

## Wood Anatomy of *Dubautia* (Asteraceae: Madiinae) in Relation to Adaptive Radiation<sup>1</sup>

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**ABSTRACT:** Qualitative and quantitative features are reported for stem wood of 13 collections of 12 species of the Hawaiian genus *Dubautia*. Although the species share a basic wood plan, quantitative expressions range widely, especially with respect to vessel element dimensions, vessel density, vessel grouping, length of libriform fibers, and dimensions of multiseriate rays. Ecology and habit explain most of the diversity. Variations in the ratio between vessel element length and libriform fiber length are correlated with habit both within *Dubautia* and when *Dubautia* is compared with *Argyroxiphium* and *Wilkesia*. Other variation in wood is related mostly to ecology. The *Dubautia* species of wet forest have high mesomorphy ratio values. Low mesomorphy ratio values occur in species of recent or dry lava (e.g., *D. scabra*) or dry alpine areas (*D. menziesii*); mesomorphy ratio values in the xeric species are comparable with those in *Argyroxiphium*. Highly xeromorphic wood in the bog species *D. waialealae* may reflect recent immigration from a dry habitat or peculiar features of the bog habitat. The lianoid *D. latifolia* has notably xeromorphic wood, which may reflect recent entry into wet forest or else the tendency for lianas in general to have xeromorphic features that confer conductive safety. All species of *Dubautia* show fiber dimorphism. *Dubautia* is a superb example of adaptive radiation, in contrast to the Hawaiian *Schiedea* (Caryophyllaceae), which has shifted into various habitats with little change in wood anatomy, or the Galápagos genus *Scalesia*, all species of which must survive periods of drought and have xeromorphic wood.

HAWAIIAN MADIINAE (*Argyroxiphium*, *Dubautia*, *Wilkesia*) constitutes a monophyletic group (Baldwin et al. 1990, Baldwin and Robichaux 1995) often cited as a premier example of adaptive radiation in plants (e.g., Carlquist 1965, 1970, Carr 1985, Robichaux et al. 1990). *Argyroxiphium*, with five species, and *Wilkesia*, with two (Carr 1985), show distinctive aspects of this adaptive radiation, but the diversity of the 21 species now recognized within *Dubautia* (Carr 1985, 1990) illustrates entry into a wide range of habitats with attendant change in morphological, anatomical, and physiological expressions.

Wood anatomy has proven to be a sensitive indicator of adaptation to diverse ecological regimes and may be seen with special clarity in families and genera that have diversified in recent geological time, with little attendant extinction (Carlquist 1975). Thus, we would expect the wood anatomy of *Dubautia* to show adaptive radiation in wood exceptionally well. *Dubautia* ranges from subshrubs on hot, dry lava (*D. linearis*, *D. scabra*) to shrubs of mesic forest (*D. microcephala*, *D. plantaginea*), rain forest trees (*D. knudsenii*), bog shrubs (*D. waialealae*), alpine shrubs (*D. menziesii*), and a lianoid shrub (*D. latifolia*). The habitats and localities for *Dubautia* species are well described by Carr (1985, 1990).

Earlier studies that included data on wood of *Dubautia* (Carlquist 1958, 1974, 1994) dealt with a small number of the species and

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with limited data sets. Therefore, a more detailed series of studies is attempted here. Companion studies, on wood of *Argyroxiphium* (Carlquist 1997) and *Wilkesia* (Carlquist in press), lend perspective to the observations on *Dubautia* wood.

Adaptation by wood of dicotyledons to varied ecological regimes is primarily related to vessel features: vessel diameter, vessel element length, and vessel density (Carlquist 1975). To this list, degree of vessel grouping should be added (Carlquist 1984). Presence and nature of growth rings (Carlquist 1980) and occurrence of vasicentric tracheids (Carlquist 1985a) in wood are also indicative of ecology.

Degree of woodiness (subshrubs, shrubs, trees) is indicative of adaptation to various habitats in a phylad in which secondary woodiness has occurred, as appears to be the case in *Dubautia* and other island genera (Carlquist 1974). Secondary woodiness is characteristic of the Hawaiian Madiinae, judging by their terminal position in cladograms (Baldwin et al. 1990, Baldwin and Robichaux 1995). Basic to the Hawaiian genera are subshrubs of very limited woodiness, such as the Californian montane genus *Raillardiopsis*, which has been included in this study for purposes of comparison. Adaptive radiation in wood of *Dubautia* should be understood in the context of the Madiinae as a whole.

#### MATERIALS AND METHODS

The wood samples studied represent mostly wood samples I collected over a period of years from naturally occurring specimens. To these have been added stems from a few herbarium specimens. The sample of *D. linearis* wood was small (3 mm diameter), but the sample of *D. waialealae*, although ca 6 mm in diameter, was from the basal stem of a mature plant. The stem of *D. latifolia* was taken from a dead 3-yr-old branch and does not represent a basal stem, but the scarcity of this species does not permit harvesting of larger wood samples. For all other species, the wood samples represent

basal stems or major branches, portions obtainable when these plants were relatively common 40 or more years ago.

Wood samples were prepared by drying. Voucher specimens are listed in Table 1. Summaries of habitat information for the various species given by Carr (1985) are the best source for comparisons with wood anatomy, and thus localities of the individual specimens are not given here. The wood of *Raillardiopsis muiirii* (A. Gray) Rydb. has not been included in Table 1; it was collected in Tehipite Valley, Middle Fork of the Kings River, 1400 m, Fresno County, California, J. T. Howell 33960 (RSA). The specimen of *D. plantaginea* (Carlquist 1928), collected in Ko'olau Gap, is referable to *D. plantaginea* var. *platyphylla* Hillebrand, a variety now placed into synonymy under *D. plantaginea* subsp. *plantaginea* by Carr (1985).

Portions of dried wood samples were boiled in water and stored in 50% aqueous ethanol. Wood was sectioned on a sliding microtome. Sections were stained either with safranin or with a safranin-fast green combination. Macerations for measurement of vessel element length and libriform fiber length were prepared with Jeffrey's Fluid and stained with safranin.

Means shown in Table 1 are based on 25 measurements per feature except for rather variable ones: vessel wall thickness, pit diameter, and libriform fiber wall thickness figures are based on conditions judged to be typical. Number of vessels per group is computed on the basis of a solitary vessel = 1, a pair of vessels in contact = 2, etc. Vessel lumen diameter is used rather than outside vessel diameter because lumen diameter is considered a better indicator of conductive characteristics. The lumen diameter of vessels oval in transection was measured as an average between widest and narrowest diameter. Wood anatomy terms follow the IAWA Committee on Nomenclature (1964), except for the terms vasicentric tracheid and vascular tracheid, which follow earlier usages (Carlquist 1984, 1985a). Radial sections of all species were prepared, as is typical in studies on wood anatomy, but radial sections have not been illustrated here; they yield

some kinds of information well (e.g., shape of ray cells), but more numerous features relevant to the conclusions of this paper are evident on transections and tangential sections.

Statistical treatments other than means have not been undertaken here because of the nature of sampling. Wood collections of *Dubautia* are few because of rarity of the species and the infrequency with which wood collections have been made. For statistical measurements to be meaningful, one would have to sample a series of mature specimens of each species. Moreover, wood of branches and roots as well as of basal stem portions should be included for a study in which statistical methods are employed. The means given in Table 1 are suggestive of differences among the species, but do not have the statistical validity obtainable from extensive sampling of comparable samples. Statistical tests can only meaningfully analyze material studied; they cannot project what one would find in materials not studied.

## RESULTS

### Growth Rings

Growth rings were observed clearly only in two species, *D. latifolia* (Figure 5) and *D. scabra*. These growth rings can be recognized by rings of wide earlywood vessels external to narrow latewood vessels; latewood vessels are also more numerous per square millimeter. In species other than *D. latifolia* and *D. scabra*, fluctuation with respect to vessel diameter occurs, but not in the form of clearly demarcated growth rings.

### Vessel Elements

The mean number of vessels per group is shown in Table 1, column 1, and ranges widely within the genus: from 1.3 in *D. knudsenii* and *D. plantaginea* to more than 10 in *D. waialealae* (Figure 13); *D. menziesii* (Figure 11) also has some large vessel groupings, although the transection shown in Figure 11 does not suggest this. In *D. menziesii* and *D. waialealae*, narrow vessels often occur

in large radial multiples together with wide vessels; the narrow vessels often are difficult to discern because they are similar in diameter to libriform fibers. The tendency for vessel grouping to take the form of radial multiples is illustrated by *D. latifolia* (Figure 5), whereas in *D. sherffiana* (Figure 9), vessel groups are about as wide tangentially as radially.

Vessel diameter (Table 1, column 2) also ranges widely in *Dubautia*. Mean vessel diameter is widest in *D. plantaginea* (Figure 1), narrowest in *D. waialealae* (Figure 13). Other transections illustrated here show decreasing vessel diameter within these extremes: *D. paleata* (Figure 3: 50  $\mu\text{m}$ ), *D. latifolia* (Figure 5: 42  $\mu\text{m}$ ), *D. ciliolata* (Figure 7: 39  $\mu\text{m}$ ), *D. sherffiana* (Figure 9: 38  $\mu\text{m}$ ), and *D. menziesii* (Figure 11: 15  $\mu\text{m}$ ).

Vessel density (Table 1, column 3) is ordinarily considered inversely proportional to vessel diameter. This is approximately true in *Dubautia* (compare columns 2 and 3); in examining transections of species in which narrow vessels are common but easily confused with libriform fibers, this correlation may not be evident at first. In *D. latifolia* (Figure 5), the number of vessels per square millimeter is 109, well above the average for *Dubautia* as a whole (last data line of Table 1), 68, whereas the vessel diameter in this species, 42  $\mu\text{m}$ , is close to the average for the genus (46  $\mu\text{m}$ ). This is the strongest deviation in the genus away from an inverse relationship between vessel diameter and vessel density, and is in the only species with a lianoid habit, as discussed below.

Vessel element length (Table 1, column 4) ranges from 420  $\mu\text{m}$  in *D. knudsenii* to 174  $\mu\text{m}$  in *D. menziesii* (Figure 11), and for both of those species (as for most wood samples studied) mature branches rather than twigs were studied. Thus, differences among the species are mostly not attributable to juvenility of wood. Vessel element length will be discussed with relation to ecology (see below).

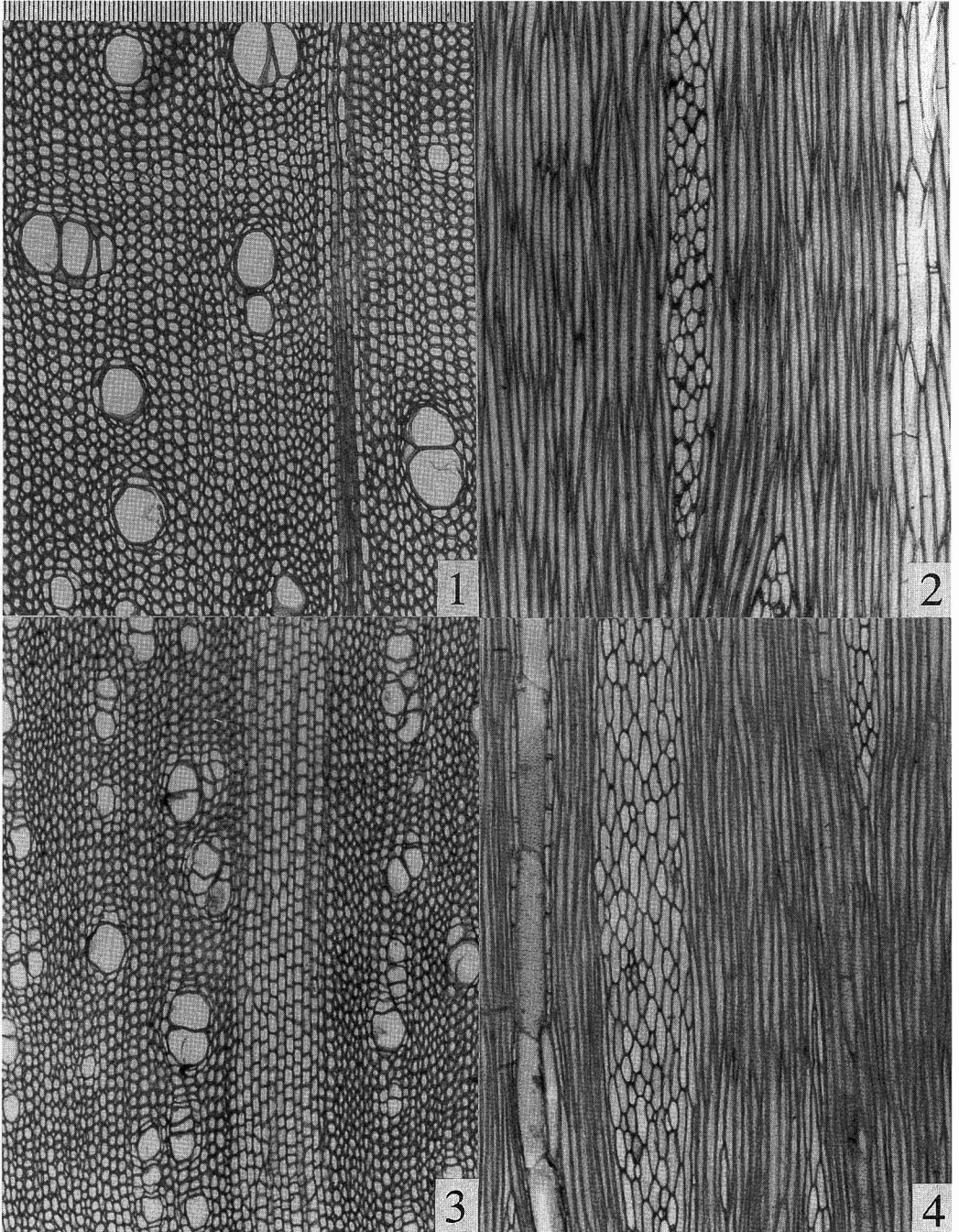
Vessel wall thickness is relatively uniform for the genus (Table 1, column 5). The thick-walled vessels of *D. paleata* and *D. latifolia* (Figure 5) differ but little from the conditions

TABLE 1  
WOOD CHARACTERISTICS OF *Dubautia*

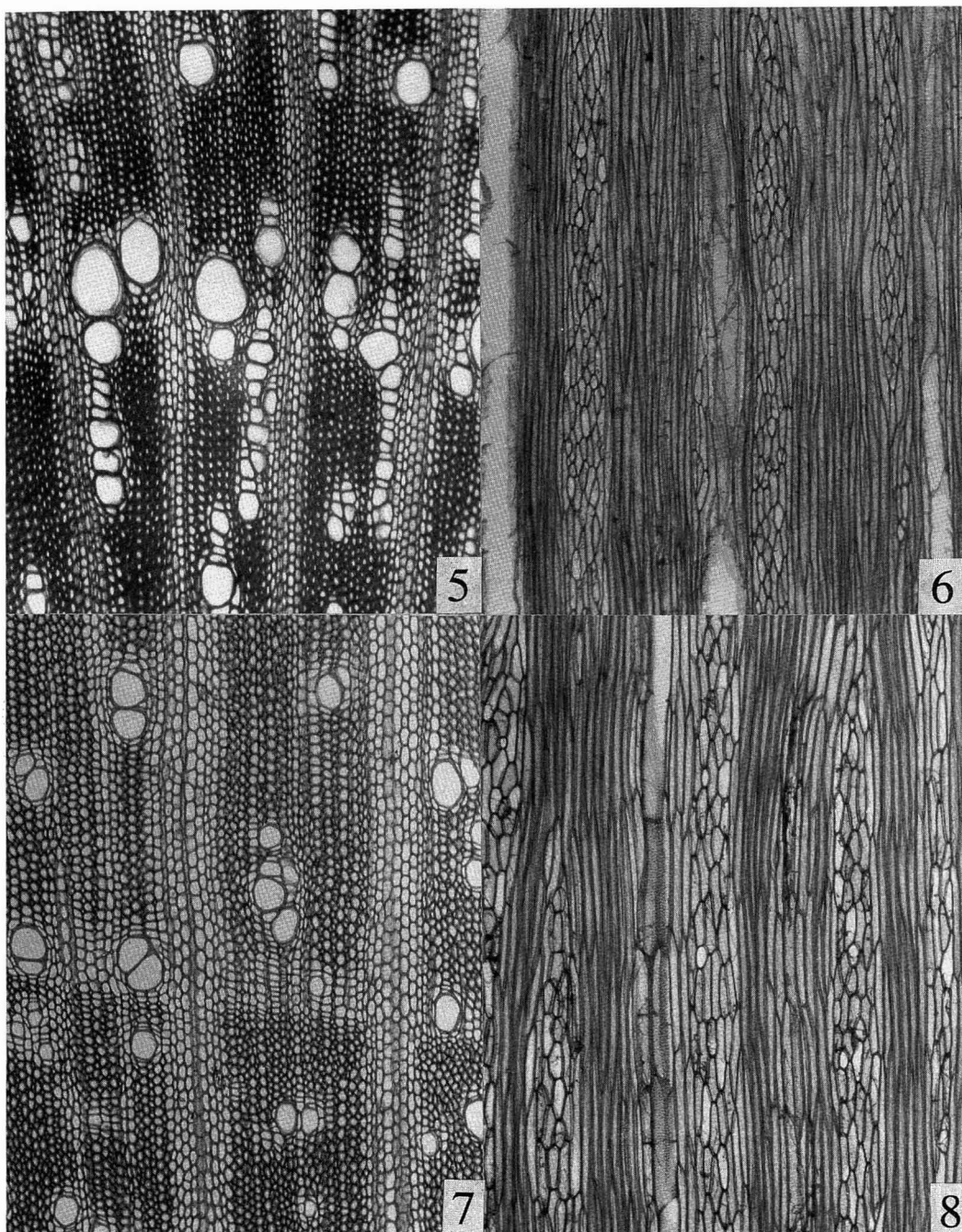
SPECIES	COLLECTION	1 VG	2 VD	3 VM	4 VL	5 VW	6 VP	7 LF	8 SF	9 FW	10 MH	11 MW	12 FV	13 MR
<i>D. ciliolata</i> (DC.) Keck	Carlquist 2051 (RSA)	1.9	39	36	184	3.0	5	448	229	4.0	1561	8.3	2.43	199
<i>D. knudsenii</i> Hillebr.	Carlquist H15 (UC)	1.3	68	13	420	2.3	4	698	472	2.6	4623	3.4	1.66	2197
<i>D. latifolia</i> (A. Gray) Keck	cult. J. Plews	4.2	42	109	296	2.7	5	650	424	5.2	2949	6.6	2.20	114
<i>D. laxa</i> Hook. & Arn.	Carlquist 1971 (RSA)	1.4	59	14	262	2.5	4	546	305	4.6	576	5.9	2.08	1104
<i>D. linearis</i> (Gaud.) Keck	Rock 8123 (BISH)	1.8	41	39	179	2.2	4	374	314	4.0	1936	6.8	2.10	188
<i>D. menziesii</i> (A. Gray) Keck	Carlquist H17 (UC)	13.4	15	157	173	2.2	5	442	286	3.0	1696	5.4	2.54	17
<i>D. microcephala</i> Skottsb.	Carlquist H14 (UC)	2.0	52	20	320	2.2	4	564	390	3.0	601	3.4	1.76	832
<i>D. paleata</i> A. Gray	Carlquist 1772 (RSA)	1.9	50	39	332	3.0	6	553	208	2.4	5972	6.3	1.67	426
<i>D. plantaginea</i> Gaud.	Carlquist 1928 (RSA)	1.3	67	13	278	2.2	5	603	327	2.5	3892	6.2	2.17	1433
<i>D. plantaginea</i> Gaud.	Carlquist 1362 (RSA)	1.5	86	13	324	2.2	5	695	536	5.0	1999	7.1	2.14	2143
<i>D. raillardoides</i> Hillebr.	Carlquist H16 (UC)	1.7	42	22	331	2.6	5	654	286	2.4	2050	4.1	1.98	632
<i>D. scabra</i> (DC.) Keck	Carlquist 2035 (RSA)	3.8	32	126	244	1.2	4	469	254	2.5	2252	7.0	1.92	62
<i>D. sherffiana</i> Fosberg	Carlquist 2356 (RSA)	1.6	38	23	224	2.2	4	539	313	3.0	922	4.4	2.50	370
<i>D. waialealae</i> Rock	Rock 5030 (UC)	>10	11	333	208	2.5	4	462	193	2.4	1101	6.1	2.22	7
<i>Dubautia</i> collections averaged		3.8	46	68	270	2.4	4.6	558	324	3.1	2295	5.8	2.25	697

KEY TO COLUMNS: 1 (VG), mean number of vessels per group; 2 (VD), mean vessel lumen diameter,  $\mu\text{m}$ ; 3 (VM), mean number of vessels per square millimeter; 4 (VL), mean vessel element length,  $\mu\text{m}$ ; 5 (VW), mean thickness of vessel walls,  $\mu\text{m}$ ; 6 (VP), mean axial diameter of lateral wall vessel pits,  $\mu\text{m}$ ; 7 (LF), mean length of longer libriform fibers,  $\mu\text{m}$ ; 8 (SF), mean length of shorter libriform fibers,  $\mu\text{m}$ ; 9 (FW), mean wall thickness of long libriform fibers at widest point,  $\mu\text{m}$ ; 10 (MH), mean height of multiseriate rays,  $\mu\text{m}$ ; 11 (MW), mean width of multiseriate rays at widest point,  $\mu\text{m}$ ; 12 (FV), F/V ratio (mean length of longer libriform fibers divided by mean vessel element length); 13 (MR), mesomorphy ratio (mean vessel lumen diameter times mean vessel element length divided by mean number of vessels per square millimeter).

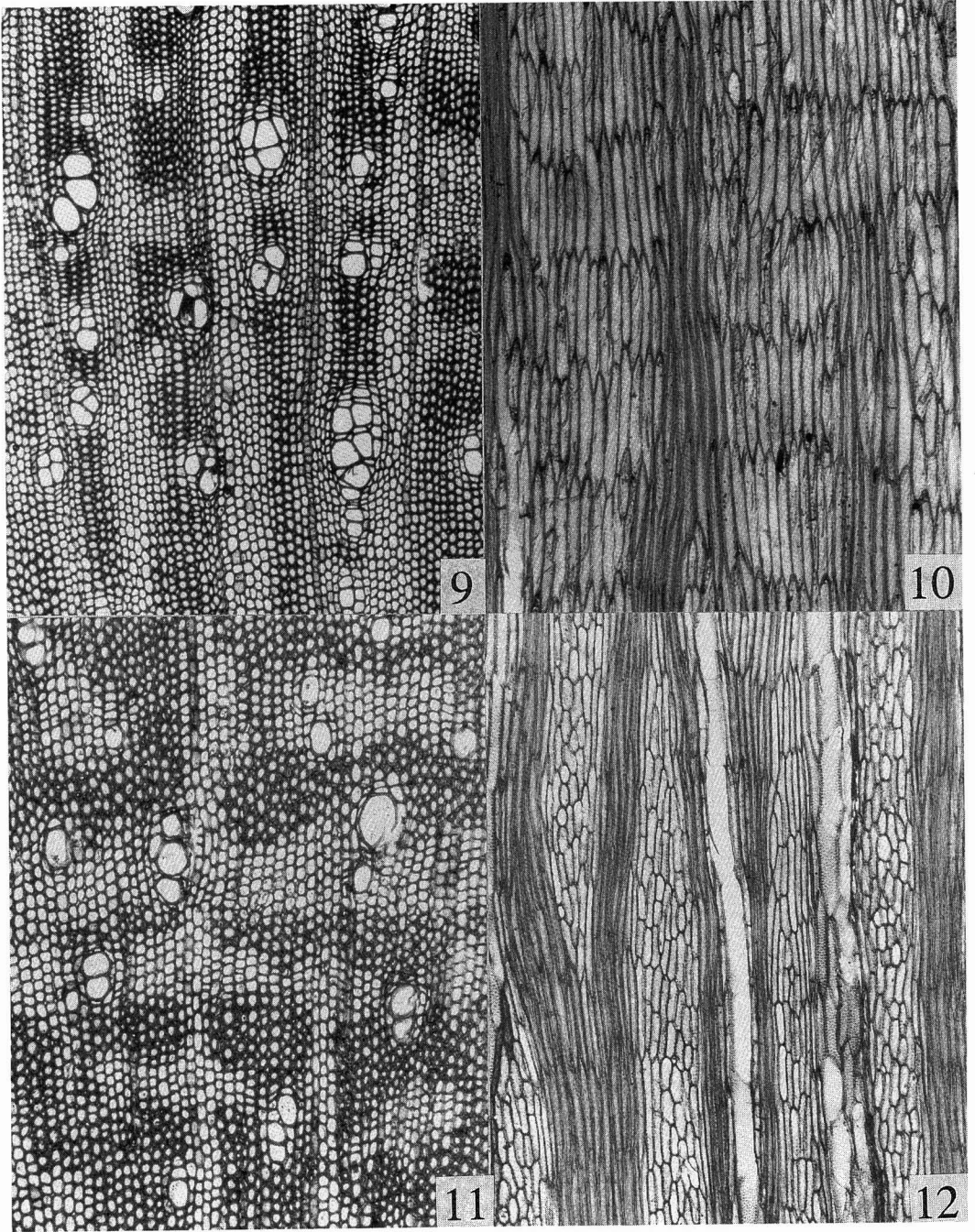




FIGURES 1-4. Wood sections of *Dubautia*. 1-2. *D. plantaginea* (Carlquist 1362). 1. Transection; vessels are wide, solitary or paired. 2. Tangential section; libriform fibers are stored. 3-4. *D. paleata*. 3. Transection; vessels are narrower, in larger groupings. 4. Tangential section; multiseriate ray (center) is typical of wide, tall rays in this species. Scale for all figures above Figure 1 (each division = 10  $\mu\text{m}$ ).



FIGURES 5-8. Wood sections of *Dubautia*. 5-6. *D. latifolia*. 5. Transection; wide vessels slightly above center of photograph are earlywood vessels indicative of a growth ring. 6. Tangential section; many libriform fibers are septate, only vaguely storied. 7-8. *D. ciliolata*. 7. Transection; a tangential band of thin-walled libriform fibers just below center. 8. Tangential section; both thick-walled fibers (*left*) and thinner-walled fibers (*right*) are storied. Scale for all figures above Figure 1.



FIGURES 9-12. Wood sections of *Dubautia*. 9-10. *D. sherffiana*. 9. Transection; vessels mostly grouped (pore multiples). 10. Tangential section; storiage both in thinner-walled fibers (most of photograph) and in thicker-walled fibers (dark strip of fibers near center). 11-12. *D. menziesii*. 11. Transection; thinner-walled libriform fibers present mostly as bands, but also as strands (e.g., upper left). 12. Tangential section; rays are tall and wide, occupy a large portion of the section. Scale for all figures above Figure 1.



seen in transections of wood of the other species (Figures 1, 7, 9, 11, 13). Likewise, diameter of lateral wall pits on vessels (Table 1, column 6) is remarkably uniform. The uniformity of vessel wall thickness and lateral wall pit diameter is one reason for saying that wood of *Dubautia* as a whole has a common plan that has been altered by adaptation of various species to particular ecological regimes.

With respect to morphology, all vessels of *Dubautia* have simple perforation plates and most frequently are cylindrical with few "tails." Lateral wall pits are alternate and mostly oval, but a few laterally elongate pits were recorded for *D. ciliolata* and *D. plantaginea*. No forms of helical sculpturing (e.g., "helical thickenings") were observed on walls of secondary xylem vessels.

#### *Imperforate Tracheary Elements*

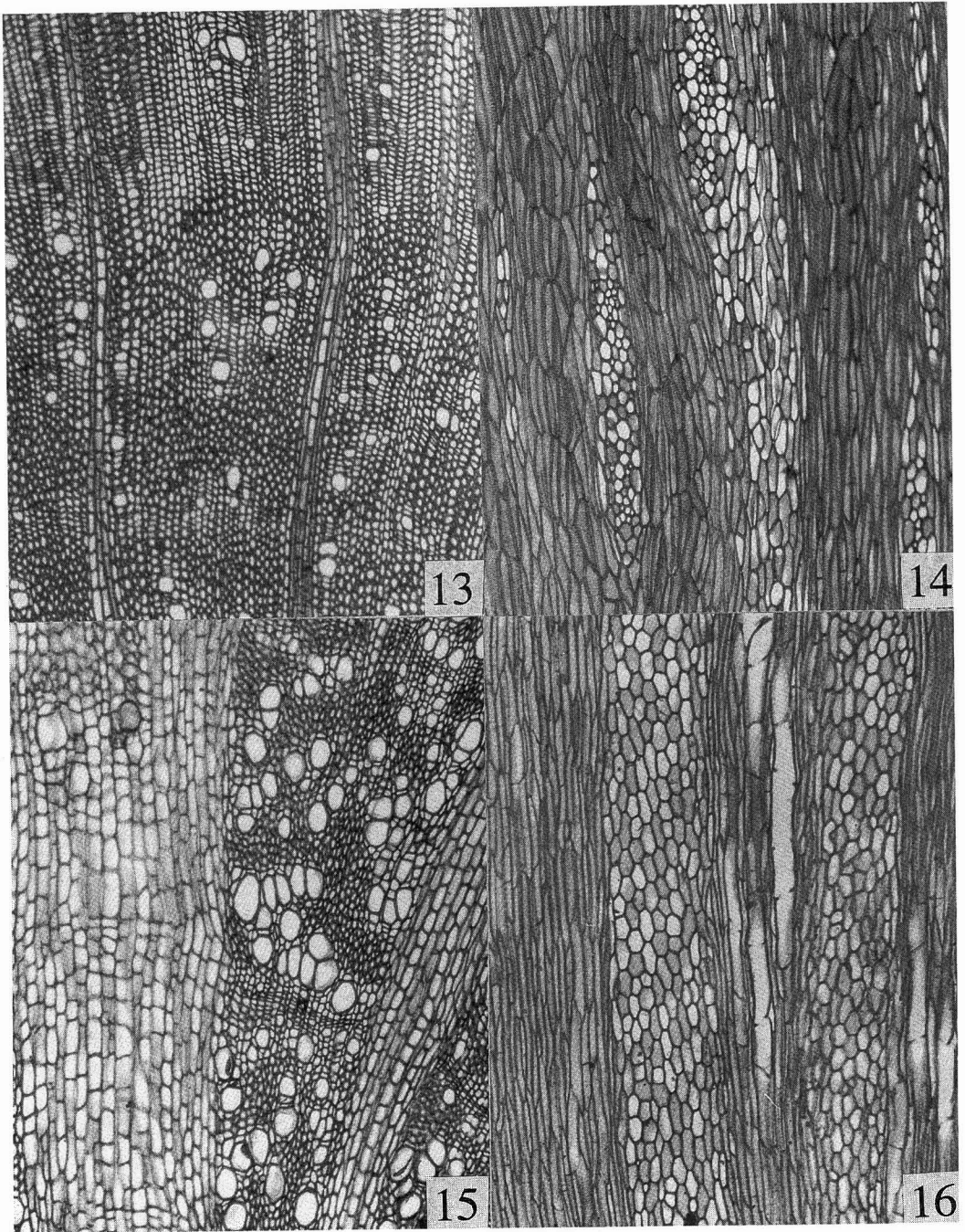
In wood of *D. menziesii* and *D. waialealae*, imperforate fusiform tracheary elements with bordered pits are present in small numbers. They are associated with narrow vessels and may be considered as vessel elements too narrow to bear perforation plates. When found at termini of growth rings, such cells are termed vascular tracheids. If distributed throughout growth rings or in species without growth rings, these cells are termed vasicentric tracheids (Carlquist 1984, 1985a). Vasicentric tracheids are indicative of xeromorphy in woods (Carlquist 1985a). Vasicentric tracheids were not observed in woods of species other than *D. menziesii* and *D. waialealae*. Macerations must be studied to ascertain if vasicentric tracheids are present, because small perforation plates can easily be missing or overlooked in sections of narrow tracheary elements with bordered pits.

Other than the very small numbers of vasicentric tracheids in the two species just cited, all imperforate tracheary elements in *Dubautia* are libriform fibers. However, within the wood of any given *Dubautia*, libriform fibers are not uniform. There are short, comparatively wide, and thin-walled libriform fibers that are usually clearly storied; these contrast with longer, relatively

narrow, and thicker-walled libriform fibers that exhibit storied less conspicuously or not at all. Fibers intermediate with respect to these features are relatively uncommon, and a bimodal distribution with respect to the quantitative features is present. The contrast between these two fiber types may be seen here most clearly in the tangential sections of Figure 10 and Figure 12. The bands and patches of thin-walled fibers for these particular species are illustrated in the corresponding transections, Figure 9 and Figure 11.

The phenomenon of fiber dimorphism was first observed in the wood of *D. laxa* and *D. menziesii*, as well as in the wood of *Wilkesia gymnoxiphium* A. Gray (Carlquist 1958, 1994), and was assigned the term fiber dimorphism by Carlquist (1961). In the monograph on woods of Heliantheae (Carlquist 1958), fiber dimorphism was not observed in all species of *Dubautia*. However, better materials and more extensive preparations have permitted me to recognize the occurrence of fiber dimorphism in all of the species of *Dubautia* studied here, although it is relatively inconspicuous in some, such as *D. plantaginea* (Figures 1, 2), *D. latifolia* (Figure 5), and *D. paleata* (Figures 3, 4). As seen in transections, the shorter, thinner-walled fibers may occur as long tangential bands (Figure 7) or in shorter tangential bands (Figures 9, 11), some of which are very short tangentially and can be termed strands (e.g., Figure 11, upper left). Earlier, I concluded that the shorter, thinner-walled fibers should be called axial ("vertical") parenchyma (Carlquist 1958). In this study, I have seen no instances in which the shorter fibers are subdivided into strands as is the vasicentric axial parenchyma in *Dubautia* (see below), so I now consider the shorter fibers still to be libriform fibers, although possibly functionally similar to axial parenchyma.

In Table 1, mean lengths are given for longer fibers (column 7) and shorter fibers (column 8) for each collection. A few fibers of length intermediate between the two classes do occur in macerations, and these were omitted from the measurements because assignment to one class or the other would have been arbitrary. These omissions may



FIGURES 13-16. Wood sections of *Dubautia* (13-14) and *Raillardiopsis* (15-16). 13-14. *D. waialealae*. 13. Trans-section; vessels are narrow (narrowest vessels are narrower than libriform fibers). 14. Tangential section; all fibriform cells in left quarter of photograph are narrow vessels. 15-16. *R. muirii*. 15. Transsection; wide rays are present. 16. Tangential section; vague storing present in fibriform cells, left quarter of photograph. Scale for all figures above Figure 1.

have the effect of widening the differences between the means for the two fiber types in any given species, but because intermediate fibers are relatively scarce, relatively little bias is introduced.

The mean length of shorter fibers in *Dubautia* as a whole is 324  $\mu\text{m}$ ; this is somewhat greater than the mean vessel element length for the genus (270  $\mu\text{m}$ ), indicating that appreciable elongation of the derivatives of fusiform cambial initials does occur as they mature into shorter fibers. Indeed, some shorter fibers characteristically have a wide cylindrical body at either end of which is an abruptly narrower tail; the tails are interpretable as products of intrusive growth during cell elongation after derivation from a fusiform cambial initial. The ratio in length between longer fibers and shorter fibers in the genus as a whole is 1.7, a ratio sufficiently high that the dimorphism is evident in numerical terms.

Wall thickness is given for the longer fibers only (Table 1, column 9). The range in this feature is from 5.2  $\mu\text{m}$  in *D. latifolia* to 2.4  $\mu\text{m}$  in *D. paleata* (Figure 3) and *D. scabra*. Some septate fibers were observed in *D. latifolia*.

#### Axial Parenchyma

Axial parenchyma in *Dubautia* is vasicentric: an incomplete sheath one cell in thickness around vessels or vessel groups. The parenchyma occurs in strands of two to four cells: mostly two in most species studied, but more commonly four cells in *D. knudsenii* and *D. microcephala*. Strands of two cells may be seen in axial parenchyma cells in Figure 2 (vertical strip of pale cells at far right). Elongate diagonally oriented pits can be seen on the walls of axial parenchyma cells, all of which are lignified in *Dubautia*. These diagonal pits face helices of alternate oval pits on adjacent vessel elements.

#### Rays

Rays are almost exclusively multiseriate in *Dubautia* except for *D. microcephala*. In that species, uniseriate rays are nearly as common

as multiseriate rays and average 188  $\mu\text{m}$  in height.

The mean height of multiseriate rays is given in Table 1, column 10. There is no correlation between height of multiseriate rays and length of vessel elements within *Dubautia*. Notably short rays characterize *D. laxa*, *D. microcephala*, and *D. sherffiana*. The tallest rays in the genus were observed in *D. paleata* (Figure 4), but tall rays are also common in *D. latifolia* (Figure 6), *D. plantaginea* (Figure 2), *D. raillardioides*, and *D. scabra*.

Rays occupy a relatively large proportion of the wood in *D. menziesii* (Figure 12) and *D. scabra*, both of which are small shrubs or subshrubs. The Californian *Raillardioopsis muiirii* is relevant in this regard, because it, too, is a subshrub and wide rays occupy a large proportion of the woody cylinder (Figures 15, 16).

Ray width (Table 1, column 11) varies markedly within *Dubautia*. Relatively wide rays may be observed in *D. ciliolata* (Figure 8), *D. latifolia* (Figure 6), *D. linearis*, *D. paleata* (Figure 4), *D. plantaginea*, and *D. scabra*.

Ray cell walls are lignified but only moderately thick in the genus. The range observed was from 1.5  $\mu\text{m}$  to 2.4  $\mu\text{m}$ . Borders were observed (especially on tangentially oriented ray cell walls) on many of the pits in ray cells of *D. knudsenii*, *D. latifolia*, and *D. sherffiana*, and on a smaller proportion of the pits in ray cells of the other species.

#### Storying

Storied patterns can be seen clearly in the shorter libriform fibers (e.g., Figure 10), but also, to a lesser extent, in all fibers (Figures 2, 4, 8, 12, 14). Vessels, vasicentric tracheids, and axial parenchyma conform to the storied pattern.

#### Deposits and Other Features

Oleoresins, commonly seen as droplets or massive deposits in cells of some Asteraceae, are scarce in woods of *Dubautia*. No crystals were observed in wood of *Dubautia*. A few



small starch grains were observed in ray cells. Tyloses were not observed.

#### CONCLUSIONS

One figure correlates with habit rather than with moisture regimes: the F/V ratio (libriform fiber length divided by vessel element length), which is given for *Dubautia* in Table 1, column 12. For *Dubautia* as a whole, the ratio is 2.25. This compares with 1.89 in *Argyroxiphium* (Carlquist 1997) and 2.86 in midlevel stems of *Wilkesia* (Carlquist in press). The stems of *Argyroxiphium* range from acaulescent to condensed; in such stems, mechanical strength is likely of low selective value and the short fibers in that genus may reflect that. On the contrary, the unbranched polelike stems of *W. gymnoxiphium* (which often occurs in exposed sites) may correlate with the higher F/V value in that genus. The intermediate F/V value of *Dubautia* is appropriate for a genus that ranges mostly from large to small shrubs. The highest F/V values within *Dubautia* occur in *D. ciliolata*, *D. menziesii*, and *D. sherffiana*, species that are relatively small shrubs with a limited number of branches, but which occur in more exposed and thus likely windier sites than do the majority of *Dubautia* species.

Moisture regimes of the *Dubautia* species are well revealed by the mesomorphy ratio (Table 1, column 13), which incorporates vessel lumen diameter, vessel density, and vessel element length. The highest mesomorphy ratio figures occur in the trees and shrubs of rain forest: *D. knudsenii* (2197), *D. laxa* (1104), *D. microcephala* (832), *D. plantaginea* (1433, 2143), and *D. raillardoides* (632) are notable in this regard. At the other end of the spectrum, with relatively small mesomorphy ratio figures, are *D. ciliolata* (199), *D. linearis* (188), *D. latifolia* (114), *D. menziesii* (17), *D. scabra* (62), and *D. waialealae* (7). One can compare this series of relatively low figures with those obtained for stems of *Argyroxiphium* (Carlquist 1997): the range is from 8 in *A. kauense* (Rock &

M. Neal) Degener & I. Degener to 165 in *A. grayanum* (Hillebrand) Degener, a bog margin species. *Argyroxiphium caliginis* Forbes, a bog species, has a mesomorphy ratio value of 24, which is very close to that of the Haleakalā silversword, *A. sandwicense* DC. subsp. *macrocephalum* (A. Gray) Meyrat, 22. If *A. sandwicense* subsp. *macrocephalum* is similar to plants that gave rise to *A. caliginis*, shift to the bog habit has not been reflected by release to a more mesomorphic wood pattern. The interpretation given (Carlquist 1997) is that this shift has been recent and that xeromorphic wood is not disadvantageous in the bog habitat. Transpiration that would require vessels of wide diameter does not characterize bog shrubs of limited size and relatively small foliar surface. These same considerations might apply to *D. waialealae*, which grows in the Hawaiian locality with the greatest rainfall (Carlquist 1980), but which, ironically, has the lowest mesomorphy ratio value of any *Dubautia* species. *Dubautia waialealae* might be a relatively recent immigrant to the bog habitat, perhaps from a dry zone on Kaua'i or even possibly from another island. A similar explanation may apply to *D. latifolia*, the sole scandent shrub in the genus; it has a relatively low mesomorphy ratio value (114) compared with those of other species of *Dubautia*. The ancestors of this species, sole species in its subgenus, may have shifted from drier habitats into the wetter forests of the Kōke'e region of Kaua'i. Alternatively, it may exemplify selective value of a xeromorphic wood pattern in a liana; many lianas have a large number of narrow vessels or vasicentric tracheids in addition to the wide vessels for which lianas are noted (Carlquist 1985b). Lianas also have greater vessel density than arboreal dicotyledons considering their mean vessel diameter, and *D. latifolia* is the sole species of the genus that shows vessel density higher than expected on the basis of an inverse correlation between vessel density and vessel diameter. *Dubautia latifolia* thus exhibits some features expected in a liana and also possibly phyletic shift in ecological preference. The hypothesis that the bog species

*A. caliginis* and *D. waialealae* have acquired xeromorphic wood characteristics in response to the bog habitat is conceivable, but this does not seem applicable to *A. grayanum*, a bog margin species, and would require a reversion to xeromorphic wood features from a more mesomorphic plan that was ultimately likely derived from ancestors with xeromorphic wood like that of the Californian tarweeds (see below).

Vessel grouping proves closely correlated with ecology in *Dubautia*. Only in such a wide-ranging genus as *Olearia* (Asteraceae) can one find a greater span among species with respect to number of vessels per group (Carlquist 1984). When one compares the vessels per group figures for the various species of *Dubautia* (Table 1, column 1) with the mesomorphy ratio values (Table 1, column 13), one finds the relationship to be very close to inverse. This not only reinforces the concept of vessel grouping as a feature related to xeromorphy (Carlquist 1984), it also serves as another indicator of adaptive radiation in wood features of *Dubautia*. Large groupings of vessels potentially safeguard conductive pathways during times when high tensions in the secondary xylem might disable many vessels.

If, as cladograms show (Baldwin et al. 1990, Baldwin and Robichaux 1995), montane California subshrubs such as *Raillardiopsis* are basal to the Hawaiian Madiinae, the features of these subshrubs are essential to our understanding of adaptive radiation in *Dubautia*. If the wood of *Raillardiopsis* (Figures 15, 16) is indicative, the Hawaiian Madiinae began with xeromorphic wood: vessel elements of narrow diameter and short length, numerous per square millimeter of transection, in relatively large groups. *Raillardiopsis* and *Madia bolanderi* have tall, wide multiseriate rays and few or no uniseriate rays, like wood of xeromorphic species such as *D. menziesii* or *D. scabra*. If the wood of *Raillardiopsis* or *Madia bolanderi* represents ancestral features, the diversification in wood features of *Dubautia* represents widening of vessels to accommodate greater peak transpiration of broader leaves and loss

of large numbers of narrow, short vessels that offer redundancy and serve for conductive safety where moisture availability fluctuates, but are of no selective value where soil moisture is abundant.

One notes that vessel dimensions correlate well with leaf area in *Dubautia*, as illustrated for a selection of species earlier (Carlquist 1974:153). Leaf area is an indicator of transpirational characteristics in *Dubautia*, several features of which are discussed by Robichaux et al. (1990).

The ecological significance of fiber dimorphism in *Dubautia* is uncertain. This phenomenon is present in *Argyroxiphium* and *Wilkesia* also (Carlquist 1997; in press), but has not been observed in the Californian Madiinae (Carlquist, unpubl. data). Further studies of fiber dimorphism both with respect to physiology and to details of histology are desirable.

In summary, adaptive radiation in woods of *Dubautia* is truly exceptional when one compares it with wood anatomy of other endemic island genera. For example, *Scalesia* (Asteraceae, tribe Heliantheae) on the Galápagos Islands is relatively uniform with respect to vessel features (Carlquist 1982). The upland Galápagos forest, habitat for some *Scalesia* species, is really not mesic because rainfall is seasonal, so that wood of the upland *Scalesia* species must cope with the demands of a dry season. *Schiedea* (Caryophyllaceae) is a Hawaiian genus of shrubs or subshrubs that is present in both dry and genuinely mesic habitats, but its wood anatomy is xeromorphic with only minimal shift toward mesomorphy in the species of more mesic habitats (Carlquist 1995). *Schiedea* may be unable to form large shrubs and trees because of a combination of features. One indicator is that *Schiedea* has rayless woods, and rayless woods are not found in large shrubs or trees. Certainly in island genera that have radiated autochthonously into a range of habits and habitats, wood anatomy may parallel that radiation to various degrees. *Dubautia* is exceptional in the degree to which adaptive radiation is illustrated by quantitative features of wood anatomy.

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