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WOOD ANATOMY OF HYDROPHYLLACEAE. I. *ERIODICTYON*

Sherwin Carlquist, Vincent M. Eckhart, and
David C. Michener

INTRODUCTION

Hydrophyllaceae is a characteristically herbaceous family; only *Eriodictyon* Benth., *Wigandia* H.B.K., and the monotypic *Turricula* Macbr. can be considered woody (stems attaining a diameter of more than 1 cm). Are plants such as these relicts from a woody ancestry, or is the family secondarily woody? The nature of wood anatomy offers some features useful in the attempt to answer this question.

Wood anatomy is also applicable to analysis of the curious growth form of *Eriodictyon*. Unlike most shrubs, *Eriodictyon* is characterized by a well-developed root system from which aerial innovations of various height and duration arise. Such a growth form is ideal for resisting drought and fire in the chaparral and chaparrallike areas where *Eriodictyon* grows. The majority of *Eriodictyon* plants (using that term to denote an aerial stem) in any given locality may ultimately result from root innovations rather than events of seed germination. Indeed, attempts to grow *Eriodictyon* from seed have been unsuccessful (Everett 1957). Because roots are persistent, large, and of ecological significance in the genus, wood of them has been analyzed for three species (Table 1). For two other species, a portion termed underground stem has been studied. In *E. trichocalyx* Heller subsp. *lanatum* (Brand) Munz the underground stem immediately subtending the aboveground stem was collected. In *E. traskiae* Eastw. subsp. *smithii* Munz, the underground stem was similar, but further buried beneath the ground by the fallen rubble of diatomaceous earth typical of its habitat. Shrubs of *Eriodictyon* range in size from a maximum of 4 m in *E. altissimum* P. V. Wells (Wells 1962) or 3 m in *E. crassifolium* Benth. (Munz 1959) to shrubs barely reaching $\frac{1}{4}$ m in some subalpine populations of *E. californicum* (H. & A.) Torr. and *E. trichocalyx* subsp. *trichocalyx*.

Wood anatomy is also worthy of investigation with respect to the ecological range of the genus. *Eriodictyon* is a remarkably characteristic shrub of several regions of California; nine of the 10 species occur in the state. All of the species currently recognized as valid according to recent floras (e.g., Munz 1959, with the addition of *E. altissimum*; Wiggins 1980) are included in the present study, and the two subspecies recognized for two of the species are represented (Table 1). Dubiously distinct varieties of *E. crassifolium* have not been included. *Eriodictyon sessilifolium* Greene is restricted to coastal

regions of northern Baja California, Mexico (Wiggins 1980). Of the nine species indigenous to California, some range into other states. *Eriodictyon angustifolium* Nutt. extends from the eastern Mojave Desert of California to Utah, Arizona, and Baja California (Munz 1959), and could be said to occupy drier and (in summer) hotter sites than do the other species. *Eriodictyon californicum* occurs in the Sierra Nevada and northern Coast Ranges of California, from which it extends into Oregon. *Eriodictyon trichocalyx* subsp. *lanatum* grows both in the southernmost portion of California and in the adjacent parts of Baja California. Only *E. traskiae* subsp. *traskiae* occurs on an offshore island, Santa Catalina Island. None of the habitats occupied by *Eriodictyon* could be said to be mesic. While some of the habitats occupied by the genus have moderated temperatures by virtue of proximity to the seacoast (habitats of *E. altissimum*, *E. capitatum* Eastw., *E. sessilifolium*, and *E. traskiae*), other habitats (those of *E. californicum* and *E. trichocalyx*) experience considerable frost.

Although *Eriodictyon* grows in dry places, the vegetative aspect of most species is not extremely xeromorphic. To be sure, the narrow leaves of *E. angustifolium* suggest adaptation to excessive heat loading of leaf tissue and water loss from transpiration by virtue of adoption of a narrow leaf shape. The leaves of the coastal *E. altissimum* are also notably narrow, however. Because leaves of *Eriodictyon* are not truly microphyllous, they must have mechanisms other than size and shape for minimizing heat loading and water loss. The surface characteristics of indument and varnish, although they may well function primarily against herbivore and insect predation, may have some function in protection from heat and drought. The wood anatomy of *Eriodictyon* may well be an important water-management device, but the nature of the foliage doubtless is important and must ultimately be taken into account.

Woods of Hydrophyllaceae are notable in having tracheids bearing full bordered pits rather than libriform fibers with simple pits (Record and Hess 1943; Metcalfe and Chalk 1950). Some other tubiflorous families of dicotyledons have such tracheary elements, notably Convolvulaceae (Metcalfe and Chalk 1950), Dipsacaceae (Carlquist 1982) and Goodeniaceae (Carlquist 1969). However, this allegedly primitive feature is not common in the tubiflorous families of dicotyledons. Do Hydrophyllaceae have other primitive wood features? Wood anatomy is potentially of interest in assessing phylogenetic position, degree of specialization, and shift to or from woody habit in Hydrophyllaceae.

MATERIAL AND METHODS

The taxa studied and the specimens documenting them are shown in Table 1. Portions of wood from the plant parts indicated in column 1 were mostly

Table 1. Wood characteristics of *Eriodictyon*.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>E. altissimum</i> P. V. Wells	<i>D. Dingus XI-24-1982</i>	SS	33	119	420	1.40	1.8	25	662	3.5	2.2	181	92	VD	0.28	116
		SM	35	178	365	1.36	1.8	25	620	3.5	2.1	231	159	VD	0.20	72
		SL	50	127	386	1.07	2.1	21	638	4.0	2.2	234	126	VD	0.39	152
<i>E. angustifolium</i> Nutt.	<i>D.C. Michener 3945</i>	R	90	36	410	1.05	1.5	30	880	2.0	3.9	410	120	IC	2.53	1037
		S	60	137	360	1.32	2.0	24	740	2.5	3.0	330	100	X	0.44	158
<i>E. californicum</i> (H.&A.) Torr.	<i>D.C. Michener 4018</i>	S	48	208	430	1.45	2.0	20	620	2.5	2.3	280	120	VD	0.23	99
<i>E. capitatum</i> Eastw.	<i>G. Hannan 299</i>	R	120	26	460	1.05	2.7	26	910	3.0	4.2	360	170	ID	4.60	2131
		S	48	118	390	1.10	2.2	21	730	2.4	2.1	240	110	X	0.41	158
<i>E. crassifolium</i> Benth.	<i>S. Carlquist 15646</i>	S	38	209	610	1.15	2.1	18	870	2.6	2.6	340	130	VD	0.18	111
<i>E. sessilifolium</i> Greene	<i>L. Shultz 6034</i>	S	40	93	460	1.20	2.0	15	910	2.1	2.7	310	130	IB	0.43	197
<i>E. tomentosum</i> Benth.	<i>D.C. Michener 4035</i>	S	50	199	360	1.12	2.1	18	560	2.4	2.5	400	140	VD	0.25	90
<i>E. traskiae</i> Eastw. subsp. <i>smithii</i> Munz	<i>S. Carlquist 7389</i>	US	63	55	335	1.45	2.3	23	655	3.7	3.9	275	97	X	1.15	384
		S	45	134	427	1.16	1.4	23	642	2.3	2.4	229	141	X	0.33	142
<i>E. traskiae</i> Eastw. subsp. <i>traskiae</i>	<i>S. Carlquist 1827</i>	S	45	152	330	1.12	2.1	20	660	2.6	2.4	200	99	VD	0.29	97
<i>E. trichocalyx</i> Heller subsp. <i>lanatum</i> (Brand) Munz	<i>D.C. Michener 3982</i>	US	83	69	290	1.35	2.1	22	760	3.0	3.7	370	88	VD	1.20	349
		S	57	232	350	1.15	2.2	19	660	2.7	2.4	350	100	VD	0.25	86
<i>E. trichocalyx</i> Heller subsp. <i>trichocalyx</i>	<i>S. Carlquist 15649</i>	S	45	201	240	1.25	1.7	15	620	2.3	2.7	230	90	X	0.22	54
	<i>S. Carlquist 15650</i>	R	82	39	375	1.45	1.8	28	627	3.4	4.6	735	226	ID	2.10	788
	<i>S. Carlquist 15651a</i>	S	40	241	360	1.40	2.0	16	690	3.0	2.1	380	140	VD	0.17	60
		S	40	412	340	1.36	1.6	16	550	2.2	4.0	330	120	VD	0.10	33

Legend for numbered columns: 1, plant portion (R = root, S = stem of maximal diameter near base of plant, SS = stem of small plant in unfavorable locality, SM = stem of medium-sized plant in intermediate locality, SL = stem of large-sized plant in favorable locality, US = underground stem). 2, mean vessel diameter, μm . 3, mean number of vessels per mm^2 . 4, mean vessel-element length, μm . 5, mean number of vessels per group. 6, mean vessel wall thickness, μm . 7, mean tracheid diameter at widest point, μm . 8, mean tracheid length, μm . 9, mean tracheid wall thickness, μm . 10, mean width of multiseriate rays at widest point, cells. 11, mean height multiseriate rays, μm . 12, mean height uniseriate rays, μm . 13, Growth-ring type according to scheme of Carlquist (1980). 14, Index "Vulnerability" (Carlquist 1977). 15, Index "Mesomorphy" (Carlquist 1977).

preserved in 50% ethyl alcohol. The use of pickled wood specimens revealed few details not also visible in dried woods other than presence of nuclei in axial and ray parenchyma. Woods were sectioned on a sliding microtome. In a few, hardness made use of Kukachka's (1977) ethylenediamine softening method desirable. Sections were stained in a safranin series, as were macerations, which were prepared with Jeffrey's Fluid. Quantitative data in Table 1 are based on 25 measurements for each feature.

The majority of sections and data were prepared by Vincent M. Eckhart. Dr. David C. Michener contributed wood of four of the taxa, as shown in Table 1. Dr. Leila Schultz kindly collected the material of *E. sessilifolium*. Two of the species are in localities of limited access. Of these, Dr. Gary Hannan provided material of *E. capitatum*, while Dr. D. D. Dingus of California State Polytechnic University at San Luis Obispo kindly collected stems of *E. altissimum*. He collected three stems of *E. altissimum* (see Table 1, column 1). These stems were 1.5, 3.2, and 4.3 cm in diameter, respectively. These correspond to sites judged by Dr. Dingus to be dry, less dry, and moderately moist, respectively. No herbarium specimens were preserved for the collection of *E. altissimum*. Herbarium specimens documenting the other taxa of *Eriodictyon* are located in the herbarium of Rancho Santa Ana Botanic Garden, with the exception of *E. capitatum*, the specimen of which is located at University of California, Santa Barbara.

ANATOMICAL DESCRIPTIONS

Growth rings.—The types of growth rings found in *Eriodictyon* are listed in Table 1. The types are not, of course, sharply demarcated from each other and intergradation among them is to be expected. Minimal growth ring activity is shown by *E. sessilifolium* (Fig. 9), in which earlywood vessels are a little wider than vessels in latewood (Type IB), although not greatly so. In certain taxa of *Eriodictyon*, growth rings are not strongly demarcated, but tracheids as well as vessels are wider in earlywood than in latewood (Type ID: *E. capitatum* roots, Fig. 13). If growth rings are sharply delimited, with wider vessels and wider tracheids in earlywood, Type VD is said to exist (most *Eriodictyon* collections: e.g., *E. altissimum*, Fig. 5; *E. traskiae* subsp. *traskiae*, Fig. 15). In a few, parenchyma tends to substitute for tracheids in earlywood, and thus Type IC can be said to be present (e.g., *E. angustifolium* roots, Fig. 2, 3). There is in some collections a conspicuous tendency for vessels not to be largest in the earliest-formed earlywood, but to increase after the beginning of the growth ring. Designated Type X (Carlquist 1980), such growth rings are shown here for stems of *E. angustifolium* (Fig. 1) and, less conspicuously, stems of *E. capitatum* (Fig. 11). When a Type X growth ring occurs, one presumes that the cambium becomes active before the period of maximal water flow begins. Thus, smaller vessels would be produced as

the wet winter months begin, but larger vessels would follow during the wet, but warmer, spring months. This presumption was confirmed chronologically in the stems of *E. traskiae* subsp. *smithii*, collected on December 22, 1982, after appreciable winter rainfall had already occurred, and some earlywood containing smaller vessels had been produced at the periphery of the stem.

Vessel elements.—Vessels are round in shape as seen in transection (Fig. 1, 2, 3, 5, 9, 11, 13, 15), compressed when in contact with other vessels but never truly angular. Record and Hess (1943) claim that vessels in Hydrophyllaceae are solitary (their descriptions based on *Eriodictyon* plus *Wigandia*). Although vessels are very nearly solitary in *Wigandia*, various degrees of grouping are exhibited by *Eriodictyon* (Table 1, column 5). Figures below 1.20 for this feature certainly indicate a predominance of solitary vessels, but half of the collections lie above this value. The larger number of vessels per group tend to occur in the species from drier and colder areas: *E. altissimum*, *E. angustifolium*, *E. californicum*, and *E. trichocalyx*. One could say, however, that more numerous vessels per group is an inevitable byproduct of having more numerous vessels per mm² of transection. That correlation is generally close, and one notes from comparing columns 3 and 5 in Table 1 that roots tend to have both few vessels per mm² and few vessels per group compared to stems. The correlation between vessels per mm² and vessels per group is not entirely linear, however; if it were, there would be no value in presenting both measurements. Of the two measurements, vessels per mm² is probably more significant, because it is a direct expression of the indicator of redundancy (or lack of it) in the conductive system. Although some groups, such as Asteraceae (Carlquist 1966) show increased numbers of vessels per group with increasing xeromorphy, some families of dicotyledons show little or no such elevation in these values.

Mean vessel-element diameters (Table 1, column 2) in *Eriodictyon* are typical of xeromorphic woods in the case of stems, but the wider vessel elements in roots are clearly mesomorphic by comparison. Such side-by-side comparisons of stems and roots are offered for *E. angustifolium* (Fig. 1, 2) and *E. capitatum* (Fig. 11, 13). The taxa with wider vessels tend to have fewer per mm², within limits.

The length of vessel elements in *Eriodictyon* (Table 1, column 4) is below the median for dicotyledons as a whole (cf. Metcalfe and Chalk 1950, p. xxiv). The average vessel-element length for the 20 collections of *Eriodictyon* is 385 μ m. This is certainly moderately xeromorphic, but longer than the average vessel-element length for Asteraceae as a whole, 235 μ m (Carlquist 1966).

Vessel walls (Table 1, column 6) are uniformly thinner than tracheid walls (column 9) in *Eriodictyon*.

Fibriform vessel elements.—*Eriodictyon* wood as seen in transection il-

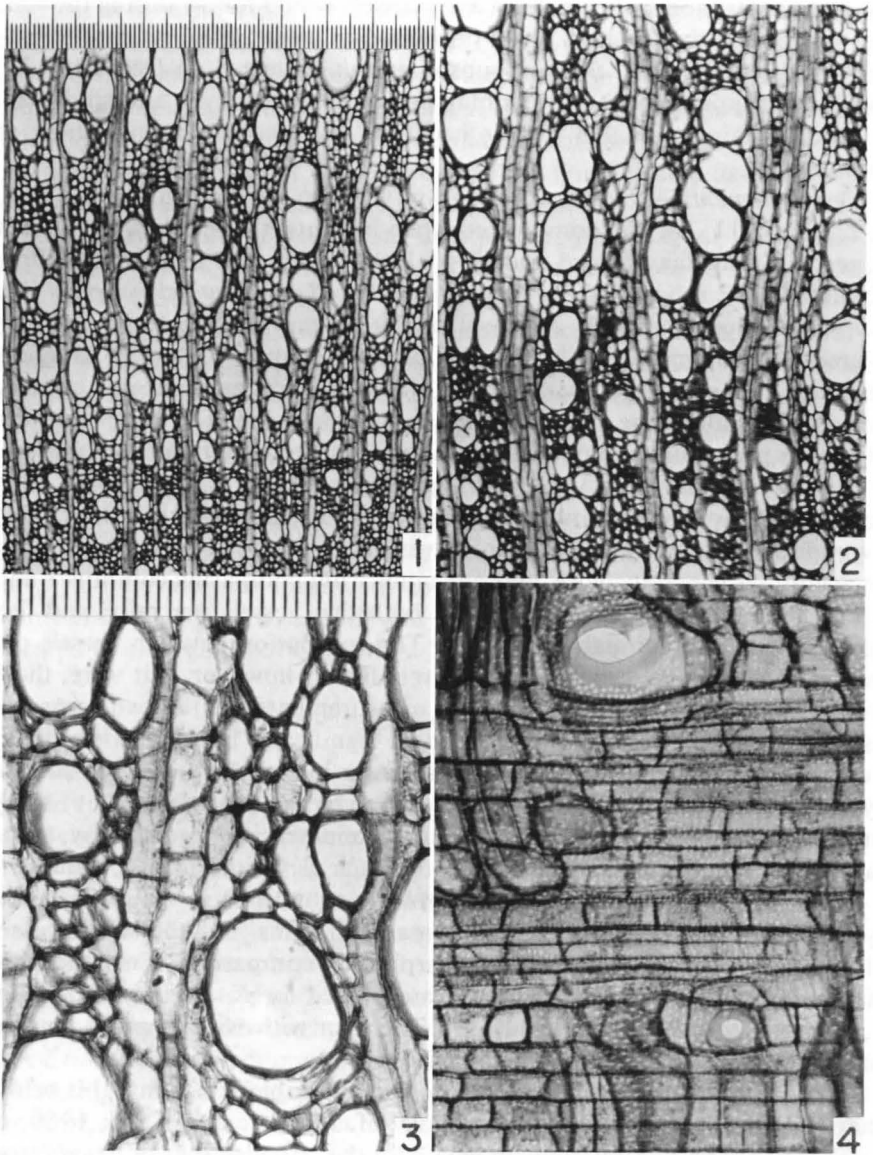


Fig. 1-4. Wood sections of *Eriodictyon angustifolium* (Michener 3945).—1. Transection of stem, showing sharply demarcated growth ring; end of latewood near bottom.—2. Transection of root; growth ring not sharp, but markedly larger earlywood vessels in upper part of photograph.—3. Transection of root, showing abundance of axial parenchyma in earlywood.—4. Radial section of stem, showing procumbent ray cells and two perforate ray cells. (Fig. 1, 2, magnification scale above Fig. 1 [finest divisions = 10 μ m]; Fig. 3, 4, magnification scale above Fig. 3 [divisions = 10 μ m].)

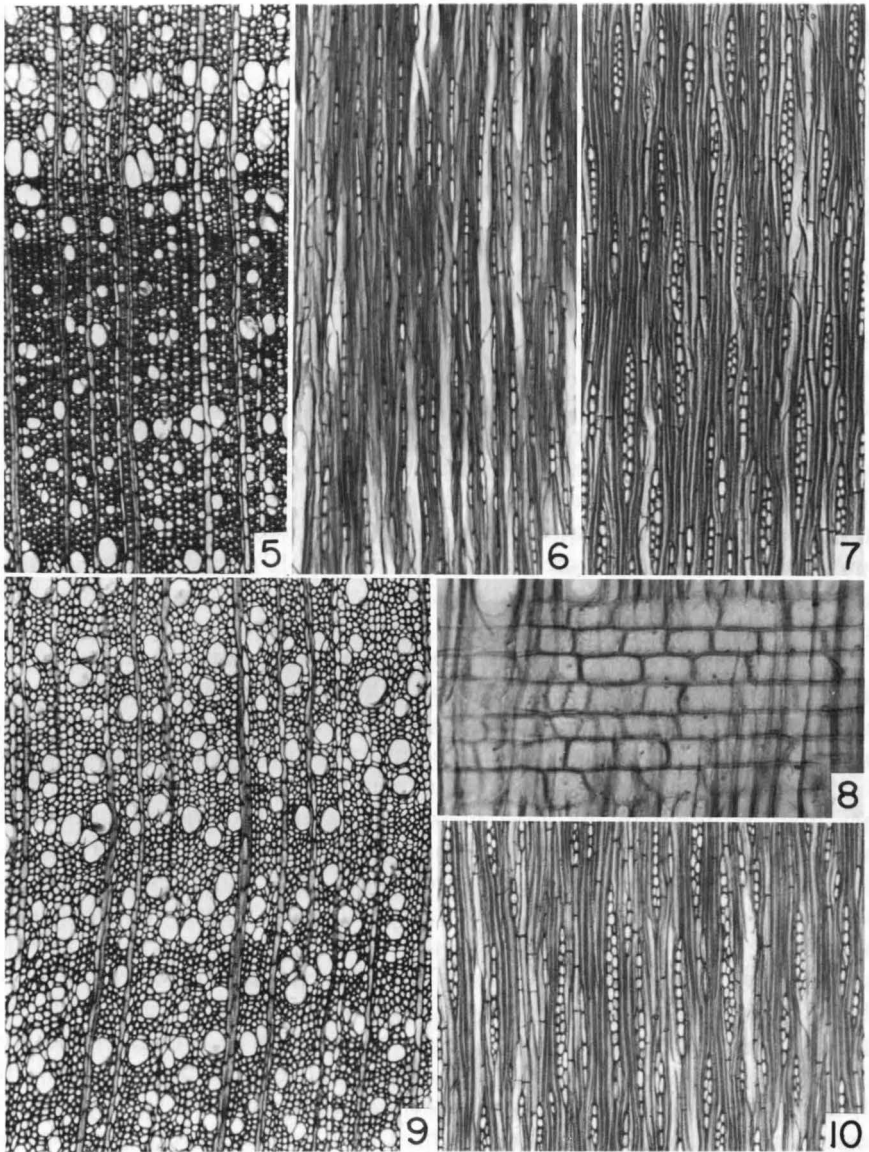


Fig. 5-10. Wood sections of *Eriodictyon*.—5-8. *E. altissimum* (Dingus XI-24-1982), large stem.—5. Transection, showing moderate differentiation between latewood (lower two thirds of figure) and earlywood, above.—6. Tangential section near center of stem; rays are exclusively uniseriate.—7. Tangential section from periphery of stem; multiseriate rays evident.—8. Radial section; all cells in photograph are procumbent ray cells.—9-10. *E. sessilifolium* (Schultz 6034).—9. Transection; growth ring activity virtually absent.—10. Tangential section; multiseriate rays are narrow. (Fig. 5-7, 9, 10, scale above Fig. 1; Fig. 8, scale above Fig. 3.)

lustrates a range of vessel diameter, so that vessels are difficult to differentiate from parenchyma cells (which have wall thickness approximately the same). In a maceration of *Eriodictyon* wood one sees some narrow vessels also. These are fusiform in shape, and the perforation plates are lateral rather than terminal thereby. In length, these narrower vessel elements, which I am terming fibriform here, tend to be longer than the wide vessel elements. That may, in part, account for the fact that mean vessel element length in Hydrophyllaceae is appreciably greater than that of Asteraceae. This greater length for fibriform vessel elements may, in developmental terms, be the product of greater intrusiveness of tips during maturation as compared with wider vessel elements. The vessel-element length of Hydrophyllaceae, however, may at least in part represent a lower degree of phylogenetic specialization than Asteraceae represents.

As seen in radial sections (Fig. 17–19), fibriform vessel elements can be seen to have very small perforation plates. Indeed, some of these plates have wide borders and look much like exceptionally wide bordered pits, such as the bordered pits seen on lateral walls of vessels. Some of the fibriform vessel elements have more than one perforation (Fig. 18, 19). Study of such double perforation plates reveals that most of these do not relate to branching of a vessel, but interconnect only a pair of vessel elements.

The fibriform vessel elements of *Eriodictyon* might at first glance be regarded as similar to vascular tracheids, although perforated. This interpretation is rejected, and the following reasons are advanced for regarding the fusiform vessel elements as quite different from vascular tracheids. (1) The fibriform vessel elements do not occur merely at the end of growth rings; they may be found in the most mesomorphic of the *Eriodictyon* woods, those of roots, where they can be found in association with wider vessels. (2) The fibriform vessel elements are longer than wide vessel elements, whereas in most instances vascular tracheid lengths agree with the lengths in any given wood sample. (3) Thus far all known instances of vascular tracheids are reported from woods of great specialization, where libriform fibers are the imperforate element type. If *Eriodictyon* had vascular tracheids, therefore, one would also expect libriform fibers to be present; none are. The only wood reported in which vascular tracheids do not coexist with libriform fibers is that of *Loricaria thuyoides* (Carlquist 1961), in which all vessels are narrow at most, and in which narrow vessels and vascular tracheids are so abundant that no mechanical cell type is present and thereby a remarkable gymnospermlike condition occurs. (4) The selective value of a vascular tracheid lies in its ability to confine an air embolism within a single conductive cell, so that air embolisms do not spread to other cells. True tracheids have the same selective value. Therefore, one cannot imagine any reason why a plant which already has tracheids as the imperforate tracheary element type should evolve vascular tracheids. In order to have

the advantage of tracheids under water stress conditions, a tracheid-bearing plant merely could produce tracheids only in the later portions of a growth ring. In fact, there are various woods (*Ephedra*; Bruniaceae) in which this happens, and vessels are absent from the latter part of a growth ring.

Fusiform vessel elements are more common in *Eriodictyon* than in *Wigandia*, and presumably relate to the selective value of narrower vessel elements, more numerous per unit transection, in a plant or plant organ adapted to a highly seasonal climate.

Tracheids.—Hydrophyllaceae are claimed by Record and Hess (1943) and Metcalfe and Chalk (1950) to have tracheids ("fibres with bordered pits") rather than fiber-tracheids or libriform fibers. This is confirmed by the present study (Fig. 16). While Hydrophyllaceae are unusual in this regard among tubiflorous families, one can cite Convolvulaceae (Metcalfe and Chalk 1950), Dipsacaceae (Carlquist 1982) and Goodeniaceae (Carlquist 1969) as families in which tracheids are the imperforate element type. Chloanthaceae (Carlquist 1981) is a tubiflorous family in which fiber-tracheids occur. Vestigial borders on pits of imperforate tracheary elements have been reported so far only in a scattering of species in the families Bignoniaceae, Boraginaceae, Loganiaceae, Polemoniaceae, Scrophulariaceae, Solanaceae, and Verbenaceae. Presence of tracheids in a wood is statistically correlated with other primitive features (Metcalfe and Chalk 1950, p. xlv) in dicotyledons as a whole, and it may be regarded as one of several relictual primitive features in Hydrophyllaceae. Tracheids can be claimed to have a strong selective value in the ecological regimes where *Eriodictyon* exists, however, as mentioned below.

Axial parenchyma.—Record and Hess (1943) described the axial parenchyma of Hydrophyllaceae as having a diffuse distribution, with a tendency toward reticulate patterning, of these cells as seen in transection. That can be confirmed on the basis of the present materials, among which those patterns appear most clearly in Fig. 15. In some collections, such as the roots of *E. angustifolium* (Fig. 2, 3), early portions of growth rings feature more abundant axial parenchyma, so that apotracheal bands of parenchyma could be said to be present. Roots have parenchyma more abundantly than do stems in *Eriodictyon*. Axial parenchyma comprises less than a fourth of the axial tissue shown in the stem tangential sections of Fig. 6, 7, 10, and 12, but it comprises more than a third of the cells in the root tangential section shown as Fig. 14. Axial parenchyma is formed as strands of four to six cells in *Eriodictyon*.

Vascular rays.—Ray cells are predominantly procumbent in multiseriate rays of *Eriodictyon* (Fig. 4, 8). Uniseriate wings are infrequent on multiseriate rays (Fig. 7, 10, 12). Most frequently, the upper and lower tips of multiseriate rays consist of a single cell as seen in tangential section; such cells are most commonly square or procumbent, sometimes erect. Erect cells do not sheathe

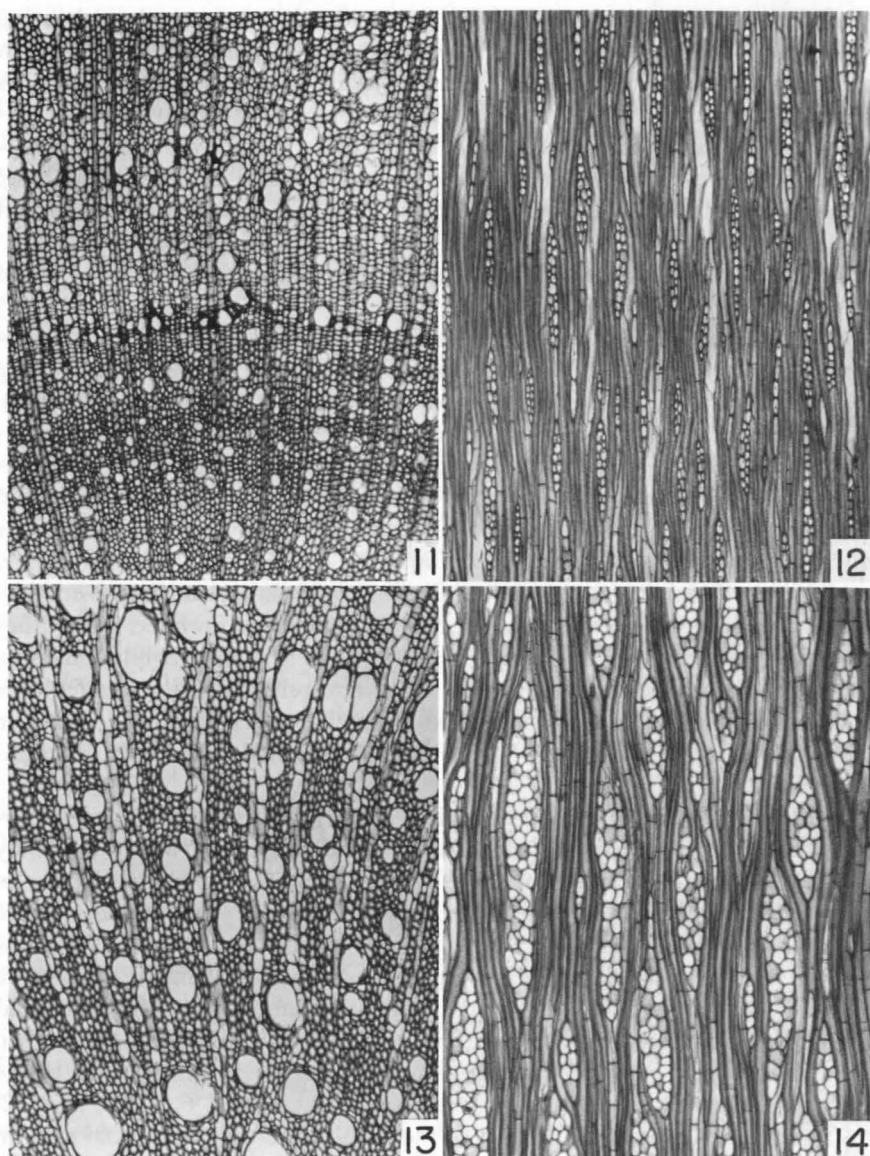


Fig. 11-14. Wood sections of *Eriodictyon capitatum* (Hannan 299).—11-12. Sections of stem.—11. Transection; growth ring not sharply demarcated, vessels small.—12. Tangential section; rays relatively narrow, short.—13-14. Sections of root.—13. Transection; growth ring poorly demarcated, vessels wide.—14. Tangential section; rays tall, wide, large-celled. (Fig. 11-14, magnification scale above Fig. 1.)

multiseriate portions of multiseriate rays in the genus. Uniseriate rays may be composed, in any given section, wholly of erect cells or wholly of procumbent cells or of both cell types. Rays in *Eriodictyon* correspond to Kribs's (1935) Heterogeneous Type IIB except for the marked procumbence of cells in the multiseriate rays and the lack of sheathing erect cells on the multiseriate portions of multiseriate rays.

At earlier stages in ontogeny of rays (nearer the pith), erect cells are more frequent, although not dramatically. However, multiseriate rays are lacking near the pith in *Eriodictyon*, as shown in *E. altissimum* (Fig. 6). Multiseriate rays are initiated by radial longitudinal subdivision of ray initials. Such ontogeny can be found in a scattering of dicotyledons, and is not a clue to relationships of Hydrophyllaceae. In the experience of the senior author, origin of rays ontogenetically as uniseriate rays exclusively is much less common in herbaceous groups than in woody ones.

Multiseriate rays in stems of *Eriodictyon* are characteristically narrow, mostly averaging less than three cells wide (Fig. 7, 10, 12). Multiseriate rays of roots appear to be much larger than those of stems as seen in tangential section. This proves to be true in three respects: size of cells (e.g., compare Figs. 12 and 14); average number of cells wide at widest point (Table 1, column 10); and average height (Table 1, column 11). The mean height of uniseriate rays in *Eriodictyon* is not well correlated with height of multiseriate rays for any particular sample. The greater size of multiseriate rays in roots as compared to stems can be considered related to water storage. Although all of the samples of root wood and many of stem wood in the present study were pickled, storage of starch was noted (as numerous small grains) only in stem rays of *E. angustifolium*.

Perforate ray cells, shown for *E. angustifolium* in Fig. 4, were observed in most of the samples of *Eriodictyon* wood. These cells may be related to breakup of rays during increase in diameter of the stem or root.

Other features.—No storying was observed in wood of *Eriodictyon*. Deposits of resinlike compounds were seen infrequently (center of Fig. 11; parenchyma cells of Fig. 15). However, such deposits are probably not characteristic of particular taxa, and may at least in some cases represent a trauma response.

ECOLOGICAL SUMMARY OF WOOD ANATOMY

Eriodictyon wood seems strongly adapted to dry habitats, based on criteria developed earlier (Carlquist 1975). *Eriodictyon* wood has simple perforation plates, which permit rapid flow of water at times of high transpiration and water availability. However, tracheids, which prevent the spread of air embolism during episodes of water stress, are the imperforate tracheary element type. Thus one can add *Eriodictyon* to the list of desert and dry habitat

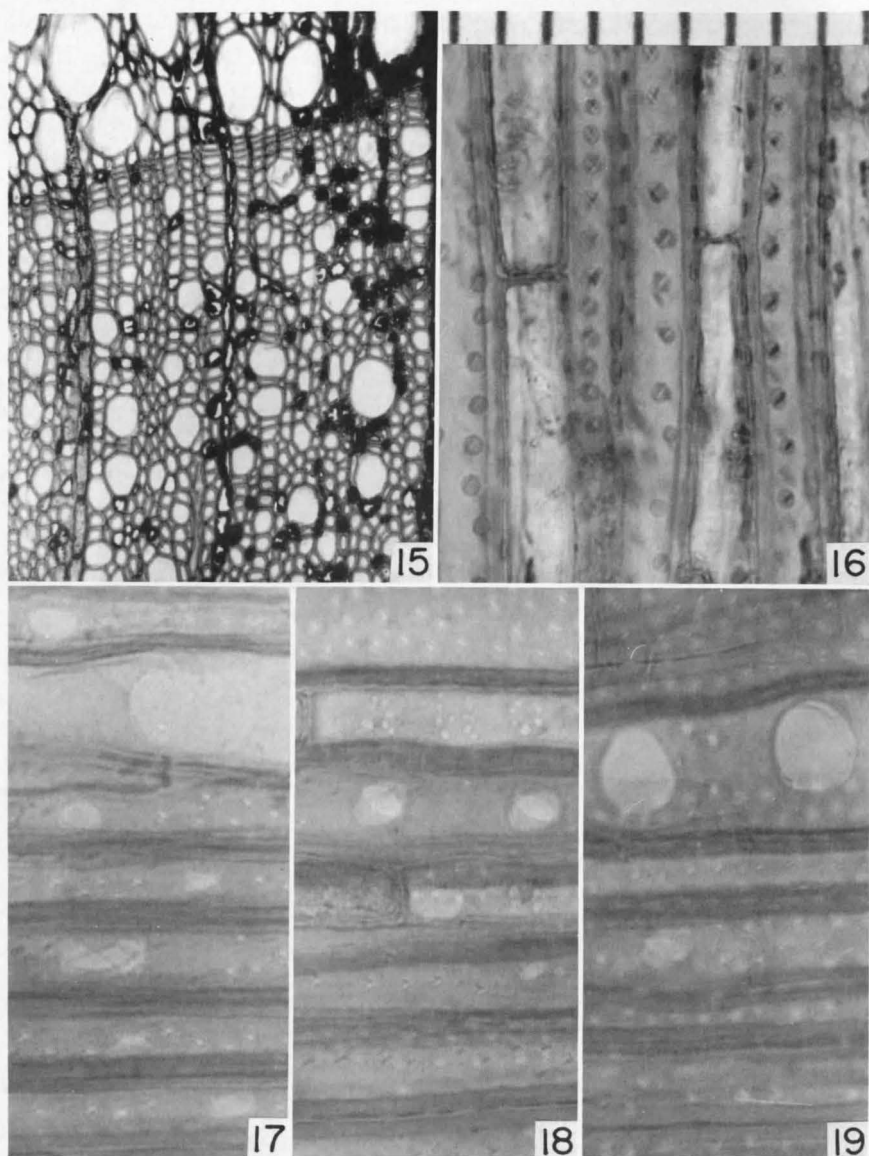


Fig. 15–19. Wood sections of *Eriodictyon*.—15. Transection of *E. traskiae* subsp. *traskiae* (Carlquist 1827) stem; resinlike deposits occur in parenchyma cells.—16. Radial section of *E. trichocalyx* root (Carlquist 15650); pits on tracheid walls are fully bordered.—17–19. Portions of radial section of *E. crassifolium* stem (Carlquist 15656).—17. A series of small perforation plates, mostly in very narrow (fibriform) vessels.—18. Vessel with a pair of pitlike perforations on end wall, above; a smaller perforation below center.—19. Vessel with two perforations on end wall above; a second pitlike perforation below. (Fig. 15, magnification scale above Fig. 3; Fig. 16–19, scale above Fig. 16 [divisions = 10 μ m].)

Californian shrubs with tracheids as the imperforate tracheary element type, a list which includes *Adenostoma*, *Cercocarpus*, *Crossosoma*, *Ephedra*, *Fal-lugia*, *Forsellesia*, *Krameria*, *Larrea*, *Mortonia*, and *Purshia* (Carlquist 1980). Functionally similar are those woods of this region which have libriform fibers as the imperforate tracheary element type but which produce vascular tracheids at the end of a season; the list of these includes *Arctostaphylos* and *Artemisia* (Carlquist 1980) as well as *Keckiella* (Michener 1981).

Another striking adaptation by *Eriodictyon* to dry conditions is found in the divergence between root and stem in wood features. The xeromorphic features of stem woods include narrowness of vessels (notably the fibriform vessel elements), high number of per mm^2 of transection, and possession of growth rings with wider vessels at the beginning (Type VD) or after the beginning (Type X) of the growth ring but narrow vessels elsewhere in the growth ring. The indices for vessel features termed Vulnerability and Mesomorphy have been calculated according to the formula advanced earlier (Carlquist 1977) and presented in Table 1, columns 14 and 15. Stems of *Eriodictyon* have Vulnerability and Mesomorphy index values in the ranges found in dryland plants. If figures given for an assemblage of desert shrubs given by Carlquist (1975, p. 206) were translated into the indices, V would be 0.08 and M would be 17.9. That *Eriodictyon* stems lie in the range from $V = 0.10$ and 0.45 and $M = 33$ to 197 makes them somewhat higher than the average of desert shrubs in these indices, but in a close order of magnitude.

That *Eriodictyon* stem wood is xeromorphic but not extremely so may be explained on the basis of the compensatory effect of roots as succulent storage and shoot innovation organs; possibly foliar characteristics have a mediating effect as well. If shoots can die back to roots in severe conditions, then obviously the role of wood anatomy in water management by stems is moderated. Compared to stems, roots have much more axial parenchyma; rays are taller in dimensions, wider in cell number, and are composed of much larger cells. Roots have wider vessels, fewer per mm^2 compared to those of stems. Because *Eriodictyon* roots have some succulent characteristics, we may compare their wood to that of an assemblage of succulents (Carlquist 1975, p. 206). These succulents have the values $V = 1.12$, $M = 290$. *Eriodictyon* roots have even higher values. Figures for roots from Table 1 are $V = 2.53$, 4.60 , and 2.10 ; $M = 1037$, 2131 , and 788 for the roots studied, respectively. Roots of *Eriodictyon* do not appear succulent in gross aspect to the extent tubers would, but their texture and hardness is different from what one finds in stems. Perhaps the higher figures in *Eriodictyon* roots may be related to the fact that these are underground succulent organs, whereas the figures based on an assemblage of succulents were derived from stems.

Pickled material was available for all roots of *Eriodictyon* studied; this

did not reveal appreciable quantities of starch. For the present, therefore, roots of *Eriodictyon* qualify primarily as water-storage rather than photosynthate-storage organs.

Underground stems, as mentioned earlier, were studied for two species of *Eriodictyon*. Vulnerability and Mesomorphy values for these prove to be between intermediate between stem and root values, not surprisingly.

If species of *Eriodictyon* are compared with each other, some differences in wood anatomy related to habitat appear. Using only stems as the means of comparison, growth rings tend to be absent (*E. sessilifolium*) or less marked (*E. capitatum*, *E. traskiae* subsp. *smithii*) in taxa of southerly and coastal localities. Inland and montane taxa have sharply demarcated growth rings (most notably *E. angustifolium*, *E. californicum*, *E. trichocalyx*). In any given species, roots have much less marked growth rings than do stems.

Marked fluctuations in humidity and temperature may relate to the xeromorphic woods found in *E. californicum* (Sierra Nevada) and *E. trichocalyx* (mountains and valleys of southern California). Elevational differences are apparent, although not statistically significant, in the *E. trichocalyx* plants studied. The *E. trichocalyx* subsp. *trichocalyx* collections *Carlquist 15649* and *15651a* are from elevations in the San Gabriel Mountains (near Claremont) where snow occurs, and these have lower mesomorphy values than does *Carlquist 15650*, from Claremont (elevation ca. 400 m) where snow in winter is virtually unknown.

The number of vessels per group is elevated in the collections of *Eriodictyon* from more extreme localities, but this is very likely an expression of the greater number of vessels per mm² in these woods. The occurrence of fibriform vessels, present throughout the genus, deserves mention. Such narrow vessels, some indistinguishable from tracheids in transection, undoubtedly confer a degree of redundancy (and therefore safety under water stress conditions when a proportion of vessels may be disabled).

PHYLOGENETIC SUMMARY OF WOOD ANATOMY

Wood of Hydrophyllaceae is specialized with respect to wood anatomy, as one might expect in a tubiflorous family of dicotyledons. However, wood of Hydrophyllaceae is less specialized than that of most of those families in the following features: tracheids rather than libriform fibers or fiber-tracheids are present as the imperforate tracheary element type; axial parenchyma is diffuse rather than vasicentric or otherwise grouped; rays are Heterogeneous Type IIB rather than homogeneous (but specialized beyond typical IIB in predominance of erect cells and lack of erect sheathing cells on multiseriate portions of multiseriate rays).

The ratio in length between imperforate tracheary elements and vessel elements can be regarded as an index of phylogenetic specialization in di-

cotyledons, within limits (Carlquist 1975). From the data in Table 1, one can easily calculate such ratios. In *Eriodictyon* they range from a low of 1.43 (*E. crassifolium*) to 2.62 (*E. trichocalyx* subsp. *lanatum* underground stem). The mean ratio of tracheid length to vessel-element length for the 20 collections of *Eriodictyon* is 1.86. This is moderately, but not highly specialized.

Wood anatomy does have some evidence to offer concerning whether a group is ancestrally herbaceous or woody. Predominance of erect ray cells is conspicuous in groups which seem ancestrally herbaceous (Carlquist 1962). If this is true, *Eriodictyon* bears no traces of herbaceous ancestry, since cells of multiseriate rays are predominantly procumbent, even at or near the outset of secondary growth. A second pertinent feature is the occurrence of uniseriate rays exclusively near the pith in *Eriodictyon*. During increase in stem diameter, multiseriate rays develop from these by radial longitudinal division of ray initial cells. This phenomenon happens to occur in woody plants typically: one can cite such groups as *Bursera* (Barghoorn 1941), *Illicium*, and *Sarcococca*. Genera other than *Eriodictyon*, which will be covered in a forthcoming paper, will be important in assessing this and other criteria for whether Hydrophyllaceae are primitively herbaceous or woody.

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