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WOOD ANATOMY OF MACARONESIAN
AND OTHER BRASSICACEAESHERWIN CARLQUIST¹*Claremont Graduate School and Rancho Santa Ana Botanic Garden,
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INTRODUCTION

The tendency for herbaceous families of dicotyledons to be represented on insular areas by species and genera more markedly woody than their continental relatives is exemplified by the family Brassicaceae. This tendency, although early noted by such authors as Hemsley (1885), has not been explored to any appreciable extent genetically, experimentally, or even ecologically for any of the families in which this phenomenon occurs. The present study is one of a series of papers in which I am attempting to discern what modes of anatomical structure characterize woody insular representatives of herbaceous groups, and with the aid of ecological correlations draw conclusions concerning the occurrence and nature of what may be termed "insular woodiness."

Crucifers offer an excellent subject for such a study, for the family as a whole seems clearly an herbaceous one, and primitive tribes do not contain the woodiest members of the family. One of the tribes sometimes regarded as primitive is Stanleyeae. The genus *Stanleya* is mostly herbaceous, and the shrubby species studied here, *S. pinnata*, can be said to be exceptional in this regard (Rollins, 1939). The genus *Romanschulzia* seems to contain a greater constellation of primitive features (Rollins, 1956), although it, too, can be called essentially herbaceous.

Within the related family Capparaceae, woodiness may be primitive, although some genera appear to have increased woodiness during their evolution. The likelihood appears very great that none of the woody crucifers studied here represent vestiges of capparaceous woodiness in any case, for they belong to tribes with numerous specialized features, well removed from the capparid-like crucifers, and they grow in geographical areas in which woodiness is common in families prevalently herbaceous elsewhere. The woody habit of *Stanleya pinnata* may well be a response to longer growing seasons in the southwestern United States. In this same region, there are many woody species of Asteraceae, and this parallel suggests that climate has been influential in the production of a shrubby habit.

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Almost certainly the remainder of the genera of Brassicaceae in the present study represent woodiness acquired during evolution of herbaceous groups on insular areas. As circumstantial, though strong, evidence one may cite the fact that the genera of the present study belong to a wide diversity of tribes and even subtribes within the family. The tribal distribution of the genera is as follows according to the treatment of Schulz (1936):

Stanleyeae: *Stanleya*
Lepidieae: *Lepidium*
Brassicaceae: *Crambe*, *Sinapidendron*
Matthioleae: *Matthiola*, *Parolinia*
Hesperideae: *Cheiranthus*
Sisymbrieae: *Descurainia*

Presuming that the scheme of Schulz represents various degrees of phylogenetic specialization, these genera seem clearly to represent independent derivations of woodiness on various insular or otherwise climatically moderate areas where they grow, derivations from groups that are rich, intermediate, and poor in putatively primitive features. In addition, the geographical distribution of woody crucifers, in various islands and island-like areas all over the world, suggests independent derivations. The genera studied here, with the exception of *Lepidium* and *Stanleya*, are essentially Eurasian or with close relatives in Eurasia, especially in the Mediterranean region. One may note that Hemsley (1885) cited conspicuous woodiness in certain non-insular crucifers (*Euzomodendron*, *Vella*, and *Oudneya*) from Spain and Algeria, but these, like *Stanleya pinnata* in southwestern North America, may represent adaptation to warmer regions with long growing seasons, fewer frosts. Also, in the páramos of Colombia, woody species of *Draba* occur. These high plateaus have a cool climate, but almost uniformly cool throughout the year, because of the equatorial latitudes in which the páramos occur. Likewise, woodiness in *Romanschulzia* from typical latitudes could be said to be present in relation to the long growing season and lack of frosts of these regions. Unfortunately, *Euzomodendron*, *Vella*, *Oudneya*, *Draba*, and *Romanschulzia* could not be studied because wood samples were not available. Certain insular crucifers likewise are not included here: there are woody species of *Erysimum* on the Aegean Islands (Snogerup, 1967), and *E. moranii* on Guadalupe I., Mexico, a species somewhat woodier than related species from Mexico, such as *E. insulare* and *E. suffrutescens* (Rollins, 1970). Some annual Brassicaceae, such as *Brassica nigra*, develop enough wood at their bases so that sections could be made with a sliding microtome. However, the present study is limited chiefly to insular crucifers collected by the writer. Wood collections contain few samples from plants of habits other than arboreal or arborescent or at most shrubby, and thus nearly all samples had to be collected in the field by the writer.

Insular crucifers are probably dispersed with relative ease to island areas, especially those near continents. In those sites they have at least in some cases developed growth forms in which renewal buds, usually formed near ground level, are not killed by winter frost but instead produce continual

innovations, so that a broom-like shrub with a short, woody caudex-like stem is formed. An exception to this is *Parolinia*, in which an upright elongate stem like that of a "typical" shrub is branched at various levels. *Parolinia* also has wood of a texture much more dense than that of other crucifers.

The Brassicaceae of the present study are interesting in that unlike other phylads woody on islands, these insular crucifers are not mesic in their adaptations. Woody Lobelioideae (Carlquist, 1969a) are nearly all mesic in their ecological preferences, and show this in terms of wood anatomy. Likewise, an appreciable number of Asteraceae (Carlquist, 1966) have entered such niches. The Hawaiian and Macaronesian euphorbias (Carlquist, 1970b) have occupied a broad span of situations with respect to rainfall, although only a few could be called characteristically rain-forest species. The woody species of *Echium* (Carlquist, 1970a) are characteristic of drier situations in the Canary Islands and Madeira, and only *E. pininana* and *E. candicans* are laurel-forest species. Although this pair of species represents the most mesic adaptations of the genus, and they show this with respect to wood anatomy, the Macaronesian laurel forest cannot be called a rain forest. Brassicaceae on islands are distinctive in that the woody species studied here occur exclusively or nearly exclusively in xeric localities. Only one collection was made from a laurel-forest location: *Cheiranthus mutabilis*, Carlquist 2645. This plant, which grows along the waterfalls in the Ribeiro Frio district of Madeira, probably represents a recent invader of open rocky situations within the laurel forest, and the primary adaptation of the species as a whole, as shown by other collections, is xeric.

The xeromorphic preferences of Macaronesian Brassicaceae are clearly indicated by their presence in lowland dry situations (the site of the vast majority studied here), but also in dry alpine situations as well: *Cheiranthus scoparius*, *C. tenuifolius*, and *Descurainia bourgeauana* could be called Macaronesian alpine. Sea bluffs, the characteristic habitat of *Lepidium serra*, *Sinapidendron angustifolium*, and *S. frutescens*, are physiologically dry localities, sometimes even mildly halophytic in their vegetation. For further descriptions of ecology and habit photographs and drawings, the reader can consult Burchard (1929), Carlquist (1970c), Hillebrand (1888), Lems (1960), Lowe (1868), and Schenck (1907). Space does not, unfortunately, permit inclusion of habit photographs here.

The crucifers studied here seem good material for answering the question: what are the characteristic modes of wood structure in a basically herbaceous group, woody derivatives of which have, with few exceptions, retained a xeric or near-xeric (ca. 25 inches of rain per year or less) adaptation? One must concede that information from woody species of *Draba* and *Romanschulzia* is necessary before a full assessment of wood anatomy of Brassicaceae can be made. One might also benefit from knowledge of wood anatomy of cabbages on subtropical islands, like the Canary Islands or the West Indies. On such islands, cabbages often become unbranched or little-branched rosette herbs with stems up to perhaps three meters tall. This phenomenon is a phenotypic response to the moderate maritime cli-

mates of these islands, and although it does not represent, as far as known, a genetic change to the rosette-tree habit, it forms an interesting parallel to those genera of other families (e.g., *Dendroseris* of Asteraceae; *Cyanea* of Campanulaceae—Lobelioideae) that have developed the rosette-tree habit during evolution on islands.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

Wood specimens were collected in the field, with the exception of *Stanleya pinnata*, samples of which were obtained from plants cultivated in the Rancho Santa Ana Botanic Garden, Claremont, California. Wood samples were dried without artificial heat after they were collected. Basal portions of stems have been utilized unless other portions of the plant are indicated in the table. Authors of taxonomic names for the taxa studied here are given in the table and omitted elsewhere. All wood samples studied are documented by voucher specimens in the Rancho Santa Ana Botanic Garden (RSA). Replicates of most of these specimens were prepared and distributed to other herbaria, particularly the Gray Herbarium.

Wood sections and macerations were prepared according to the usual techniques. The characteristics studied are typical of those of studies on secondary xylem, but have been influenced by features that seemed to show interesting variations in my previous studies on wood anatomy. For each quantitative feature analyzed, 50 measurements were made and a mean obtained. Significant differences in wood anatomy within a plant can occur. The data of the table show marked differences between base and upper branch of *Descurainia briquetii*, but differences among root, stem, and upper branch are relatively minor in *Cheiranthus arbuscula* and *Sinapidendron frutescens*.

I have followed the taxonomic treatment of Lems (1960) for Canarian Brassicaceae and that of Lowe (1868) for Madeiran species. I suspect, however, that Lowe was overimpressed with minor differences, and that some of his varieties or even species might correspond with what we would consider ecotypes today. Taxonomy of insular species is often difficult, apparently because some genera speciate or diversify without the formation of genetic barriers among populations that would typically accompany speciation in continental areas. Consequently, numerous intergrades can occur, despite distinctiveness of extremes, and a confusing taxonomic situation often results.

For assistance in collecting activities, I wish to thank Mr. Gunther Kunkel; the late Dr. Kornelius Lems provided much information helpful to my field work. Microtechnical assistance was provided by Mr. Gerald Benny, Mr. Arthur Gibson, and Mr. Timothy Magee. Professor Reed C. Rollins read a preliminary manuscript of this paper and provided useful suggestions and improvements.

ANATOMICAL DESCRIPTIONS

In the table, qualitative and quantitative data for woods of Brassicaceae have been summarized. Most of the items are self-explanatory. However,

abbreviations have been used in some instances. In the column headed "RAY CELL TYPES," the relative abundance of upright (erect), square, and procumbent cells as seen in radial sections are indicated: an uppercase letter indicates relative abundance, a lowercase letter relative paucity. Thus USP denotes that upright and square cells are relatively abundant, procumbent cells rather less frequent. Under "STORIED WOOD STRUCTURE," only libriform fibers are the concern (or possibly also shorter, nucleated fibers that may resemble axial parenchyma cells). Rays are not storied in the Brassicaceae studied. Thus "+" indicates storying in a least parts of the axial xylem of a section, "O" no appreciable storying. In the column headed "VESSEL WALL FEATURES," presence of grooves interconnecting adjacent pit apertures is indicated by "g"; "e" denotes that most lateral-wall pits are elliptical or elongate in face view, and "c" that most pits are circular in outline. In the column headed "GROWTH RING FEATURES," the elements in early wood differing from those in late wood are indicated: "mv" = more numerous vessels in early wood; "wv" = wider vessels; "tf" = thinner-walled libriform fibers (or possibly nucleated fibers).

VESSEL ELEMENTS

Vessel-Element Length.—Metcalf and Chalk (1950) indicated that crucifers have notably short vessel elements. As shown in the table, this seems a very accurate appraisal. The longest average vessel-element length obtained is only 200.6 μ (*Cheiranthus mutabilis*), the shortest 62.1 μ (*Descurainia briquetii*). If one takes an average of the average lengths given in this column, one obtains the figure 117.4 μ for the woody Brassicaceae studied here as a whole. The comparable figure for 328 species of Asteraceae (Carlquist, 1966) is 235 μ , which is appreciably longer, although still well below the average figure for dicotyledons as a whole (cf. Metcalf and Chalk, 1950). Shortness of vessel elements is clearly indicated in the tangential sections presented here as Figs. 2, 4, 6, 8, 11, 13, 17, 20, 22, and 25. One may ask why Brassicaceae have such notably short vessel elements. An explanation that might be offered concerns the fact that Brassicaceae is an essentially herbaceous family, and that if the herbaceous habit in dicotyledons is an indicator of specialization compared with woody dicotyledons, shorter vessel elements would, in general, be expected in herbaceous groups. This, while perhaps true, may be only a partial explanation. To be sure, the tribes of Asteraceae richest in herbaceous species do appear to have shorter average vessel-element lengths: for example, Ambrosieae (187 μ), Anthemideae (145 μ), Arctotideae (129 μ), Cynareae (185 μ), and Helenieae (167 μ) (Carlquist, 1966). However, the correlation between vessel-element length and ecology cited in that paper and others (Carlquist 1969b, 1970a; Webber, 1936) seems clear. As mentioned above, the Brassicaceae studied come from relatively dry regions. The data from *Cheiranthus* are interesting in this regard. *Cheiranthus mutabilis*, Carlquist 2645, comes from the moist laurel-forest areas of Madeira, whereas *Cheiranthus scoparius*, Carlquist 2496, represents a population from alpine regions of extreme drought on Tenerife. With regard to ecological correlations as op-

TABLE 1. Wood characteristics of Brassicaceae.

NAME	COLLECTION	
<i>Cheiranthus arbuscula</i> Lowe	Carlquist 2654 (RSA)	STEM
<i>C. arbuscula</i> Lowe	Carlquist 2654 (RSA)	ROOT
<i>C. mutabilis</i> L'Her.	Carlquist 2645 (RSA)	
<i>C. mutabilis</i> L'Her.	Carlquist 2648 (RSA)	
<i>C. scoparius</i> Brouss.	Carlquist 2496 (RSA)	
<i>C. scoparius</i> Brouss.	Carlquist 2596 (RSA)	
<i>C. tenuifolius</i> L'Her.	Carlquist 2675 (RSA)	
<i>Crambe fruticosa</i> L.f.	Carlquist 2669 (RSA)	
<i>C. strigosa</i> L'Her.	Carlquist 2507 (RSA)	
<i>C. strigosa</i> L'Her.	Carlquist 2553 (RSA)	
<i>Descurainia bourgeauana</i> Fourn.	Carlquist 2697 (RSA)	
<i>D. briquetii</i> Pit.	Carlquist 2557 (RSA)	BASE
<i>D. briquetii</i> Pit.	Carlquist 2557 (RSA)	BRANCH
<i>D. millefolia</i> (Jacq.) Webb & Berth.	Carlquist 2515 (RSA)	
<i>D. preauxiana</i> Webb	Carlquist 2617 (RSA)	
<i>Lepidium serra</i> Mann	Carlquist 1799a (RSA)	
<i>Matthiola maderensis</i> Lowe	Carlquist 2628 (RSA)	
<i>Parolinia ornata</i> Webb	Carlquist 2614 (RSA)	
<i>Sinapidendron angustifolium</i> (DC.) Lowe	Carlquist 2630 (RSA)	BASE
<i>S. angustifolium</i> (DC.) Lowe	Carlquist 2630 (RSA)	BRANCH
<i>S. frutescens</i> (Ait.) Lowe var. <i>diffusa</i> Lowe	Carlquist 2672 (RSA)	
<i>S. frutescens</i> (Ait.) Lowe var. <i>succulenta</i> Lowe	Carlquist 2661 (RSA)	ROOT
<i>S. frutescens</i> (Ait.) Lowe var. <i>succulenta</i> Lowe	Carlquist 2661 (RSA)	BASE
<i>S. frutescens</i> (Ait.) Lowe var. <i>succulenta</i> Lowe	Carlquist 2661 (RSA)	BRANCH
<i>S. rupestre</i> Lowe var. <i>chaetocalyx</i> Lowe	Carlquist 2670 (RSA)	
<i>Stanleya pinnata</i> (Pursh) Britton	cult. RSA	

posed to shortness of vessel elements on account of specialization related to herbaceous habit, I note that the above examples from Asteraceae do not include Cichorieae (average vessel-element length of species studied, 232 μ). Most Cichorieae studied by the writer (1960) were rosette trees of wet

LENGTH VESSEL ELEMENTS, AVERAGE, μ	DIAMETER VESSELS, AVERAGE, μ	DIAMETER WIDEST VESSEL, μ	VESSELS PER GROUP, AVERAGE	LENGTH LIBRIFORM FIBERS, AVERAGE, μ	GREATEST WIDTH LIBRIFORM FIBERS, AVERAGE, μ	WALL THICKNESS LIBRIFORM FIBERS, AVERAGE, μ	HEIGHT MULTISERiate RAYS, AVERAGE, mm	GREATEST WIDTH MULTISERiate RAYS, AVERAGE, CELLS	RAY CELL TYPES (SEE TEXT)	STORIED WOOD STRUCTURE (SEE TEXT)	VESSEL WALL FEATURES (SEE TEXT)	GROWTH RING FEATURES (SEE TEXT)
119.4	35	68	1.8	258	17	2.6	.49	4.5	USp	0	eg	tf
122.4	35	69	1.6	278	20	2.6	.97	5.8	USp	0	eg	tf
200.6	54	70	1.4	410	14	4.8	.44	2.9	USp	0	eg	tf
155.9	50	81	1.3	362	16	2.1	.68	5.7	USp	0	eg	tf
63.3	27	44	5.7	193	12	3.7	.34	3.3	USp	0	eg	mv, vv
101.3	32	56	2.2	186	15	2.1	.68	5.7	USp	0	g	tf
124.9	30	60	1.7	338	14	3.7	.34	3.3	USp	0	eg	tf, vv
99.6	37	58	1.7	281	12	4.8	.33	2.3	uSp	+	eg	tf
128.9	26	139	1.8	334	19	3.0	.48	4.4	USp	+	eg	tf
126.8	16	78	1.6	317	30	3.6	.37	3.0	uSp	+	eg	tf, mv
112.3	31	47	1.8	225	9	3.6	.29	1.8	USp	0	eg	tf, mv
62.1	27	45	1.6	239	13	2.4	.85	3.7	uSP	0	eg	mv, vv
162.0	82	116	1.4	422	26	4.2	.76	3.0	USp	0	eg	mv, vv
99.2	31	50	2.0	216	11	2.4	.72	3.7	USp	0	eg	tf
78.5	29	42	1.9	203	11	5.6	1.09	4.3	USp	0	eg	tf, vv
79.6	36	64	1.6	243	14	3.6	.76	5.2	USp	0	cg	tf
121.0	52	78	1.7	331	19	4.2	.72	3.9	USp	0	cg	tf
118.8	37	70	2.1	307	7	3.0	.14	1.4	uSP	0	c	tf, vv
91.6	50	72	1.7	221	12	5.6	.40	6.3	USp	+	eg	tf
154.8	42	70	1.4	338	14	4.2	.55	2.3	USp	+	eg	tf
102.5	36	81	1.5	251	13	3.0	.79	3.7	USp	+	cg	tf
149.3	72	114	1.8	499	20	1.8	.61	2.7	USp	+	c	tf
145.0	55	92	1.7	389	21	3.6	.51	2.8	USp	+	cg	tf
121.0	50	89	1.5	291	16	2.4	.66	3.9	USp	+	eg	tf
67.6	36	56	1.7	194	13	3.0	.38	4.2	USP	+	eg	tf
143.9	41	75	5.9	240	11	3.6	.70	3.7	USp	0	eg	tf, vv

forest areas; only a few were temperate herbs, and this doubtless accounts for the greater vessel-element length in Cichorieae. Indeed, the annual species (*Lactuca serriola*) and a shrub from a dry island (*Stephanomeria blairii*, also known as *Malacothrix blairii* or *Munzothamnus blairii*) have

Fig. 1-4. Sections of wood of *Crambe*.—Fig. 1-2. *Crambe strigosa*, Carlquist 2553.—Fig. 1. Transection; a growth ring is evident.—Fig. 2. Tangential section. The storied condition is clearly evident in the libriform fibers.—Fig. 3-4. *Crambe fruticosa*, Carlquist 2669.—Fig. 3. Transection. Fibers are thicker-walled than those of *C. strigosa*.—Fig. 4. Tangential section. Storied structure is present, although less clear than in *C. strigosa*.—Scale for figs. 1-4 is given by the stage micrometer shown above Fig. 1.

the shortest vessel elements for Cichorieae. Because vessel-element length is controlled by length of fusiform cambial initials and thereby may be assumed to be a deep-seated characteristic genetically, not readily subject to phenotypic modification, the dual explanation of shortness due to specialization of an herbaceous phylad and also due to adaptation to ecologically dry conditions may account for the figures in Brassicaceae. However, one may still ask why herbaceous groups have shorter vessel elements. I am inclined to relate this correlation, also, to ecology, for many annuals and woody herbs accomplish growth, especially the later or last-formed secondary xylem, during warm, dry parts of the year when water near the surface of the soil—where their roots are located, as opposed to those of trees and shrubs—reaches minimal levels most rapidly. In fact, water-stress conditions appear decisive, together with other factors, in termination of the life span of many annual or biennial species.

Vessel Diameter.—Although undoubtedly under genetic control, width of vessels seems subject to a greater degree of phenotypic modification than does vessel-element length. Vessels vary considerably in diameter within a single growth ring, for example. Thus, vessel diameter may be an even more sensitive indicator of xeromorphy than vessel-element length (Carlquist, 1969b). Vessel diameter in Brassicaceae does parallel vessel-element length rather closely, suggesting that ecology is important to both diameter and length. Notable are the figures for average vessel diameter in the alpine collection from Tenerife of *Cheiranthus scoparius* (27 μ), relatively wide diameter in the more nearly mesic populations of *C. mutabilis* (54 μ , 50 μ). The average of averages for vessel diameters in Brassicaceae in the present study is 40.3 μ , which is rather narrow for dicotyledons as a whole (cf. Metcalfe and Chalk, 1950), and appreciably narrower than that for Asteraceae as a whole (51 μ : Carlquist, 1966). This suggests that the woody Brassicaceae studied have adapted to fewer mesic situations than the woody Asteraceae summarized by the writer (1966). In other families in which I have studied wood anatomy, wider vessels seem correlated with mesomorphy, narrower ones with xeromorphy, with the exception of vining or scandent species, which throughout dicotyledons have wider vessels than do their non-vining relatives.

Vessel Grouping.—As can be seen from the table, average number of vessels per group does not vary over a wide gamut in crucifers. However, the species of more xeric localities (*Cheiranthus scoparius*, Fig. 19; *Parolinia ornata*, Fig. 12; and *Stanleya pinnata*, Fig. 21) do have an appreciably higher figure. The most mesomorphic species studied here, *Cheiranthus mutabilis* (Fig. 16), has the lowest figure for vessels per group. This correlation is clearly shown in Asteraceae, where woody species divided into mesic, dry, and desert categories showed marked differences in this feature (Carlquist, 1966). This correlation is not as marked in some other families, for woody Goodeniaceae (Carlquist, 1969b) and *Echium* of the Boragi-

photographed at the same magnification as the wood sections. The scale shows 1.2 mm, the finest divisions of the scale = 10 μ .

Fig. 5-9. Wood sections of Brassicaceae.—Fig. 5-6. *Lepidium serra*, Carlquist 1799a.—Fig. 5. Transection. Note narrowness of vessels.—Fig. 6. Tangential section, showing conspicuous rays.—Fig. 7-9. *Sinapidendron angustifolium*, Carlquist 2630, base of plant.—Fig. 7. Transection. Slightly thinner-walled fibers demarcate a growth ring in upper half of photograph.—Fig. 8. Tangential section. Storied structure is evident in libriform fibers and parenchyma cells.—Fig. 9. Portion of vessel wall, showing mixture

naceae (Carlquist, 1970a) seem to show a much lower degree of vessel grouping, although the correlation could still be said to hold within these families. Vessel grouping in Brassicaceae tends to take the form of short radial chains in most species (Fig. 1, 3, 7, 10, 12), but those with a higher degree of vessel grouping (Fig. 19, 21) are characterized by irregular pore clusters.

Pitting.—As shown by the column in the table labeled "VESSEL WALL FEATURES," elliptical or markedly elongate pits characterize the vessels of most crucifer woods. Such pitting is shown for *Sinapidendron angustifolium* (Fig. 9). Pits circular in outline characterize some species, as shown for *Cheiranthus mutabilis* in Fig. 18. In *Stanleya pinnata* (Fig. 23), pits are closely crowded and notably polygonal rather than circular in outline. Both circular and elliptical pits may be found in a single species. Predominance of circular pits seems related to mechanical strength. The most markedly shrubby species, such as *Parolinia ornata* and *Stanleya pinnata*, are characterized by circular pits. The suggestion that elongate pits tend to occur in predominantly herbaceous families in those species with growth forms not seemingly related to pronounced mechanical strength has been made earlier (Carlquist, 1969a). Because most woody crucifers are at most small shrubs, often branched from near the base, abundance of elliptical pits on this basis might be expected. Broader contact areas among tracheary elements as provided by elliptical pits would seem conducive to maximal water conductivity but provide a weaker wall, viewed in mechanical terms.

Superficial examination of vessel walls in some crucifer woods gives an appearance of elliptical pitting in some cases where the pits are, in fact, circular, but where pit apertures are interconnected in lateral series by grooves. This is shown for *Cheiranthus mutabilis* in Fig. 18. As the table indicates, such grooves are almost universally present in woody crucifers, but they are not conspicuous, nor do marked forms of sculpturing sometimes called "tertiary helical thickenings" occur in the crucifers under study. Presence of grooves and other types of helical sculpture seems a clear indicator of xeromorphy in vessels of Asteraceae (Carlquist, 1966) and other families (Webber, 1936).

LIBRIFORM FIBERS

No tracheids or fiber-tracheids are present in Brassicaceae; pits of all imperforate elements are simple. This is expected for a rather specialized herbaceous family, and is true in such families as Boraginaceae, Asteraceae, Campanulaceae, Lamiaceae, Solanaceae, etc. The length of libriform fibers in species of Brassicaceae (see table) forms a parallel to that of vessel elements, as would be expected. Wall thickness and diameter of libriform fibers vary widely among the crucifers studied, however. Narrow wall thickness is not always correlated with narrowness of libriform fibers. For example, the narrow fibers of *Parolinia ornata* (Fig. 12, 13) have walls so thick

of elliptical and circular pits.—Scale for Fig. 5–8 shown above Fig. 1. Scale for Fig. 9 shown above Fig. 9: three divisions represent 10 μ each.

Fig. 10-15. Wood sections of Brassicaceae, tribe Matthioleae.—Fig. 10-11. *Matthiola maderensis*, Carlquist 2628.—Fig. 10. Transection. Inconspicuous growth-ring activity is visible.—Fig. 11. Tangential section. Rays are relatively tall.—Fig. 12-15. *Parolinia ornata*, Carlquist 2614.—Fig. 12. Transection. Note density, owing to thick-walled fibers.—Fig. 13. Tangential section. Rays are extremely short and narrow.—Fig. 14. Enlarged portion of a larger ray, showing thick-walled condition.—Fig. 15. Enlarged

that virtually no lumina are present in these cells. This feature makes the wood of *Parolinia ornata* extremely hard and dense, the hardest wood among the crucifers studied here. Although bands of vessel elements in growth rings of wood of *Stanleya pinnata* are accompanied by few fibers, there are narrow, thick-walled fibers mixed with the wider vessels in alternating bands, accompanied by very thick-walled fibers; these make the wood of *Stanleya pinnata* notably strong. An opposite condition is shown for the basal region of *Descurainia briquetii* (Fig. 24, 25). In such caudex-like bases, mechanical strength would be expected to have less significance than in upright, elongate stems of shrubs such as *Stanleya* and *Parolinia*.

Variations in wall thickness and diameter of fibers with respect to axial parenchyma and growth rings are discussed under those respective headings below.

AXIAL PARENCHYMA

In all the woods of Brassicaceae studied, scanty vasicentric parenchyma is present. This takes the form of complete or incomplete sheaths, usually only one cell wide, around vessels and vessel groups. This condition can be seen most clearly in the photograph of *Crambe fruticosa* (Fig. 3). As viewed in longitudinal sections, axial parenchyma is often present as strands of two cells, but perhaps more commonly is not subdivided. "Single-cell strands" might well be expected because the vessel elements they accompany are so short.

Some of the crucifer woods seem clearly to show fiber dimorphism in relation to growth rings. Thin-walled libriform fibers in early wood are to be expected in dicotyledonous woods, but where such fibers exhibit many or all of the characteristics of parenchyma cells, marginal parenchyma may be said to be present. Such a condition can be said to exist in the two species of *Crambe* (Fig. 1, 3), and *Matthiola maderensis* (Fig. 10), but is most clearly shown in *Sinapidendron* (e.g., *Sinapidendron angustifolium*, Fig. 7; Fig. 8, lower left). Liquid-preserved wood samples would be required if one is to ascertain whether the short, parenchyma-like, thin-walled fibers are nucleated at maturity and should, therefore, be termed parenchyma (or at least nucleated fibers). At any rate, the presence of a type of fiber dimorphism seems clearly present in the crucifers cited, in which the phenomenon resembles the conditions described in *Dubautia* or *Hemizonia* (Carlquist, 1958), where the concept of fiber dimorphism as a source for formation of marginal parenchyma was originally described.

RAY PARENCHYMA

Uniseriate rays are relatively infrequent in crucifer woods, and can be said to be virtually absent. A few uniseriate rays, with a maximum height of about three cells, can be seen in the photograph of *Descurainia briquetii*

position of fibers, also from a tangential section, showing a rhomboid crystal at left.—Scale for magnification of Fig. 10–13 shown above Fig. 1. Scale for magnification of Fig. 14–15 shown above Fig. 9.

Fig. 16–20. Sections of wood of *Cheiranthus*.—Fig. 16–18. *Cheiranthus mutabilis*, Carlquist 2648.—Fig. 16. Transection. Note large vessels, a few of which (below) are occluded by deposits.—Fig. 17. Tangential section. Non-lignified thin-walled ray cells have collapsed.—Fig. 18. Portion of vessel wall; grooves interconnect pit apertures of adjacent circular pits.—Fig. 19–20. *Cheiranthus scoparius*, Carlquist 2496.—Fig. 19. Transection. The very small vessels and their aggregations into pore multiples are prob-

(Fig. 25). There are interesting variations in width of multiseriate rays. Notably wide rays occur in *Cheiranthus arbuscula*, *C. scoparius* (Fig. 20), *Lepidium serra* (Fig. 6), and *Sinapidendron angustifolium* (Fig. 8). Exceptionally narrow rays characterize *Parolinia ornata* (Fig. 13) and *Descurainia bourgeauana*. Notably short rays (less than 0.3 mm in height) also characterize these two species. Rays taller than 1.0 mm, although relatively frequent in dicotyledons as a whole (cf. Metcalfe and Chalk, 1950), occur in only a few of the Brassicaceae studied. *Descurainia preauxiana* is the only species studied in which average ray height exceeds this figure, although species of *Cheiranthus* (Fig. 17, 20) have rays nearly as tall. Shortness of rays in Brassicaceae as a whole may be related to shortness of fusiform cambial initials. At any rate, such shortness does run counter to the often-expressed concept that herbs have wide, tall rays, little altered during secondary growth from tall, wide pith rays ("primary rays").

A surprisingly large proportion of Brassicaceae have a predominance of upright (erect) ray cells with respect to procumbent cells (see table). Only in *Parolinia ornata* is this situation reversed. Preponderance of erect ray cells has been cited as a possible criterion of juvenilism (Carlquist, 1962), and seems to characterize rays of dicotyledonous groups that have become woody secondarily, such as lobelioids (Carlquist, 1969a).

Ray cells of most crucifer woods are thin-walled but lignified (Fig. 2, 4, 6, 8, 11, 13, 20, 22, 25). In a few cases, such as *Cheiranthus mutabilis* (Fig. 17), or the basal portions of *Descurainia briquetii* (Fig. 24). Some ray cells, especially those in the central portions of rays, may be non-lignified, so that breaks in rays are evident when woods are sectioned. An opposed condition, that of ray cells with very thick, lignified walls, was observed in *Parolinia ornata* (Fig. 14) and *Descurainia preauxiana* (Fig. 27).

STORIED STRUCTURE

As can be seen from the table, all of the Brassicaceae studied can be said to exhibit growth-ring phenomena. Most of these patterns represent relatively minor modifications and are probably produced by fluctuations in availability of water during a season (e.g., *Matthiola maderensis*, Fig. 10) or over a series of seasons. Thinner-walled fibers are the only conspicuous indicators of growth rings in most species. The most strongly-marked growth rings were observed in *Stanleya pinnata* (Fig. 21), in which bands of fewer, markedly wider vessels mixed with thick-walled libriform fibers alternate with bands of numerous, very narrow vessels associated with axial parenchyma cells. Because *Stanleya pinnata* is the only continental crucifer studied here, and it comes from a temperate region, its pronounced growth-ring phenomena are to be expected. *Stanleya* grows in areas with marked seasonal contrasts in both temperature and water availability in comparison with the more moderate climates in which the insular crucifers grow.

able indicators of xeromorphy.—Fig. 20. Tangential section; a large group of vessels at right.—Scale for Fig. 16–17, 19–20 shown above Fig. 1. Scale for Fig. 18 shown above Fig. 9.

Fig. 21-27. Wood sections of Brassicaceae.—Fig. 21-23. *Stanleya pinnata*, specimen cultivated at Rancho Santa Ana Botanic Garden.—Fig. 21. Transection. Prominent growth rings are evident. Some vessels (below center) are occluded by deposits.—Fig. 22. Tangential section. This section represents portion of a growth ring in which wider vessels are present.—Fig. 23. Portion of vessel wall. Pits are basically circular, but appear polygonal owing to crowding.—Fig. 24-26. *Descurainia briquetii*, Carlquist 2557, base

RESIN-LIKE DEPOSITS

Stanleya pinnata shows marked accumulation of resin-like materials in vessels (Fig. 21). Other Brassicaceae in which such deposits in vessels were observed (although to a lesser extent than in *Stanleya*) included *Cheiranthus arbuscula*, *C. scoparius*, *Descurainia briquetii*, *D. preauxiana*, and *Parolinia ornata*. These species are all native to relatively dry, sunny areas, and these chemically unidentified deposits may be related to that factor.

CRYSTALS

Crystals are infrequent in the Brassicaceae studied. Prismatic and rhomboidal crystals birefringent in polarized light were observed in ray cells of *Descurainia briquetii* (Fig. 26). Minute rhomboidal crystals that showed no birefringence with my polarizing equipment were seen in fibers of *Parolinia ornata* (Fig. 15), but in no other cells of that species.

DISCUSSION AND SUMMARY

The wood anatomist, or for that matter the comparative plant anatomist, has been accustomed to presentation of his data in terms of differences and similarities among species, genera, etc. These data are sometimes expressed in terms of taxonomic criteria, or so accepted by taxonomists reading such data. I have become increasingly distressed about this tendency, because although harmless in some cases, it is definitely misleading in others (and apparently especially so when computerized). At best, it represents a myopia in which the bases for the differences and similarities are not sought. In wood anatomy, particular features may be the result of different growth forms (often between two species within a genus), they may represent the result of phylogenetic specialization with respect to dicotyledons as a whole, they may represent different degrees of mesomorphy or xeromorphy, they may stem from different degrees of juvenilism or adulthood, or they may result from such factors as different physiological processes, single-gene differences, or even be artifacts. To interpret such a wide variety of expressions as simple taxonomic criteria seems to me a dubious procedure.

A few examples from the present study will suffice to illustrate this point. Although *Matthiola maderensis* (Fig. 10, 11) and *Parolinia ornata* (Fig. 12–15) belong to the same tribe, Matthioleae, their woods are as different quantitatively and qualitatively as those of almost any other species of crucifers selected at random from the present study. Does this mean that this particular pair of species should not be placed in the same tribe? Decidedly not. *Matthiola* and *Parolinia* have quite different growth forms and ecological preferences: *Parolinia* is a large shrub (perhaps the largest

of plant.—Fig. 24. Transection. Vessels are wide, fibers notably thin-walled.—Fig. 25. Tangential section. Note large size of ray cells.—Fig. 26. Prismatic and rhomboidal crystals from a ray cell, photographed with polarized light.—Fig. 27. *Descurainia preauxiana*, Carlquist 2617. Ray cells, enlarged, from a tangential section. Note relatively thick, lignified walls.—Scale for Fig. 21–22, 24–25 shown above Fig. 1. Scale for Fig. 23, 26, 27 shown above Fig. 9.

in the family), *Matthiola* an annual or biennial; *Parolinia* grows in sub-desert areas, *Matthiola* grows during the wet season in seasonally moist localities and is therefore a mesomorphic genus in essence.

This case can be put even more strongly by saying that of the Brassicaceae studied, any given species falls quantitatively and qualitatively within the range of xylem expressions found in Asteraceae. Are these two families closely related? Obviously not—and many other families could be shown to overlap completely with respect to secondary xylem features. Similarities between woods of Brassicaceae and Asteraceae probably derive merely from the facts that both families have woods with numerous specialized features, both families have at least a large proportion of ancestors derived from herbaceous ancestors, and both families have numerous species in relatively dry, pioneer habitats. Relevant data from evolution, growth form, etc., are all-too-rarely invoked by the wood anatomist. Can we expect blind use of wood characteristics, with or without a computer, to counteract these deficiencies? Clearly not. If a wood anatomist does not understand the significance of his own data, others unfamiliar with wood anatomy can hardly be expected to lessen confusion and may merely increase it.

Ecology obviously guides wood evolution, but often indirectly and with numerous alternatives, compromises, and shifts in direction. Wood features may be related to more than a single factor. To illustrate the complexity of this situation, I will attempt to cite which characters are, in my opinion, related to particular factors:

Level of Specialization of the Family Brassicaceae.—Because herbaceous dicotyledonous families are, in general, more specialized than their most closely related truly woody counterparts, we may expect a relative abundance of specialized features in Brassicaceae. Woody species of this family are all or nearly all probably derived from more herbaceous ancestors. High level of specialization for the family as a whole is shown by the very short vessel elements with exclusively simple perforation plates and nearly transverse end walls; absence of tracheids and fiber-tracheids in favor of libriform fibers; scanty vasicentric axial parenchyma; and absence of uniseriate rays. Presence of storying in two genera is a specialized feature (Bailey, 1923), but one that can occur sporadically in families containing many fewer specialized features than do those of Brassicaceae.

Ecology.—The very short vessel elements of the crucifer woods of the present study seem related, in part, to the fact that these woody crucifers grow mostly in xeric localities. Within the family, more mesomorphic species have longer vessel elements (*Cheiranthus mutabilis*), more xeric species shorter ones (*Cheiranthus scoparius*), but the range is not great, probably because the woody crucifers studied have not adapted to as wide a gamut of ecological niches as have such genera as *Euphorbia* and *Scaevola* in the Hawaiian Islands. Narrowness of vessels in crucifers is also exceptional compared to those of dicotyledons at large, and this seems most easily interpreted as an expression of xeromorphy. Presence of grooves interconnecting pit apertures is suggestive of another xeromorphic indicator: it clearly seems to be in such other families as Asteraceae and Gooden-

iaceae. Number of vessels per group increases in the more markedly xeromorphic crucifers (*Cheiranthus scoparius*, *Parolinia ornata*, *Stanleya pinnata*). Conspicuousness and complexity of growth rings is directly related to ecological extremes, so it is not surprising that the only continental species included in this study (*Stanleya pinnata*) has the most clearly-demarcated growth-ring phenomena. Deposits of an unidentified resin-like material are most abundant in vessels of the more xeromorphic crucifers. In citing ecological correlations, however, I again call attention to the fact that woody species of *Draba* and *Romanschulzia* are not included in this study, and these might prove informative in broadening conclusions.

Growth Form.—Most crucifers in this study are subshrubs, branched from near the base. The clearest exceptions, where renewal buds can be more than a meter above the surface of the ground, are *Parolinia ornata* and *Stanleya pinnata*. Mechanical strength by virtue of thick-walled fibers is pronounced in these two species. These two species also have lateral-wall vessel pitting in the form of circular pits exclusively, whereas the remainder mostly have elliptical pits predominantly or exclusively, some with near-scalariform conditions. Presence of elliptical pits is regarded here as a feature, perhaps preserved into older stems from metaxylem by a kind of juvenilism, which is not disadvantageous because the growth forms of most woody crucifers do not seem to stress maximal mechanical strength. *Parolinia ornata* has exceptionally short, narrow rays that may possibly be related to increased mechanical strength of this species.

Juvenilism.—In addition to the relative abundance of elliptical pits cited above, predominance of erect ray cells in most woody crucifers might be explained as a form of juvenilism, or paedomorphosis. Wide, tall rays might be expected in a basically herbaceous group of dicotyledons. Such rays do not occur in Brassicaceae: perhaps short ray initials in the cambium bear a correlation with short fusiform cambial initials characteristic of these woods.

Taxonomic Criteria.—Under this heading one can cite a residue of features that are not obvious adaptations to particular factors; to be sure, some of the characteristics cited above could be utilized taxonomically, given a proper perspective. For example, presence of storying in two genera of the same tribe, the Brassiceae (*Crambe*, *Sinapidendron*) as opposed to absence in the other crucifer genera studied may be significant. However, presence or absence of crystals of particular sizes and shapes and in particular cell types (*Parolinia ornata*, *Descurainia briquetii*) is the sort of characteristic easily used taxonomically—provided comparable materials are studied. However, there are no wood features one could cite properly as species, genus, or even family characteristics on the basis of the present study—or very likely ever. One cannot really compare xylem of a markedly woody shrub to that of an ephemeral annual any more than one could extract taxonomic value from comparison of a proembryo of one species with a mature embryo of another. The present study can only be a survey of some Brassicaceae woody enough to provide convenient objects for investigation of secondary xylem. True comparability and a monographic approach must, in my

opinion, be the basis for taxonomic assessment of materials. These options are impossible where study of secondary xylem of Brassicaceae is concerned.

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