontia daphnoides*, multiseriate ray portions interconnected by uniseriate portions can be seen (Fig. 2); this condition is not common in other Myoporaceae. Such rays were termed "zusammengesetzt" rays by Metcalfe and Chalk (1983), although that term is confusing, since "zusammengesetzt" can perhaps be most accurately translated as "compound" or "aggregate," yet the rays just described should not be confused with the compound rays of Fagaceae or Casuarinaceae; we suggest the term "interconnected multiseriate rays" for the condition seen in *Bontia daphnoides*.

If multiseriate rays are more common than uniseriate rays in a wood sample of Myoporaceae, the multiseriate rays also tend to be relatively wide (e.g., more triseriate than biseriate rays); thus, the data on ray width in Table 1 are indirectly related to abundance of multiseriate versus uniseriate rays. This is an ontogenetic matter, since rays tend to become wider with age, although not in such species as *Eremophila alternifolia*, where rays remain nearly exclusively uniseriate. Ray heights are also shown in Table 1. Ray heights appear closely related to vessel

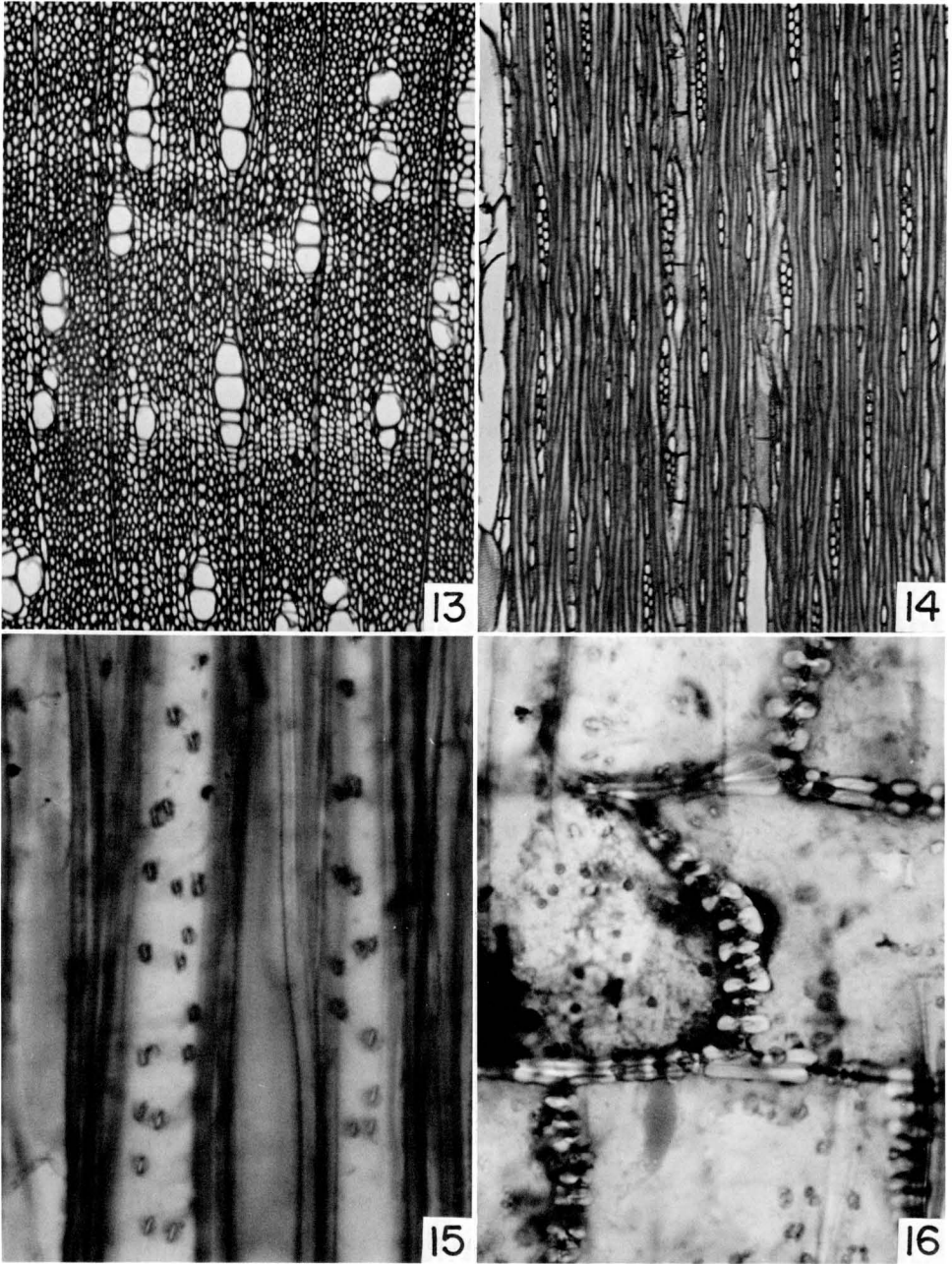


Fig. 13-16. Wood sections of *Myoporum laetum* (SJRW 25470).—13. Transection; two tangential bands of axial parenchyma are present, only slightly different in appearance from the ground mass of fiber-tracheids.—14. Tangential section; multiseriate rays are almost all biseriate.—15. Fiber-tracheids from radial section, showing characteristic sizes and shapes of bordered pits.—16. Ray cells, showing bordered pits in sectional view. (Scale for Fig. 13-14 above Fig. 1; scale for Fig. 15-16 above Fig. 3.)

element length, as was shown statistically for Staphyleaceae (Carlquist and Hoekman 1985). The species of Myoporaceae with the tallest rays, *Myoporum laetum* (568  $\mu\text{m}$ ) does have the longest vessel elements for the family also. This sample probably came from a relatively old stem. The second tallest rays reported here are those of *Oftia africana* (535  $\mu\text{m}$ ) (Fig. 22), which ranks below a number of Myoporaceae in vessel element length; this is worth noting with respect to the relationships of *Oftia*.

Myoporaceae show a predominance of procumbent cells in multiseriate rays. By far the majority of species have multiseriate rays with erect cells only in uniseriate wings; uniseriate rays in these species are composed of upright and square cells, with relatively few procumbent cells. This type of ray histology is seen in Fig. 2, 4, 8, and 18. Exceptions to this pattern can be observed in *Eremophila alternifolia* (Fig. 5), *E. oppositifolia*, and *Myoporum montanum*; in all of these species, uniseriate rays are predominant and are composed mostly of procumbent cells, with square (rarely erect) cells also present. Bordered pits on tangential walls of ray cells in the central portions of multiseriate rays were observed in all Myoporaceae; they are shown here for *Myoporum laetum* (Fig. 16).

### Storied Structure

In *Eremophila bignoniiflora* (Fig. 8), *E. mitchelli*, and *Myoporum platycarpum* (Fig. 18), storied structure is visible in rays, although not in all rays. Fiber-tracheids in these species do not show storying, presumably because fiber-tracheids elongate so much in Myoporaceae (approximately 2.5 times the length of fusiform cambial initials, assuming that vessel elements are the same length as fusiform cambial initials). Storying of rays in other Myoporaceae is absent or only vaguely present (Fig. 2, 6, 14). Storying of some axial parenchyma may be seen in some of the parenchyma cells, although generally only a portion, in the Myoporaceae for which tangential parenchyma bands were observed. One must assume that storied fusiform cambial initials are not uncommon in Myoporaceae.

### Crystals and Other Intracellular Substances

Rhomboidal crystals can be observed in ray cells of several Myoporaceae. They were reported by Metcalfe (1935) for *Eremophila mitchelli*. The presence of these is confirmed, on the basis of the present study. Rhomboidal crystals can be found, one per cell, in occasional ray cells of *E. alternifolia* (Fig. 9). However, ray cells of *E. duttonii* (Fig. 10) commonly contain one crystal per cell as do ray cells of *E. oppositifolia*. These crystals have a characteristically hexagonal shape and show layering, with one or more spaces near the center of many crystals.

Crystals were observed in axial xylem cells of *Eremophila polyclada* (Fig. 11, 12). The cells that contain these crystals are fibriform, but bear no evident pits; walls are thinner than those of fiber-tracheids, but secondary wall materials appear to occlude the cells in the interstices between the crystals; the cells are not chambered or septate. The term "crystal-bearing fiber" is suggested for this unusual mode of occurrence. The crystal-bearing fibers may be considered idioblastic, but they can occur in tangential groupings like the axial parenchyma cells which also occur in *E. polyclada*.

Amorphous deposits, often appearing as resinlike deposits, may be seen in ray

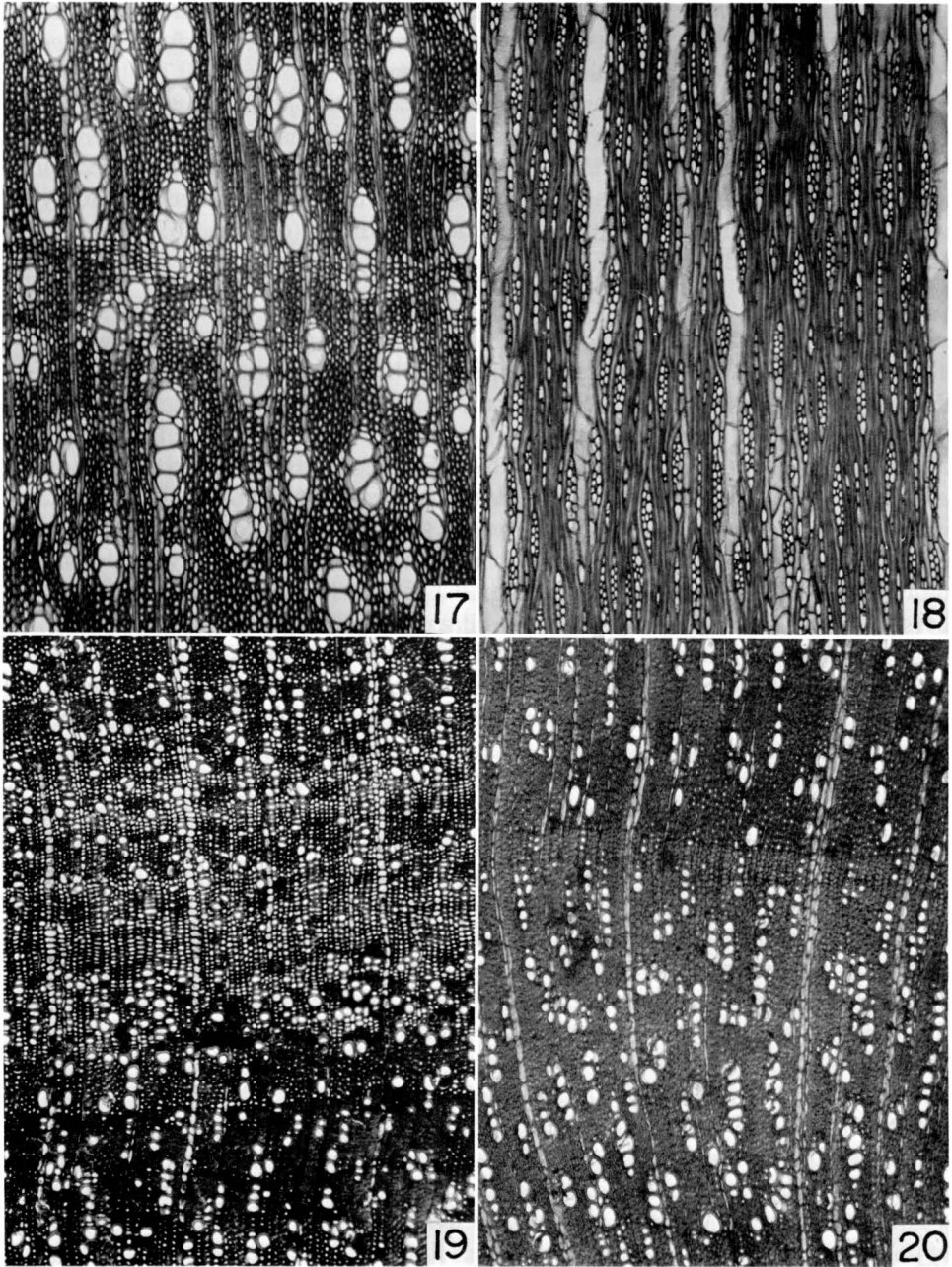


Fig. 17-20. Wood sections of Myoporaceae.—17-18. *Myoporium platycarpum* (SFCw-R 274.1).—17. Transsection; a growth ring terminates just above center of photograph.—18. Tangential section; many of the rays conform to a storied pattern.—19. *Myoporium rapense* (SJRw 24304). Transsection; vessels are narrow, fiber-tracheids fluctuate in wall thickness.—20. *Eremophila latrobei* (Carlquist 5184). Transsection; a growth ring terminates in the upper portion of the photograph. (Scale for Fig. 17-20 above Fig. 1.)

cells and axial parenchyma of *Eremophila longifolia*, *Myoporum acuminatum*, and *M. rapense*. These deposits were reported by Metcalfe (1935) for *Eremophila mitchelli* and may occur in a number of Myoporaceae.

Starch grains were figured in axial parenchyma for *Myoporum laetum* by Meylan and Butterfield (1978). In the present study, starch grains were observed in axial parenchyma and ray cells of *Eremophila alternifolia*, *Myoporum platycarpum*, and *M. stokesii*. Starch grains may be assumed to occur much more widely in woods of Myoporaceae, and microtechnical methods (e.g., use of ethylene diamine) may have destroyed them in some species studied here.

#### ECOLOGICAL CONCLUSIONS

The ratio termed "Mesomorphy" in Table 1 can be viewed as a possible indicator of ecology of Myoporaceae. If calculated for each genus, the figure would be: *Bontia*, 181; *Eremophila*, 53.1; *Myoporum*, 160; *Oftia*, 222. Note should be taken of two species of *Myoporum* with unusually low figures for this ratio, *M. platycarpum* and *M. rapense*. *Myoporum platycarpum* is unusual within its genus in being an Australian desert species (most species can be called predominantly maritime); the low ratio for *M. rapense* is unexpected and may represent an unusual sample. If these two species had been excluded from *Myoporum*, the Mesomorphy figure for the genus would have been 387, more than twice that for *Eremophila*, and indicative of the maritime and interior dryland habitats, respectively, for the two genera. The highest figure within *Myoporum* occurs in *M. sandwicense* var. *fauriei*, from a pocket of rain forest (Kipuka Pualu) near Kilauea, Hawaii. The lowest figures within *Eremophila* occur in *E. latrobei*, from near Norseman, Western Australia, and *E. oppositifolia*, from near Mildura, Victoria. Both of those localities annually experience as great climatic extremes as any habitat where *Eremophila* is found. Although the Mesomorphy ratio figures clearly follow the ecology of the species of Myoporaceae, the figures are not as low as one might expect, especially for *Eremophila*, if one may judge by other groups for which this ratio has been calculated. One can speculate that wood of *Eremophila* and perhaps the other Myoporaceae do not exhibit as great safety in construction as one would expect in habitats of the various species because some other factor, such as the evergreen and semisucculent leaves, may play an important role in water economy of the family.

The number of vessels per group, a feature not incorporated into the Mesomorphy ratio, may be considered as corroborative of the trends that ratio demonstrates. Thus, *Bontia* averages 1.66 vessels per group, but *Eremophila* is appreciably higher, 2.61. However, this range is not so great as in other groups with a comparable ecological span, as can be seen in the figures for Asteraceae (Carlquist 1966). A modifying effect of the evergreen foliage of Myoporaceae may again be hypothesized.

Growth ring presence is also indicative of relative xeromorphy of woods. In Myoporaceae, the range of diffuse porous to semi-ring-porous is not great. Of the seven species of Myoporaceae cited as semi-ring-porous, only two have vessels wider than the mean for the family, showing that semi-ring-porous species do have greater wood xeromorphy, but not by a wide margin.

Helical sculpture has been considered to represent a form of xeromorphy (Weber 1936), but the form of it seen in Myoporaceae (grooves interconnecting pit

apertures) is the least pronounced manifestation of this phenomenon, and it occurs in a minority (eight taxa) of the representatives studied.

Thus, all of the features currently used as indicators of wood xeromorphy are consistent with each other and consistent with the interpretation that woods of Myoporaceae show an ecological range, but do not exhibit as pronounced safety as do woods of other families that occupy similar habitats. Study of foliar apparatus of Myoporaceae with respect to transpirational characteristics would be very desirable.

#### SYSTEMATIC CONCLUSIONS

The woods of Myoporaceae reveal a number of instances in which species characters are demonstrated. The most distinctive of these is represented by the crystal-bearing fibers of *Eremophila polyclada*. This mode of crystal occurrence was observed in no other species of the family. Rhomboidal crystals, one per cell, were seen in some or many of the ray cells of a few species of *Eremophila*: *E. alternifolia*, *E. duttonii*, *E. mitchelli*, and *E. oppositifolia*. The occurrence of tangential bands of axial parenchyma appears limited to some taxa: *Eremophila alternifolia*, *E. bignoniflora*, *E. polyclada*, *E. scoparia*, *E. serrulata*, *Myoporum laetum*, *M. montanum*, *M. platycarpum*, and *M. sandwicense* var. *sandwicense*.

The taxonomic history of *Ofelia* has been traced by Dahlgren and Rao (1971), who decided that *Ofelia* should be included in Scrophulariaceae rather than Myoporaceae. Their decision seems defensible on the basis of the present study. *Ofelia* possesses the following features not observed in Myoporaceae: occasional double perforation plates; relatively large pits on lateral vessel walls; septate libriform fibers (rather than nonseptate fiber-tracheids); very scarce axial parenchyma; and predominance of erect cells in rays. The last-named feature, as well as the moderately tall rays of *Ofelia*, suggests some juvenilism in ray structure (despite the relatively mature nature of the sample studied, a woody stem 2.6 cm in diameter). These ray features reflect a degree of herbaceousness in *Ofelia*, whereas woods of Myoporaceae have rays characteristic of typically woody dicotyledons. Metcalfe and Chalk (1950) report intraxylary phloem in *Ofelia* with some degree of uncertainty; our material does not show any intraxylary phloem, and thus there is as yet no evidence for suggesting inclusion of *Ofelia* in any of the families in which intraxylary phloem characteristically occurs (e.g., Solanaceae). The sum of wood features is compatible with the idea of Dahlgren and Rao (1971) that *Ofelia* should be included in Scrophulariaceae.

As noted in the Introduction, another group of uncertain affinity that may impinge upon Myoporaceae is the tribe Leucophylleae (containing *Eremogeton*, *Faxonanthus*, and *Leucophyllum*) of Scrophulariaceae. Niezgodna and Tomb (1975) demonstrated pollen features that link Leucophylleae with Myoporaceae. We have studied material of two species of *Leucophyllum*, *L. frutescens* (Berl.) I. Johnston (*Carlquist 15913*, RSA) and *L. minus* Gray (*Michener 4394*, RSA). These materials reveal presence in *Leucophyllum* of the following wood features that do not occur in Myoporaceae as far as presently known: vessels with prominent helical thickenings; vascentric tracheids present; imperforate tracheary elements other than the vascentric tracheids with apparently simple pits (and therefore libriform fibers); axial parenchyma scarce at least near the smaller vessels; and erect cells common in rays. The vascentric tracheids are like those of Lamiaceae



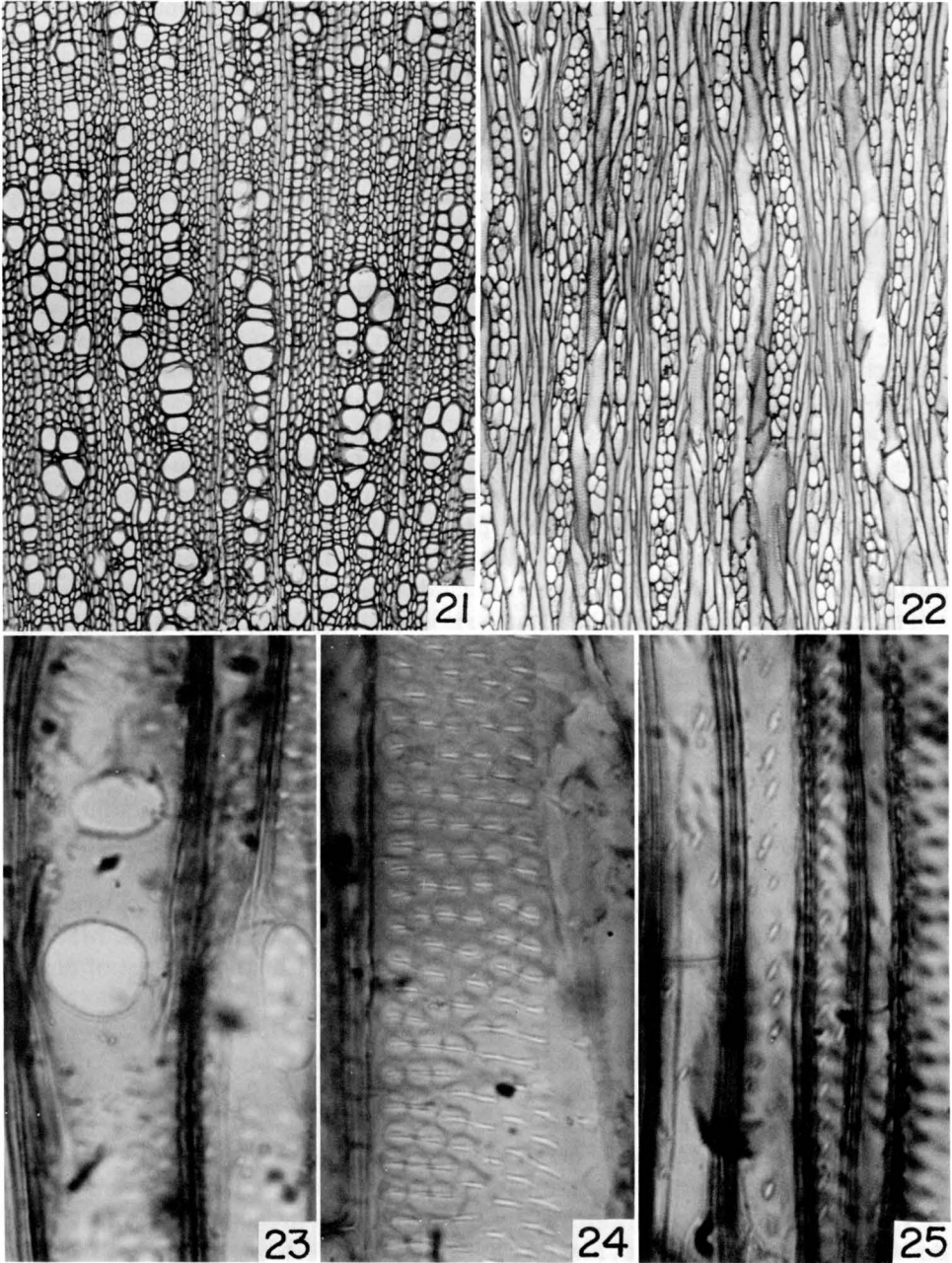


Fig. 21–25. Wood sections of *Ofiia africana* (Carlquist 4032).—21. Transection; vessels in radial multiples.—22. Tangential section; ray cells are relatively large, and erect cells are abundant and scattered throughout the rays.—23–25. Radial sections.—23. Double perforation plate interconnecting a pair of vessel elements.—24. Lateral wall pitting of vessels; grooves interconnect pit apertures, lower right.—25. Libriform fibers (left) and vessel elements; septum in the libriform fiber at left. (Scale for Fig. 21–22 above Fig. 1; scale for Fig. 23–25 above Fig. 3.)

and Verbenaceae, present in latewood but so abundantly that they exceed the typical occurrence of vascular tracheids (last few layers of latewood where no vessels occur), so that they are intermixed with vessels. This mode of occurrence has been regarded as transitional between vascular and vasicentric tracheids, and for purposes of definition has been considered an instance of vasicentric tracheid occurrence because of the key feature of adjacency to vessels (Carlquist 1985). In *Leucophyllum* there are numerous libriform vessel elements intermediate between ordinary vessel elements and vasicentric tracheids. The features by which *Leucophyllum* differs from Myoporaceae on the basis of material thus far studied seem appreciable, and deter one from adding *Leucophyllum* to Myoporaceae at present. These features, however, do not decisively place *Leucophyllum* in a particular family. No occurrence of vasicentric tracheids has as yet been reported in Scrophulariaceae (Carlquist 1985), although the difference between the vascular tracheids of some xeric Scrophulariaceae and the vasicentric tracheids of *Leucophyllum* is not great.

Wood features seem to place Myoporaceae in Scrophulariales (Bignoniales of some authors). Some Scrophulariaceae agree with Myoporaceae in having fiber-tracheids with small bordered pits rather than libriform fibers (Metcalf and Chalk 1950). Fiber-tracheids also occur in one genus of Gesneriaceae, *Coronanthera* (Carlquist and Hoekman 1986), and wood anatomy of Gesneriaceae is compatible with relationship between Gesneriaceae and Scrophulariaceae. In turn, that pair of families shows no feature that would rule out relationship with Myoporaceae. Wood anatomy of Myoporaceae is more specialized than that of those two families in its storied wood structure and lack of any scalariform perforation plates (present in Gesneriaceae and Scrophulariaceae only in metaxylem and early secondary xylem of certain species). There seems no reason to contradict the concept of leading phylogenists (Thorne 1976; Dahlgren 1980; Takhtajan 1980; Cronquist 1981) that Myoporaceae is a member of Scrophulariales. The rays of Myoporaceae seem to indicate a woody ancestry for the family; at least some segments of Gesneriaceae and Scrophulariaceae may have had an herbaceous ancestry (Carlquist and Hoekman 1986).

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