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WOOD ANATOMY OF *ECHIUM* (BORAGINACEAE)SHERWIN CARLQUIST¹*Claremont Graduate School and Rancho Santa Ana Botanic Garden,
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INTRODUCTION

Echium is a genus of interest with relation to islands: annual and short-lived perennial species occur within the Mediterranean region, but species on the Atlantic Islands have a great variety of growth forms, most notably some shrubs much woodier than any non-insular echiums. Other typically herbaceous dicotyledonous groups in which species of the Atlantic Islands are appreciably woodier than non-insular ones include *Centaurea* and *Sonchus* (Asteraceae); *Cheiranthus*, *Crambe*, *Descurainia*, *Parolinia*, and *Sinapodendron* (Brassicaceae); *Convolvulus* (Convolvulaceae); and *Plantago* (Plantaginaceae).

The tendency for Macaronesian species to be woodier than their mainland relatives has naturally given rise to interpretations. The rosette shrubs of these islands are quite characteristic; such shrubs were termed "Federbuschgewächse" by Schenck (1907). These suggest to some workers herbaceous groups in which the notably moderate climate of islands has permitted continued growth; in these groups there is natural selection for plants that are of longer duration and increased woodiness, suiting the year-long growing season of such insular areas. This theory has had a number of adherents: Schenck (1907), Rikli (1912), Johnston (1953), and Carlquist (1965). Johnston's commentary is directed to *Echium* in particular, and is, in my opinion, a very well worded and pertinent description of the probable phylexis in *Echium*. To be sure, other workers have regarded the Macaronesian rosette shrubs as relicts: Meusel (1952) and Lems (1961). Lems did modify his views, both in a subsequent paper (Lems and Holzapfel, 1968) and in conversations with me prior to his death. Those who hold the relict hypothesis are generally not familiar with island floras on a world basis, for one must explain why the same phenomena happen not merely on the Canary Islands and Madeira, but on volcanic islands all over the world. These islands are relatively recent. The groups which are represented on islands by rosette shrubs and rosette trees are the weediest, most plastic, and most evolutionarily active groups of dicotyledons: Asteraceae, Lobelioideae of Campanulaceae, Brassicaceae, Solanaceae, Chenopodiaceae, Plantaginaceae, etc. Insular rosette shrubs and rosette trees in these groups are not easily confused with true trees and truly woody shrubs;

¹Work on insular woods, including the present study, has been aided by two grants from the National Science Foundation: GB-4977X and GB-14092.

they have such herbaceous features as wide pith and wide cortex, lack of extraxylary fibers in the stem, limited longevity, and herb-like wood patterns (Carlquist, 1962, 1966, 1970a, 1970b, 1970c). Those who hold that such rosette shrubs and rosette trees are relicts on islands must still explain how such plants, obviously derived from herbaceous ancestors, have evolved in any case, so that the question of their occurrence on islands and island-like areas is not answered in any respect. The insular forms have virtually no similar relatives on mainland areas, and one would have expected at least a few to survive, for maritime climates occur along coasts of continents. The hypothesis that these represent herbaceous groups that have arrived on islands by means of their superior dispersal ability and have, in the strongly disharmonic floras of oceanic islands evolved to suit the moderate climatic conditions seems the hypothesis that offers the fewest difficulties.

Wood collections rarely contain more than a few samples from herbaceous or even shrubby plants, so woods had to be collected in the field. Such field experience, however, is especially valuable because it permits direct acquaintanceship with the ecological conditions under which the various species of *Echium* or other taxa grow. Although I cannot take space to detail my own field observations, the reader will find helpful data and photographs in papers by Schenck (1907), Burchard (1929), Lems (1960), and Lems and Holzapfel (1968).

The species for which wood anatomy is studied here represent a wide range of ecological extremes and growth forms. For example, *E. bourgeaunum* is an acaulescent monocarpic rosette plant with a single giant inflorescence. It is endemic to a small alpine area: the caldera of El Teide, about 3000 m on the island of Tenerife, Canary Islands. The plant studied here probably flowered in its third year, for it produced three concentric rings of secondary xylem, rings connected by thin-walled parenchyma cells which break down when dried, so that the rings are separate (wood from the outermost was studied here). The caldera of El Teide is a decidedly xeric locality, and wood anatomy ought to demonstrate xeromorphy most clearly.

Echium strictum is a short-lived shrub which perhaps dies after only two or three years. It is native to rocky openings in the laurel forest, as on the Anaga Peninsula, Tenerife, at about 500 m elevation. *Echium decaisnei* and *E. onosmaefolium* are shrubs native to markedly dry lowland situation on Gran Canaria, Canary Islands. However, *E. leucophaeum*, *E. giganteum*, *E. nervosum*, *E. aculeatum*, *E. virescens*, and *E. webbii* are shrubs native to dry situations also. Such situations include dry barrancos, open slopes, rubble slides, and new cinders. Most areas occupied by these *Echium* species are between sea level and 1000 m elevation. Several of these species occupy both the subtropical and temperate life zones of Lems and Holzapfel (1968). Rainfall is more important than temperature where wood anatomy is concerned. Of the shrubby species above, *E. giganteum* grows in the most mesic situations, *E. onosmaefolium* in the most xeric. However, all areas in the Canary Islands other than the laurel forests could be described as dry, so the range between these two species in ecology is not very great.

On the Canary Islands, one peculiar *Echium* is native to the laurel-*Myrica* forests: *E. pininana* of La Palma. This plant is an unbranched monocarpic rosette tree. The stem becomes two to three meters tall before flowering; the massive cone-like inflorescence increases the height of the plant two or three meters more. The habit seems well suited to the forest, for the rosette is raised to the forest canopy on the slender unbranched stem, and the inflorescence protrudes conspicuously. On Madeira, *Echium candicans* (the *E. fastuosum* of cultivation) is a large shrub found in openings in the moist laurel-*Myrica* forests; the closely related *E. nervosum* is perhaps a sort of lowland ecotype or vicarious species, found at elevations down to sea level.

Woods of *Echium* are of potential anatomical interest because basically herbaceous groups of dicotyledons represented by woodier species on islands show close relationship between wood anatomy and habitat. Do woods of *Echium*, too, show these relationships, and show alterations in wood anatomy as they evolve into the various ecological situations on islands? This is true of groups in the Hawaiian Islands: lobelioids (Carlquist, 1970a), *Scaevola* (1970b), and *Euphorbia* (1970c). The Macaronesian species of *Euphorbia*, although included in the paper just cited, are not really comparable to patterns in *Echium* because Macaronesian euphorbias are all succulent and therefore the relationship between wood anatomy and ecology is definitely modified.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

While most wood samples of *Echium* were collected in the field, some were taken from cultivated specimens (these bear collecting numbers of the 4000 series in Table 1). Dr. Kornelius Lems began a planting of *Echium* species in the Rancho Santa Ana Botanic Garden in 1966. The experimental garden of this institution proved a successful place for growing these, for the Mediterranean climate of southern California approximates the climate of the Canary Islands. Unfortunately a severe freeze in 1968 killed many specimens, but this in itself was informative, for the species that survived were those of dry upland areas. Wood samples were taken from surviving individuals in 1969. I am grateful to the late Dr. Lems both for the use of this planting and for his numerous helpful comments regarding field work in the Canary Islands and Madeira.

Wood anatomists are often asked whether wood anatomy of a plant is altered under cultivation. Woods from the cultivated *Echium* specimens were interesting in this respect. The data of Table 1 are not a total answer to this question, but they are a contribution. The great similarity between cultivated and naturally-occurring specimens of *E. onosmaefolium* is evident. This is true in *E. pininana* data also. This similarity is unexpectedly close, in fact.

The two samples of *E. nervosum* are from the base of a plant and from a branch, respectively. In the case of *Echium pininana*, an entire plant collected in its native habitat was cut into segments that were labeled. These segments were each about 14 inches long. One of these included the base.

Segments above the base are labeled "level 1," "level 2," etc. In the case of other species, wood samples were routinely taken from the bases of mature plants. Sections and macerations were in all cases prepared from peripheral regions of the samples.

Sections and macerations were prepared according to the usual techniques. With the exception of *E. bourgeauanum*, in which the small amount of wood formed and the narrowness of the rings provided problems, no unusual difficulties were experienced in sectioning. Analysis of preparations was undertaken, much in the style of my earlier studies on wood anatomy, to explore sources of divergence among the species of *Echium*. Quantitative and qualitative characteristics of interest in this regard are summarized in Table 1. Most of the measures used are obvious. Vessel grouping was determined by counting the number of vessels in a group as seen in a transection, and dividing by the number of such groups; solitary vessels would yield a figure of 1.0 in this method. Fiber width is a measure based on the greatest width of a fiber as seen in a maceration, and diameters from measurements of fibers averaged. In the case of all quantitative characters, averages are based on 50 or more measurements for each feature. There is no special merit in the use of 50; statistical reliability for measures in wood anatomy is nearly always very low, so that attempts to increase reliability by using, say, 100 measure rather than 50 are futile. The variability between different portions of a plant of between different individuals would override the value of a statistically reliable determination of quantitative features within a single sample.

Thanks are due a number of individuals for various kinds of assistance. My field work on the Canary Islands and Madeira was aided not only by Dr. Lems, but by Mr. Günther Kunkel. For work in sectioning woods and measuring wood features, thanks are due Mrs. Jane Benjamin Baker and Mr. Timothy O. Magee.

ANATOMICAL FEATURES

EXPLANATION OF TABLE

In Table 1, quantitative and qualitative features of *Echium* woods are summarized; qualitative features are given in abbreviated form. In the column labeled "Uniseriate Ray Abundance," "+" = presence of rays to an appreciable extent, "I" = infrequent (one per mm² or fewer), and "O" = very few or absent. In the column labeled "Ray Histology," upper case letters denote abundance of a cell type, lower case denotes infrequency, and no letters for a given cell type indicates virtual absence; "U" or "u" = upright (erect) ray cells; "S" or "s" = square; "P" or "p" = procumbent. These cell types are seen in radial sections, of course. In the column headed, "Pits of Imperforate Tracheary Elements," presence of borders on pits is indicated by the letters "v" (vestigial borders) or "n" (no perceptible borders). The letter "w" in this column indicates that pit apertures are wide, elliptical rather than slit-like as seen in face view of a wall. Under the heading "Pore Grouping," the letter "M" denotes pore multiples — circular or elliptical clusters; "R" indicates that in addition to pore multiples, radial chains are frequent. In the column headed "Storied Elements," "af"

indicates that virtually all of the fibers (or fiber-tracheids) conform to a storied pattern; "ff" indicates that some or a few fibers conform to the storied pattern; a question mark indicates that the storied condition could not be confirmed. If only a few fibers are storied, even a series of tangential sections may not include a storied portion. There seems a tendency for storying in early wood of growth rings, so that tangential sections not including early wood may well not show storying. Another problem is that where the grain of a wood is markedly rippled (as in *E. bourgeauanum*, Fig. 2) storied structure may not be demonstrable in tangential sections.

VESSELS

Dimensions.—Vessel elements are shorter in *Echium* than in dicotyledons as a whole. The average for dicotyledons at large is about 500 μ (Metcalfe and Chalk, 1950); the average vessel-element length in *Echium* is about 200 μ . This suggests that *Echium* is relatively specialized, as one might expect for a group of herbs. More significantly, the shortness of vessel elements seems a good indicator of xeromorphy. The only species that could be described as mesophytic with respect to vessel-element length are *E. candicans* (Fig. 12; average vessel-element length 233 μ), *E. giganteum* (Fig. 14; 241 μ), *E. hierrense* (237 μ), and *E. pininana* (Fig. 18; average vessel-element length at base 233 μ). The correlation between longer vessel elements and mesic habitat is close. In contrast, the most xeromorphic species of *Echium* in terms both of habitat and vessel-element length is the alpine *E. bourgeauanum* (Fig. 2; average vessel-element length 138 μ). Other species of *Echium* between these extremes have vessel-element length approximately correlated with differences in habitat, although the gamut is not a wide one.

Vessel-element length was determined for a series of levels within the plant body in the case of *E. pininana*. The trend within this plant is quite clear: vessel elements are slightly longer in the root than in the base of the stem. Upward from the base, vessel-element length increases rather sharply. In the inflorescence region, vessel-element length is more than double that found in the base of the plant. Is this an indication of more juvenilistic wood in upper portions, where less wood is formed? Longer vessel elements would be expected there if juvenilism does in fact operate (Carlquist, 1962). Longer vessels in the root than in the stem may relate to the mesomorphy of underground structures as opposed to above-ground structures. This possibility needs to be analyzed in other groups. Apparently this trend does occur in Fouquieriaceae (James S. Henrickson, personal communication).

Vessel diameter also appears to correlate with xeromorphy. In Goodeniaceae (Carlquist, 1970b), vessel diameter appeared to be an even more sensitive indicator than vessel-element length. One would expect this, because diameter is not controlled by the patterns of cambial cell length; diameter appears more easily altered during ontogeny. Narrow vessels would be expected for *E. bourgeauanum* (Fig. 1). Other species in which notably narrow vessels occur include *E. strictum* (Fig. 3), *E. virescens* (Fig. 7), and *E. aculeatum* (Fig. 9). Relatively wide vessels, on the contrary, characterize *E. candicans* (Fig. 11) and *E. pininana* (Fig. 17). These two species are the only echiums native to moist laurel forest.

TABLE 1. Wood Characteristics of *Echium* Species.

NAME	COLLECTION	
<i>Echium aculeatum</i> Poir.	Carlquist 2484 (RSA)	
<i>E. bourgeauanum</i> Webb	Carlquist 2498 (RSA)	
<i>E. candicans</i> L. f.	Carlquist 2647 (RSA)	
<i>E. decaisnei</i> Webb	Carlquist 2548 (RSA)	
<i>E. giganteum</i> L. f.	Carlquist 2539 (RSA)	
<i>E. hierrense</i> Webb	Carlquist 4343 (RSA)	
<i>E. leucophaeum</i> Webb	Carlquist 2724 (RSA)	
<i>E. leucophaeum</i> Webb	Carlquist 2517 (RSA)	
<i>E. nervosum</i> Ait.	Carlquist 4345 (RSA)	LARGE STEM
<i>E. nervosum</i> Ait.	Carlquist 4345 (RSA)	SMALL STEM
<i>E. onosmaefolium</i> Webb & Berth.	Carlquist 2584 (RSA)	
<i>E. onosmaefolium</i> Webb & Berth.	Carlquist 4344 (RSA)	
<i>E. pininana</i> Webb & Berth.	Cultivated at RSA (NO SPECIMEN)	
<i>E. pininana</i> Webb & Berth.	Carlquist 2730 (RSA)	ROOT
<i>E. pininana</i> Webb & Berth.	Carlquist 2730 (RSA)	BASE
<i>E. pininana</i> Webb & Berth.	Carlquist 2730 (RSA)	LEVEL 3
<i>E. pininana</i> Webb & Berth.	Carlquist 2730 (RSA)	LEVEL 6
<i>E. pininana</i> Webb & Berth.	Carlquist 2730 (RSA)	LEVEL 10
<i>E. strictum</i> L. f.	Carlquist 2511 (RSA)	
<i>E. virescens</i> DC. var. <i>angustissimum</i> Bolle	Carlquist 2446 (RSA)	
<i>E. virescens</i> DC. var. <i>virescens</i>	Carlquist 4346 (RSA)	
<i>E. webbii</i> Coincy	Carlquist 4342 (RSA)	

Groupings.—The degree of vessel grouping is low compared to some other dicotyledonous groups. However, larger aggregations of vessels can be seen in *Echium bourgeauanum* (Fig. 1). The range among the other species is not very great. Examination of the transections illustrated here shows that pore multiples are the predominant groupings, but radial chains are common in a few species: *E. bourgeauanum* (Fig. 1), *E. strictum* (Fig. 3), *E. hierrense*, *E. leucophaeum* (Fig. 7), and *E. webbii*.

LENGTH VESSEL ELEMENTS, AVERAGE, μ	LONGEST VESSEL ELEMENT, μ	VESSEL DIAMETER, AVERAGE, μ	WIDEST VESSEL, μ	VESSELS PER GROUP	DIAMETER VESSEL PITS, μ	LENGTH LIBRIFORM FIBERS OR FIBER-TRACHEIDS, AVE., μ	DIAMETER LIBRIFORM FIBERS OR FIBER-TRACHEIDS, AVE., μ	THICKNESS WALLS LIBRIFORM FIBERS OR F.-TRACHEIDS, μ	HEIGHT MULTISERiate RAYS, AVERAGE, <i>mm</i>	WIDTH MULTISERiate RAYS, AVERAGE, CELLS	UNISERiate RAY ABUNDANCE (SEE TEXT)	RAY HISTOLOGY (SEE TEXT)	PITS OF IMPERFORATE TRA- CHEARY ELEMENTS	PORE GROUPINGS	STORIED ELEMENTS
228	326	53	112	1.5	5	354	22	5	0.6	3.0	+	USP	v	M	ff
138	204	41	89	4.4	7	217	19	3	0.8	10.8	+	usP	w,n	R	?
233	298	77	164	1.5	5	373	21	4	0.6	3.4	0	USp	v	M	ff
205	296	67	107	1.6	5	309	32	4	0.8	4.9	0	USP	v	M	af
241	296	64	125	1.3	5	365	23	5	0.3	2.3	+	USp	v	M	af
237	357	58	99	2.1	5	375	25	5	0.5	3.6	0	USP	v	R	?
183	245	46	78	1.7	5	362	21	4	0.4	2.5	I	USp	v	R	ff
233	296	29	70	1.6	5	322	18	4	0.7	2.8	I	USp	v	R	ff
163	296	68	99	1.5	5	236	29	3	0.4	4.1	0	USP	w,n	M	ff
126	265	65	104	1.6	5	253	30	3	0.3	3.4	I	USP	w,n	M	?
164	275	68	107	2.4	6	276	33	5	0.4	3.5	+	USP	v	M	ff
182	275	67	109	2.3	6	290	34	4	0.4	3.5	+	USP	v	M	ff
193	286	85	148	2.2	5	363	28	3	0.6	4.0	I	Usp	n	M	ff
268	380	127	260	1.5	7	485	27	3	1.3	4.0	I	Us	n	M	ff
233	296	81	135	1.7	6	407	29	4	0.8	5.3	I	Usp	n	M	ff
291	612	94	161	1.8	6	519	26	5	0.9	3.7	I	Usp	n	M	ff
322	644	86	156	2.1	6	518	27	6	0.7	2.8	I	Us	n	M	ff
576	1030	87	160	2.2	6	840	27	6	0.6	2.2	I	Us	n	M	ff
184	255	54	104	1.7	4	300	22	3	0.3	3.6	+	USP	w,n	R	ff
225	316	53	107	1.5	5	326	25	5	0.3	2.1	+	USP	v	M	ff
182	275	56	91	1.5	5	313	30	3	0.5	6.3	+	uSP	n	M	?
163	234	76	140	2.5	5	299	27	4	0.8	4.6	+	uSP	v	R	f

Pitting.—All species of *Echium* have simple perforation plates, and no aberrant plates were observed. With respect to lateral-wall pitting, alternate pits characterize all the species (Fig. 19–22). One might expect, on the basis of paedomorphosis considerations, that elliptical or scalariform pits might occur. A few such pits were seen in *E. candicans* (Fig. 20). Because this is a mesic species, one would expect that elliptical pits might be present: such pits characterize only a few Goodeniaceae, but all are

rain-forest species (Carlquist, 1970b). *Echium* has not entered true rain forest, for there are no such areas on the Atlantic islands. Some species of *Echium* do appear at first glance to have elongate pits. This appearance is caused by presence of grooves which interconnect pit apertures in a helix. These can often be demonstrated where portions of a vessel wall are shaved away by sectioning; they are illustrated here for *E. aculeatum* (Fig. 21) and *E. bourgeauanum* (Fig. 22). These grooves were observed in all species of *Echium*, but seemed most conspicuous in species of xeric localities: *E. bourgeauanum*, *E. onosmaefolium*, and *E. virescens*, for example.

In many species of *Echium*, vessel-wall pits appear to have rough margins on apertures. This is suggested in Fig. 19–22. This roughness could be a form of vesturing, but should not yet be designated as such; it could be merely aggregation of droplets of the resin-like substances so common in these woods, even though the roughness is rather uniform. Ultra-thin sections would be needed to clarify this matter.

Pits on vessels of *E. pininana* (Fig. 19) and *E. bourgeauanum* (Fig. 22) are somewhat larger than those of other species.

FIBER-TRACHEIDS AND LIBRIFORM FIBERS

There are vestigial borders on some imperforate tracheary elements in *Echium*, as shown in Table 1. Presence of such borders was noted for *Echium* by Metcalfe and Chalk (1950). Elements with such borders may arbitrarily be designated as fiber-tracheids, while elements with simple pits can be termed libriform fibers.

In species of *Echium* with growth rings, early wood contains fibers that are wider, thinner-walled, and generally shorter than those in other portions of the axial xylem. In addition, these shorter fibers have a greater tendency to be storied than do fibers in other parts of a growth ring. All of these features characterize woods of Heliantheae in which "fiber dimorphism" was said to be present (Carlquist, 1958). This also characterizes other woods, such as certain legumes (Cumbie, 1960). The shorter fibers in *Echium* cannot be described as parenchyma cells as they can in certain of the Heliantheae or in certain legumes. These shorter fibers are visible as lighter zones in the transections shown (Fig. 3, 9, 11), but they can also be seen in tangential sections illustrated (at left in Fig. 10, 12). One species, *E. bourgeauanum*, is exceptional in that at the end of each year's xylem accumulation, a band of thin-walled parenchyma cells are formed.

There is a perceptible change in wall thickness of libriform fibers from root to inflorescence in *Echium pininana*. In the root, the fibers are thin-walled, whereas farther up the stem, fibers become thicker walled. This seems reminiscent of the condition in certain lobelioid woods: in *Cyanea leptostegia*, an exceptionally tall palmiform rosette tree, libriform fibers are notably thick walled in upper portions of the plant (Carlquist, 1970a).

AXIAL PARENCHYMA

Metcalf and Chalk (1950) report *Echium* as one of the Boraginaceae in which scanty vasicentric parenchyma occurs. This report was perhaps based on *E. candicans*. However, vasicentric parenchyma must be very sparse indeed. I did not observe with certainty any cells I could clearly term

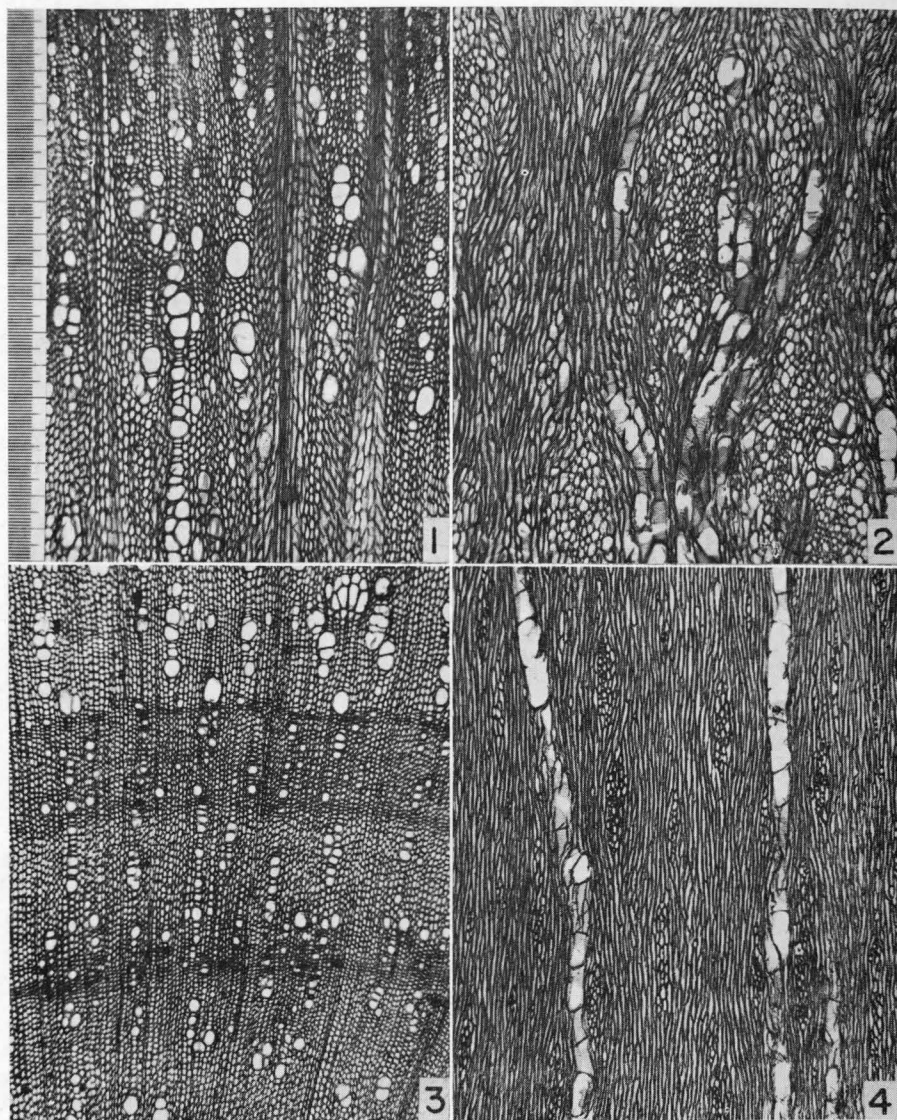


Fig. 1-4.—Fig. 1-2. *Echium bourgeauanum*, Carlquist 2498.—Fig. 1. Transection. Vessels narrow during latewood (top of photograph).—Fig. 2. Tangential section, showing wide, high rays.—Fig. 3-4. *Echium strictum*, Carlquist 2511.—Fig. 3. Transection, showing several growth rings.—Fig. 4. Tangential section. Rays are short, narrow; fibers and vessel elements are short.—Scale to left of Fig. 1 is a photograph of a stage micrometer at the same scale as the photomicrographs shown in Fig. 1-18. The scale shows 1.7 mm; subdivisions are $10\ \mu$ each.

axial parenchyma, despite the fact one would expect it in a family such as Boraginaceae. Scanty vasicentric parenchyma is present in wood of many tubiflorous dicotyledons that are basically herbaceous. One would expect at least some strands of two or more cells to be present if axial parenchyma cells do occur in *Echium* woods. Such were not observed. The parenchyma cells mentioned above for *E. bourgeauanum* are probably in the nature of shorter fibers, representing fiber dimorphism, and not related to scanty vasicentric parenchyma.

VASCULAR RAYS

Dimensions.—*Echium* has rays relatively short for a group of herbaceous dicotyledons. Within the genus, notably short rays characterize *E. giganteum* (Fig. 14), *E. hierrense*, *E. leucophaeum* (Fig. 8), *E. nervosum*, *E. onosmaefolium*, *E. strictum* (Fig. 4), and *E. virescens* var. *virescens* (Fig. 6). Relatively tall rays occur in *E. bourgeauanum* (Fig. 2), *E. decaisnei* (Fig. 16) and *E. pininana* (Fig. 18).

Width and height of rays are not related to each other: wide rays in the genus are not necessarily also tall. In fact, the rather tall rays of *E. pininana* (Fig. 18) are of moderate width. Notably narrow rays characterize *E. giganteum* (Fig. 14), *E. leucophaeum* (Fig. 8), *E. strictum* (Fig. 4) and *E. virescens* var. *angustissimum*. Wide rays may be found in *E. bourgeauanum* (Fig. 2), *E. decaisnei* (Fig. 16), and *E. virescens* var. *virescens* (Fig. 6).

Uniseriate Rays.—Most *Echium* species have uniseriate rays, as shown in Table 1, but they are relatively infrequent, as examination of the tangential sections shown here will indicate. There is not a great deal of difference between species in which uniseriate rays are reported as "present," those reported as "infrequent," and those in which uniseriates are reported as "absent." The paucity of uniseriate rays recalls the condition seen in woody Asteraceae and other families of specialized dicotyledons.

Ray Histology.—Most species of *Echium* have heterogeneous multiseriate rays with abundant erect, procumbent, and square ray cells. A tendency toward procumbent ray cells characterizes *E. bourgeauanum* and, to a lesser extent, *E. virescens* var. *virescens* and *E. webbii*. The reverse tendency, toward abundance of erect (upright) ray cells and exclusion of procumbent cells, characterizes many woods in predominantly herbaceous groups (Carlquist, 1962, 1970a, 1970b, 1970c). This condition occurs in *E. candicans*, *E. giganteum*, *E. leucophaeum*, and *E. pininana*. These are also species with relatively long (for *Echium*) vessel elements. This suggests that greater length in fusiform cambial initials is related to greater vertical length in ray initials; both may be coordinate expressions of juvenility in a wood.

STORIED STRUCTURE

As mentioned above in connection with fiber-tracheids and libriform fibers, and indicated in Table 1, storied wood structure probably characterizes all species of *Echium* to various degrees, but it could not be definitely reported for all samples studied here. It is most conspicuous in *E. giganteum* (Fig. 14) and *E. decaisnei* (Fig. 16). However, it can also be seen to some

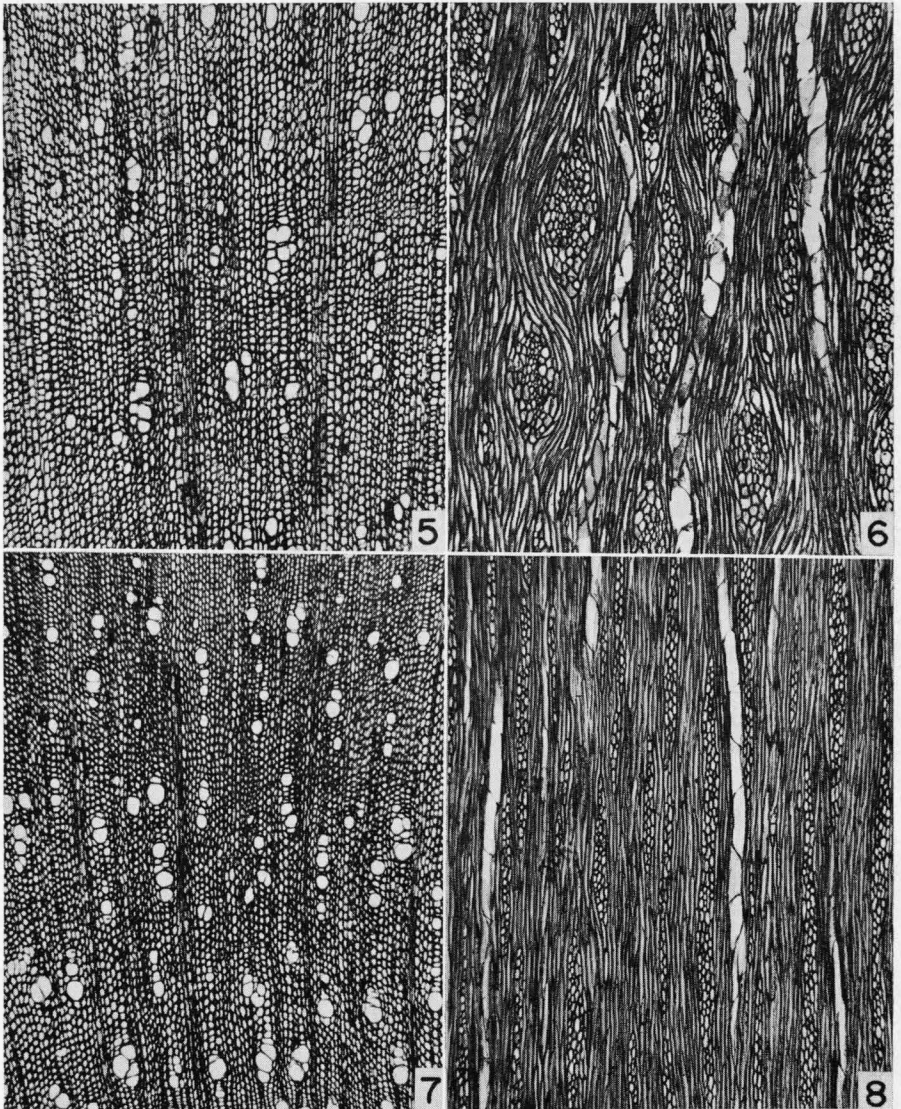


Fig. 5-8.—Fig. 5-6. *Echium virescens* var. *virescens*, Carlquist 4346.—Fig. 5. Transection. Vessels are narrow.—Fig. 6. Tangential section. Rays are notably short and wide, vessel elements are short.—Fig. 7-8. *Echium leucophaeum*, Carlquist 2517.—Fig. 7. Transection. The narrow vessels are often aggregated into radial chains.—Fig. 8. Tangential section. Rays are narrow, relatively tall.—Scale for magnification shown beside Fig. 1.

degree in all the tangential sections illustrated here. Perhaps significantly, storied structure appears most conspicuously in the largest stems. In such stems, there has been more opportunity for the radial longitudinal division of fusiform cambial initials; divisions of this type are required to produce a storied condition, and smaller stems may be expected to have less storying for this reason alone.

GROWTH RINGS

Growth rings were observed in all species except *E. pininana*. Growth rings seems a response to rainfall in *Echium* and are probably controlled by the winter and spring rains of the Atlantic islands. Ring porous wood was reported for *Echium* by Metcalfe and Chalk (1950). Where growth rings are most conspicuous, this could be said to be true, but in most species the difference between early and late wood seems relatively small. Distinct growth rings are shown here for *E. strictum* (Fig. 3), *E. aculeatum* (Fig. 9), and *E. candicans* (Fig. 11). The most marked growth ring phenomena are exhibited by *E. bourgeauanum* (Fig. 1). In this species, a growth ring begins with parenchyma (not shown), then wide vessels mixed with fibers, with vessel diameter decreasing steadily toward the end of the ring, where vessels are quite narrow.

DEPOSITS

Insoluble compounds that appear resin-like were observed in nearly all *Echium* woods studied. Such deposits were not identified, and the term "resin-like" may be misleading. Such accumulations were most abundant in *E. decaisnei* (Fig. 15, 16), where massive accumulations fill almost all parenchyma cells. *Echium onosmaefolium* also has abundant deposits. Both these species are relatively large shrubs of dry lowland situations. Moderate accumulations — droplets in many cells, massive accumulations in a few cells — were observed in *E. candicans*, *E. giganteum*, *E. hierrense*, *E. leucophaeum*, *E. nervosum*, *E. virescens*, and *E. webbii*. Little or no accumulation of the resin-like materials was observed in *E. bourgeauanum*, *E. pininana*, and *E. strictum*. These are relatively short-lived (or monocarpic) plants of upland situations.

DISCUSSION AND CONCLUSIONS

Because *Echium* has evolved into a wide variety of ecological situations, distinctions in wood anatomy within the genus might be expected to be related to these factors. The most important ecological factor in controlling wood anatomy appears to be the availability of moisture (Carlquist, 1966). Plants with succulent stems appear to fall into mesic patterns of wood anatomy, so more than mere rainfall must be taken into account (Carlquist, 1970c). Lems and Holzapfel (1968) have compared trichomes to altitudinal life zones, but a comparison to rainfall zones might have shown stronger correlations. In analyzing *Echium* woods with respect to mesomorphy versus xeromorphy, one must take into account the fact that *Echium* does not grow in real rain forest, only moist laurel forest at best. The evolution of *Echium* in wood characters is rather foreshortened, as it were, in comparison to evolution of herbaceous groups that have become woody in the

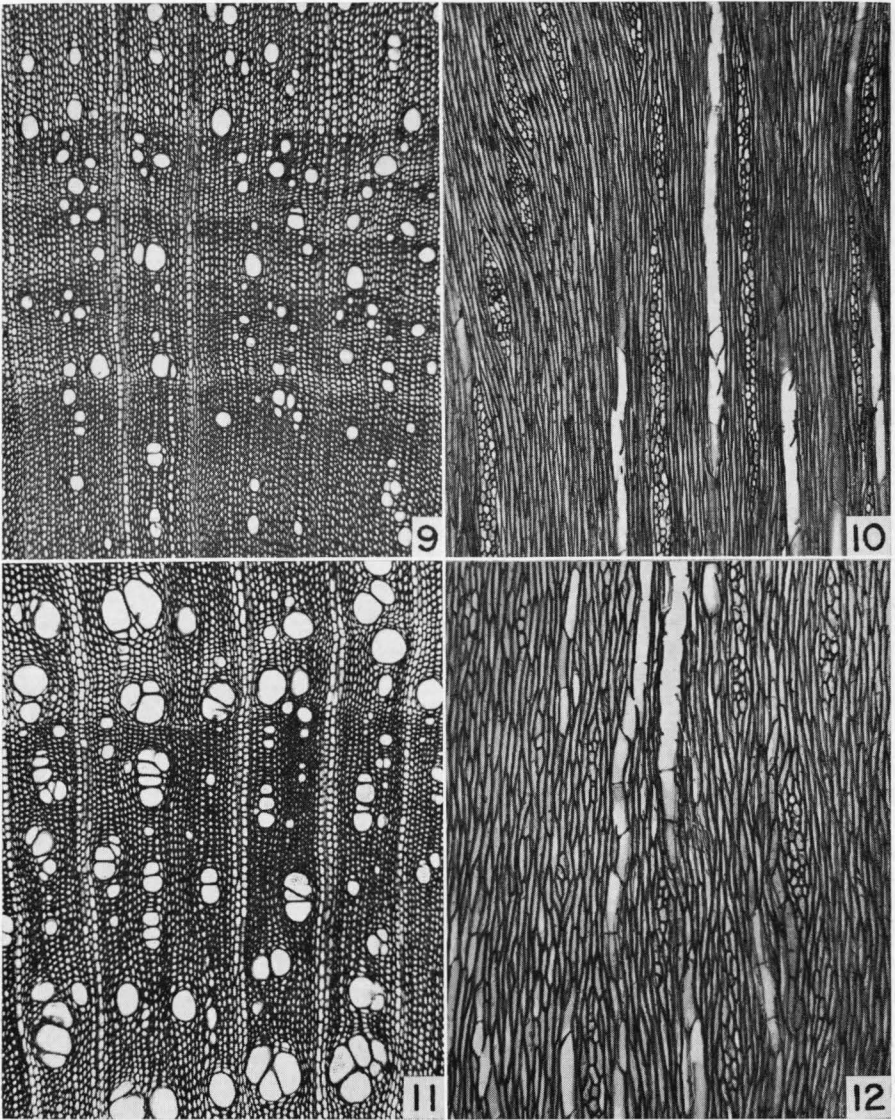


Fig. 9-12.—Fig. 9-10. *Echium aculeatum*, Carlquist 2511.—Fig. 9. Transsection. Growth rings are visible, but marked fluctuation does not occur in vessel diameter.—Fig. 10. Tangential section. The storied shorter fibers from earlywood visible at left.—Fig. 11-12. *Echium candicans*, Carlquist 2647.—Fig. 11. Transsection. Note wideness of vessels and presence of growth-ring phenomena.—Fig. 12. Tangential section; earlywood is shown. Note short, narrow rays.—Scale of magnification shown to left of Fig. 1.

Hawaiian Islands and adapted to forests where rainfall exceeds 100 inches of rain per year — for example *Scaevola* (Carlquist, 1970b) or *Euphorbia* (Carlquist, 1970c). Conceding that *Echium* as a whole has relatively short vessel elements, the gamut does correlate with moisture, from very short in the alpine *E. bourgeauanum* to long in the laurel-forest species *E. pininana* and *E. candicans*. Average diameter of vessels in a sample is likewise a good indicator of mesomorphy and xeromorphy. This figure is lowest for *E. bourgeauanum*, highest for *E. pininana*. All species of *Echium* have inconspicuous grooves interconnecting pit apertures; these are indicators of moderate xeromorphy in my opinion. Nearly all the species have growth rings the sharpness of which corresponds to severity of climate (particularly seasonality of rainfall) in the habitat of the respective species. Accumulation of the unidentified resin-like materials appears to be in proportion to either xeric conditions or size of plant.

Prevalence of erect ray cells as compared to procumbent ones is almost perfectly correlated with length of vessel elements in *Echium*. This suggests that vertical length of cambial initials — fusiform and ray — evolves with relation to a basic factor — presumably rainfall. Ray height is correlated to a lesser extent with vessel-element length. Distinctions in ray height and width appear to be species characters, with no strong correlation with ecological factors.

Presence of storied fiber-tracheids (or libriform fibers), presence of only vestigial borders or none at all on pits of imperforate tracheary elements, and near-absence of uniseriate rays are features that speak for a highly specialized level of wood structure in *Echium*, comparable only to that seen in such families as Asteraceae.

Differences in wood anatomy within a single individual are rarely investigated, but offer an interesting avenue for our understanding of factors affecting wood anatomy. In *E. pininana*, vessel-element length is slightly longer in the main root than in the base, but increases markedly as one follows a stem upward. There is a possibility that roots, which exist in an environment less subject to sudden desiccation than the aerial portions of a plant, might show more mesomorphy in wood anatomy. Wall thickness in libriform fibers increases with height in the plant; fibers have thinnest walls in the root, thickest in the inflorescence. Such patterns as variation of these ought to be analyzed in other genera of dicotyledons.

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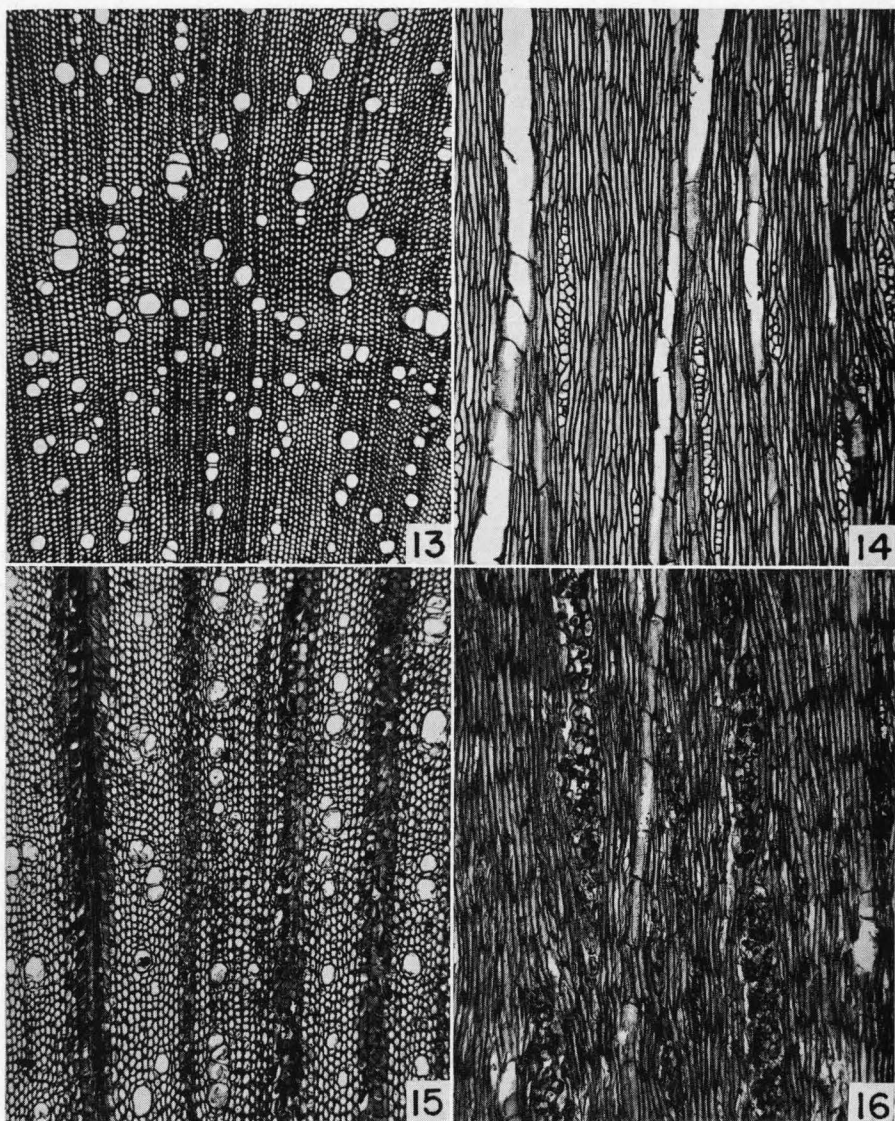


Fig. 13-16.—Fig. 13-14. *Echium giganteum*, Carlquist 2539.—Fig. 13. Transection.—Fig. 14. Tangential section. Most of the fibers are storied. Rays are narrow for the genus.—Fig. 15-16. *Echium decaisnei*, Carlquist 2548.—Fig. 15. Transection. Vessels are mostly solitary.—Fig. 16. Tangential section. The tall, wide rays are filled with an unidentified resin-like deposit. The fibers, all of which are storied, are also discolored by these deposits.—Scale of magnification shown to left of Fig. 1.

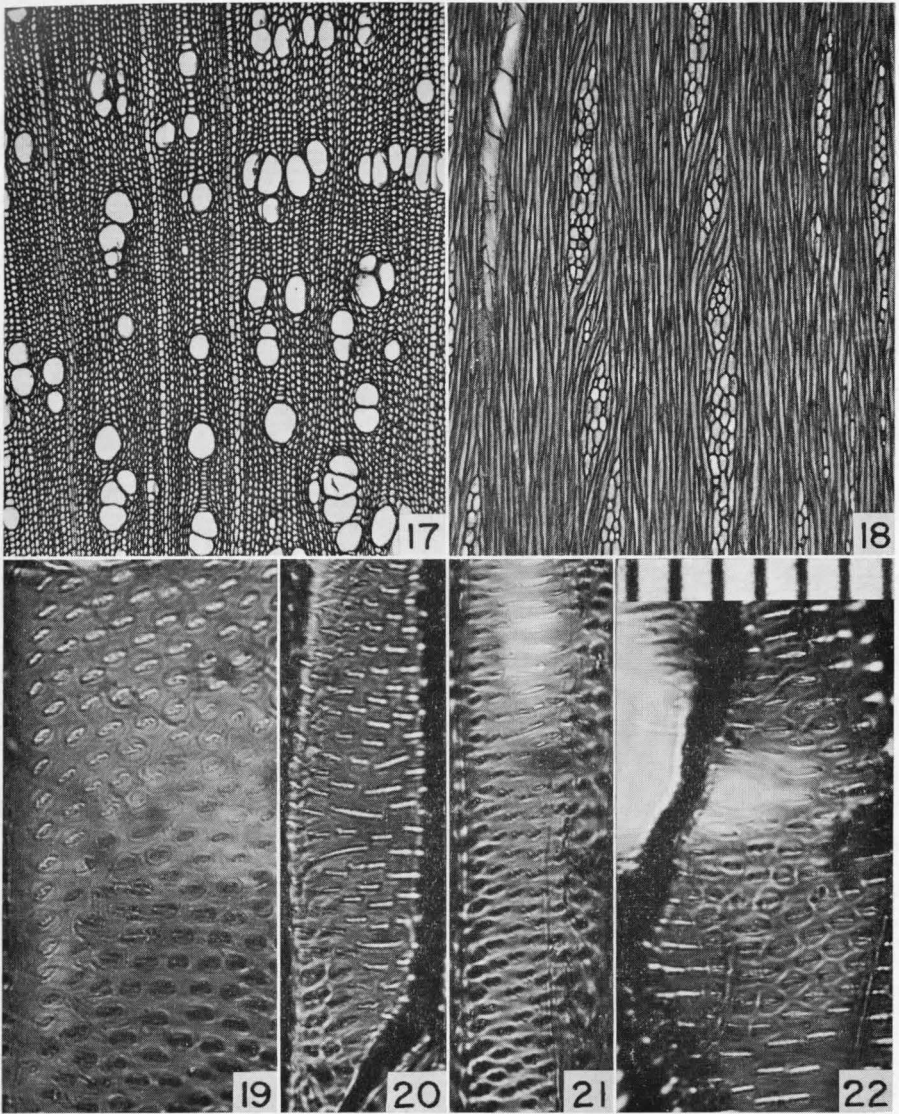


Fig. 17-22.—Fig. 17-18. *Echium pininana*, Carlquist 2730 (level 3).—Fig. 17. Transection. Note wide vessels.—Fig. 18. Tangential section; fibers in center are stored.—Fig. 19-22. Portions of vessel walls from tangential sections.—Fig. 19. *Echium pininana*, Carlquist 2730. Pits are large, alternate.—Fig. 20. *Echium candicans*, Carlquist 2647. A few elliptical pits are visible.—Fig. 21. *Echium aculeatum*, Carlquist 2484. Grooves connecting pit apertures shown where wall shaved away, at top.—Fig. 22. *Echium bourgeaunum*, Carlquist 2498. Pits are crowded; a few grooves interconnecting pit apertures

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are visible.—Fig. 17-18, scale of magnification shown to left of Fig. 1.—Fig. 19-22, scale of magnification shown above Fig. 22; each division = 10 μ .