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WOOD ANATOMY OF CYNAREAE (COMPOSITAE)

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INTRODUCTION

Few thistles or thistle-relatives develop much secondary xylem. Because many of them have an annual, biennial, or sometimes perennial rosette habit, the only cylinder of wood of any appreciable thickness occurs at the base of the stem. From pith to cambium, accumulation of secondary xylem rarely exceeds a centimeter. Cynareae are thus not notably woody, and this may explain the virtual absence of any literature on their woody anatomy. Studies on wood anatomy are with few exceptions pursued in groups of plants which are primarily shrubby or arboreal in habit. To be sure, study of woods in a group such as Cynareae is primarily a study in woods which are, because of the herbaceous nature of the species, juvenile in character. Although some taxonomic dividends accrue from such a study, the main value in examination of woods of Cynareae may lie in better understanding of woods with a strongly juvenilistic aspect. Viewed in this light, Cynareae are an excellent group for analysis, for regardless of the woody origins which appear likely for Compositae as a whole, Cynareae can all be called herbs. The only exceptions to this statement are the Juan Fernandez rosette "trees" *Centaurodendron* and *Yunquea*. Even these two genera accumulate only a relatively small amount of secondary xylem. *Centaurodendron* and *Yunquea* seem best interpreted as genera which have attained greater stature as a result of evolutionary response to conditions afforded on islands. Such an evolutionary curriculum has seemingly been followed by a number of other insular representatives of primarily herbaceous groups, such as Cichorieae (Carlquist, 1960), Lobeliaceae and Plantaginaceae.

Cynareae is a tribe widely distributed, but the greatest number of species occur in the North Temperate Zone. A prime center of diversity is Europe and Western Asia. Because many of these lands have been subjected to long agricultural usage, a number of Cynareae have become converted to weedy habits, and, by introduction, are now weeds in the New World as well as the Old. About half of the species in the present study fall into this category. Thus many species of Old World Cynareae can be collected in the field in California. During the long growing season afforded by the California climate, considerable xylem accumulation is possible, perhaps more than would be afforded in the native habitats of some of these species.

In addition, some native California thistles (*Cirsium californicum; C. occidentale*) are included in ths study. *Centaurea americana* is native to the west-

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ern and central United States. *Cirsium subcoriaceum* is an unusually robust thistle native to Mexico. *Centaurodendron* and *Yunquea* are genera endemic to the Juan Fernandez Islands; the wood anatomy of these peculiar "trees" has been discussed and illustrated in some detail earlier (Carlquist, 1958b). Much data on these insular genera has been offered in various papers by Skottsberg (1929, 1938, 1953, 1957).

Warionia saharae is a woody perennial of North Africa. Bentham (1873) claimed that *Warionia* and a related genus of southwestern Europe, *Berardia*, belong in Cynareae near *Jurinea* and *Saussurea*. *Warionia* and *Berardia* were transferred to Mutisieae subtribe Gochnatinae by Hoffmann (1890), a treatment followed as recently as 1951 by Augier and du Merac. The sum of morphological characteristics mark *Warionia* and *Berardia* as cynareoid, and one can agree with the affirmation by Small (1917) of Bentham's placement for this pair of genera.

MATERIALS, METHODS AND ACKNOWLEDGMENTS

Because wood samples of Cynareae are rarely found in wood collections, most of the materials were collected in the field from plants growing wild or in cultivation. The species utilized for this study do not necessarily represent all of the woodiest Cynareae. Species were collected if unusually woody individuals could be found. Similar individuals doubtless occur in many other Cynareae which could not be collected because of the remote localities in which they grow. Some of the samples studied here were kindly provided by Dr. Loran G. Anderson. The late Dr. Carl Skottsberg sent me in 1955 a good collection of Juan Fernandez Compositae which included wood samples of *Centaurodendron* and *Yunquea*. His interest in my studies and kindness in providing these materials are gratefully acknowledged. Dr. Hugh Iltis thoughtfully provided the wood sample of *Cirsium subcoriaceum*.

The materials for sectioning and staining wood samples are the same as those outlined earlier (Carlquist, 1958a), although samples preserved in formalin-acetic-alcohol rather than dried samples were used in most instances. Counterstaining with fast green permitted demonstration of the crassulae illustrated in fig. 9. The basal woody portions of many Cynareae, such as thistles, are difficult subjects for anatomical study because the woody cylinder is often excessively tortuous. Marked twisting of libriform fibers and other cells, as illustrated for *Silybum marianum* in fig. 10, characterizes many cynareoid wood samples. As a consequence, many portions of a section are inevitably oblique, a fact which makes analysis and illustration difficult. Some sections utilized in this study were prepared by Dr. Loran G. Anderson, Mr. Charles F. Quibell, and Dr. Alfred G. Diboll. A set of slides documenting this study has been deposited at the Division of Plant Anatomy, Smithsonian Institution, Washington, D.C. Herbarium specimens documenting the wood samples studied here are listed in table 1, with herbarium abbreviations according to Lanjouw and Stafleu (1964).

ANATOMICAL DESCRIPTIONS

Summarized in table 1 are quantitative and qualitative features which have proved useful in comparison of Cynareae as well as other Compositae. Additional information and descriptions which cannot conveniently be presented in tabular form are provided in the text under appropriate headings. Absence of figures for uniseriate rays in table 1 indicates that few or no such rays were observed, and measurements based on fewer than five rays would be meaningless.

Explanation of symbols in table 1:

ap = axial parenchyma
f = many libriform fibers
ff = a few libriform fibers
g = grooves interconnecting many bordered pits in a helix on a vessel wall
ig = inconspicuous shallow grooves which interconnect many bordered pits in a helix on a vessel wall
nv = narrower vessels
vt = vascular tracheids
wv = wider vessels
+ = presence of characteristic
— = presence of characteristic to a limited extent
0 = absence of characteristic

Ray width could not be measured for *Centaurea ragusina* because cells were thin-walled and collapsed during preparation.

VESSEL ELEMENTS

Dimensions, Shapes, Types.—The short length of vessel elements in Cynareae seems related to the specialized herbaceous habit of most species. Longer vessel elements in *Centaurodendron. Yunquea* and *Cirsium subcoriaceum* (fig. 6) may be related to the robust habit in these taxa. Literal interpretation of long vessel lengths as indices of primitiveness within Cynareae seems unwarranted in a group of plants where perhaps all wood formed could be said the be juvenile, the result of paedomorphosis (Carlquist, 1962). Species of Cynareae characterized by short vessel elements, however, can be said to be specialized in this respect. Vessel diameter of the species studied falls into a range median for Compositae as a whole. Relatively wide vessels were observed in *Cirsium subcoriaceum* (fig. 5) and *Warionia saharae* (fig. 8), whereas rather narrow vessels characterize species of *Centaurea* (fig. 1–4). Progressive decrease in vessel diameter outward from the pith was seen in *Centaurea americana* (fig. 1). Woods of Cynareae collected near the end of their growing season, such as *Centaurea americana, C. ragusina, Cnicus benedictus* and *Onopordon acanthium,* showed marked narrowing of vessel elements formed just prior to cessation of growth. Some of these vessels were as narrow as libriform fibers, and some lacked perforation plates and are therefore vascular tracheids. Where such vessels occurred, vessel groupings were large; these vessels were accompanied by axial parenchyma rather than libriform fibers.

As with other Compositae, Cynareae have simple perforation plates. Multiperforate plates, however, could be found occasionally in many species: *Centaurea americana*, *C. melitensis*, *C. ragusina*, *Cirsium californicum*, *C. occidentale* and *C. subcoriaceum* (fig. 7), for example. Such plates have been

TABLE 1. *Wood Characteristics of Cynareae*

SPECIES	COLLECTION	DIAMETER WIDEST VESSEL, μ	DIAMETER VESSELS, AVERAGE, μ
Centaurea americana L.	Carlquist 233 (RSA)	82	37.9
Centaurea cineraria L.	Anderson 1959 (RSA)	80	47.6
Centaurea cyanus L.	Carlquist 138 (RSA)	72	43.5
Centaurea iberica Trev.	Carlquist 139 (RSA)	61	38.1
Centaurea melitensis L.	Carlquist 140 (RSA)	82	37.5
Centaurea ragusina L.	Anderson 1964 (RSA)	76	34.1
Centaurea solstitialis L.	Wolf 4169 (RSA)	72	42.3
Centaurodendron dracaenoides Johow	Sparre III–9–1955 (SBT)	93	54.3
Centaurodendron palmiforme Skottsb.	Sparre V–3–1955	106	48.8
Cirsium arvense (L.) Scop.	Anderson 1965 (RSA)	81	38.6
Cirsium californicum Gray	Carlquist 123 (RSA)	72	42.6
Cirsium occidentale (Nutt.) Jeps.	Carlquist 141 (RSA)	110	63.0
Cirsium subcoriaceum Sch. Bip.	Iltis et al. 334 (WIS, US)	156	77.3
Cnicus benedictus L.	Carlquist 135 (RSA)	70	37.5
Onopordon acanthium L.	Anderson 1291 (UTC)	81	30.0
Silybum marianum Gaertn.	Carlquist 493 (RSA)	150	82.0
Warionia saharae Benth. & Coss.	Balls B2530 (RSA)	81	74.3
Yunquea tenzii Skottsb.	Skottsberg III–6–1955 (SBT)	150	40.2

reported by Tangl (1871) in *Echinops exaltatus* and by Hartig (1859) in *Onopordon acanthium;* they occur in a scattering of species in tribes other than Cynareae as well. Some of these perforation plates, such as that shown in fig. 7, appear at first glance to resemble true scalariform perforation plates characteristic of more primitive woods. However, the bars in the perforation plate illustrated are oriented not radially, but tangentially. Beside aberration in orientation, bars in multiperforate plates of Cynareae are often branched or oddly arcuate. Thus none of the perforation plates could be said to be true

Vessels per group, average	Length vessel elements, average, μ	Length libriform fibers, average, μ	Maximum width libriform fibers, average, μ	Wall thickness fibers, μ	Diameter intervascular pits, μ	Helical sculpture on vessels	Elements distinguishing early wood of rings	Storied elements	Height multiseriate rays, average, mm.	Height uniseriate rays, average, μ	Maximum width multiseriate rays, average, cells	Ray cells isodiametric to procumbent	Ray cells isodiametric to erect
1.81	189	339	19.0	3	4				1.19	53	3.8	+	+
2.01	133	285	18.2	5	4	ig			.73	39	5.9	+	+
2.88	125	231	19.4	2	5				1.09	58	4.2	−	+
3.82	143	236	19.7	2	5	ig			1.71	60	3.6	+	+
1.93	158	360	17.6	2	4				.66	146	2.3	+	+
4.21	144	228	18.9	5	4	ig	nv, vt, ap		1.47	87	?	+	+
1.58	128	290	13.5	3	5				.43	78	4.0	+	+
1.69	238	396	27.7	2–5	5	ig	ap, nv	ap	.98	97	4.2	+	+
2.33	270	340	18.8	5	5		tf	ff	1.12	—	7.2	+	+
1.60	188	286	19.4	1	5				2.07	—	9.7	+	+
3.79	178	309	19.9	2	5	ig			2.21	—	6.2	+	+
1.90	168	377	26.1	4	5	ig			.59	118	3.2	+	+
1.81	221	450	27.6	3	4	ig			1.25	153	5.8	−	+
2.83	123	316	18.6	2	5		wv		.93	128	5.1	+	+
1.75	180	340	18.4	3	6	g			.93	86	3.5	+	+
2.02	163	439	21.3	2	5				.69	70	4.5	+	+
3.02	252	377	17.8	5	5	g			1.47	222	3.0	0	+
3.79	336	462	21.9	5	5	ig		ff	1.47	—	4.4	+	+

vestiges of a more primitive condition. If they were vestiges, one would expect not only normal shape and orientation of bars, one should find predominantly plates with only one or two bars in addition to simple perforation plates. Another tribe of Compositae in which multiperforate plates have been observed frequently is Cichorieae (Carlquist, 1960). Because both Cynareae and Cichorieae are highly herbaceous groups, the frequency of multiperforate plates might reflect a phase of paedomorphosis.

Lateral-Wall Pitting.—Cynareae are characterized by intervascular bordered pits 4 or 5 μ in diameter, round in outline with elliptical apertures. Vessel-parenchyma pitting is often scalariform to some degree. This condition was observed in *Centaurea iberica, C. ragusina, Centaurodendron palmiforme, Cirsium californicum* and *Silybum marianum.* On the narrow vessels and vascular tracheids formed near the end of the growing season in *Centaurea ragusina,* all pits tend to be laterally elongate, forming a somewhat scalariform appearance.

Helical Sculpture.—Pitted vessels of Cynareae are almost uniformly provided with grooves which interconnect apertures of pits adjacent in a helix (table 1). These grooves are like those figured for Vernonieae (Carlquist, 1964) but generally are shallower and less conspicuous. Such grooves are generally best observed where portions of a wall are cut away in sectioning, as in fig. 7, where the shaved edge of a sectioned wall shows the grooves as elongate slits. Spiral sculpture of this kind was reported by Solereder (1885) for one species of Cynareae, *Stahelina arborescens.*

Vessel Grouping.—Cynareae have a degree of vessel grouping generally higher (table 1) and thus perhaps more specialized than that of other tribes of Compositae, such as Vernonieae (Carlquist, 1964). In Cynareae, grouping usually takes the form of radial chains, as in *Centaurea americana,* (fig. 1), *C. cyanus, C. solstitialis, Cirsium californicum* and *Yunquea tenzii.* Pore multiples may also be present, as in *Centaurea cineraria* (fig. 3) and *Cirsium subcoriaceum* (fig. 5); in both of these species, alignment of pore multiples into tangential bands was perceptible.

LIBRIFORM FIBERS

As shown in table 1, libriform fibers of Cynareae are not exceptionally long. They parallel the measurements for vessel-element length in each species. Notable in Cynareae is the tendency for libriform fibers to be widened in a radial direction, a condition seen conspicuously in *Centaurea solstitialis, Cirsium arvense* and *Onopordon acanthium.* This condition seems related to the herbaceous nature of Cynareae, because radially-widened fibers were noted as characteristic of Cichorieae (Carlquist, 1960) and some annual Astereae.

Unusually thin-walled fibers characterize *Cirsium arvense,* whereas they are rather thick-walled in *Centaurea cineraria* (fig. 3), *Centaurodendron dracaenoides, C. palmiforme, Warionia saharae* (fig. 8) and *Yunquea tenzii.* The presence of all three Juan Fernandez species in this list is of interest, because the larger stature of these plants suggests that thick-walled fibers may function by providing greater mechanical support. Fibers are relatively broad in *Centaurodendron dracaenoides, Cirsium occidentale* and *Yunquea tenzii.*

A unique feature observed in *Centaurodendron dracaenoides* was the presence of crassulae on libriform fibers and apotracheal parenchyma cells. Crassulae are particularly prominent on radial walls (fig. 9). Crassulae ("bars of Sanio") are usually associated with tracheids in coniferous woods, but phenomena of this sort have been reported also in dicotyledons (Bailey, 1919). The crassulae of *Centaurodendron dracaenoides* are unusually prominent, however; they conform to the usual definition: thickenings in the middle lamella, separating pits or groups of pits. I can offer no explanation for this instance of crassulae. Crassulae may be present elsewhere in Compositae, but they have not been reported yet.

Marked curvature of fibers, corresponding with the macroscopically visible twisted nature of wood, was observed in various Cynareae, such as *Silybum marianum* (fig. 10).

AXIAL PARENCHYMA

Aprotracheal Parenchyma.—Fiber dimorphism, leading to the production both of true libriform fibers and bands of apotracheal parenchyma, has been hypothesized for Compositae earlier (Carlquist, 1958a, 1961). Parenchyma of this sort was described in *Centaurodendron dracaenoides* (Carlquist, 1958b). One may note that banded apotracheal parenchyma of this sort is also found in other insular Compositae: *Argyroxiphium, Dubautia* and *Fitchia* in Heliantheae (Carlquist, 1958a); *Robinsonia, Rhetinodendron* and *Symphyochaeta* in Senecioneae (Carlquist, 1962a); and various Cichorieae (Carlquist, 1960).

Apotracheal bands are closely related to growth-ring phenomena. In the samples studied of *Centaurea ragusina* and *Onopordon acanthium,* the end of the growing season was accompanied by production of very narrow vessels and vascular tracheids, while apotracheal parenchyma is substituted for libriform fibers. This rather strong alteration of element production with relation to season was also seen in the insular species of *Hemizonia* (Carlquist, 1958a). The apotracheal parenchyma bands of *Centaurodendron dracaenoides* appear to be a less marked version of this seasonal alteration in element production, less marked because of the relatively uniform climatic conditions of the Juan Fernandez Islands. If wood samples could have been obtained from more species of annual and biennial Cynareae at the termination of their growth and fruiting, more examples of terminal bands of narrow vessels and vascular tracheids mingled with apotracheal parenchyma could doubtless have been offered.

Paratracheal Parenchyma.—Scanty vasicentric parenchyma characterizes all Cynareae studied, as it does the majority of Compositae. Such cells are inconspicuous, and almost invariably form an incomplete sheath, a single cell layer wide, around vessels or vessel groups. Paratracheal parenchyma viewed in longitudinal sections occurs as strands of two or three cells in Cynareae.

VASCULAR RAYS

Multiseriate rays predominate in Cynareae, and in no species studied were uniseriate rays at all frequent. However, uniseriates could be said to be lacking only in *Centaurodendron palmiforme, Cirsium arvense* and *Cirsium californicum.*

Erect cells predominated in multiseriate rays of all Cynareae studied except *Silybum marianum,* of which an unusually large wood sample was available, and which may, therefore, reflect a relatively adult condition in ray histology. If, as contended by the writer (1962b), the ontogenetic change from erect to procumbent cells may follow change from juvenility to adulthood, the pre-

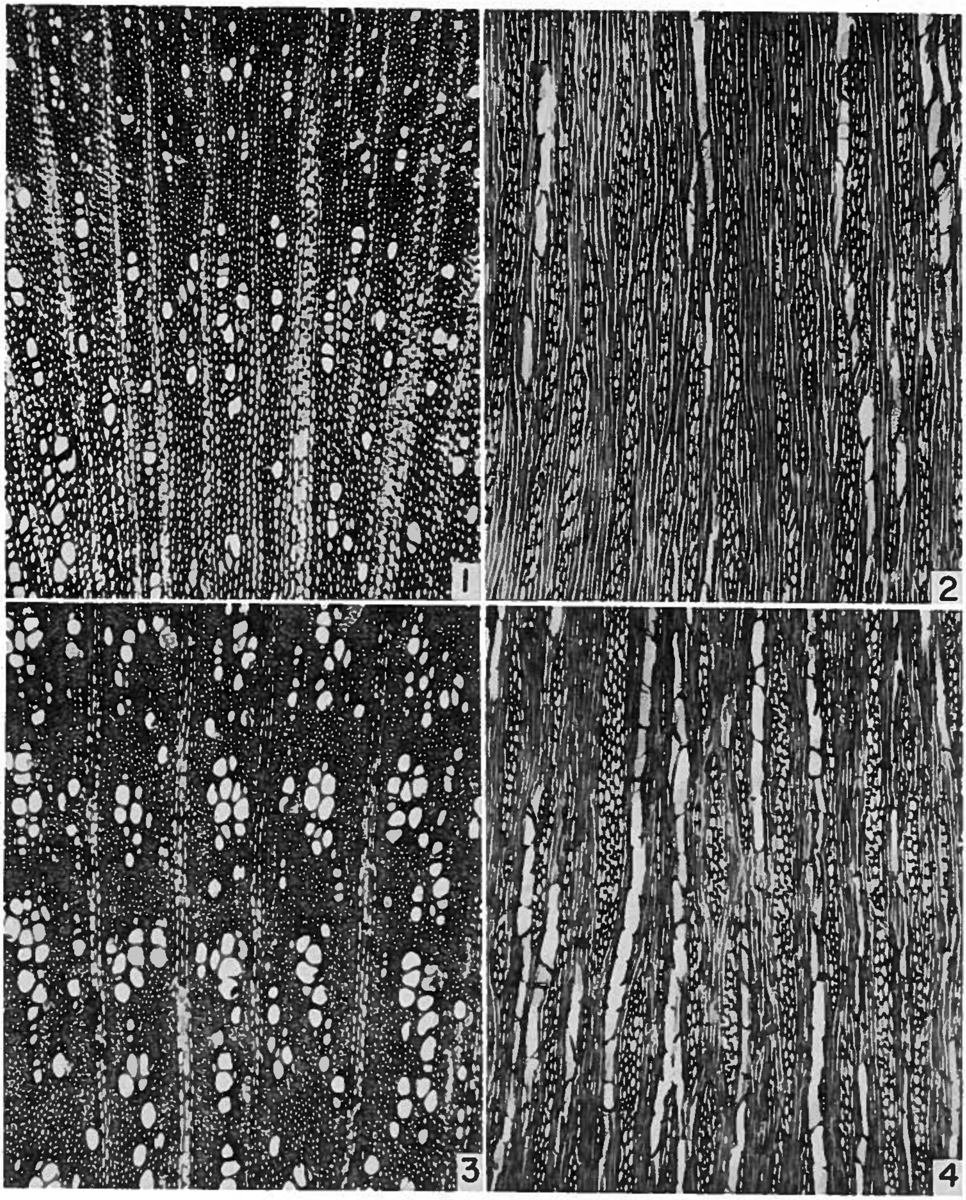

Fig. 1–4. Wood sections.—Fig. 1–2. *Centaurea americana*.—Fig. 1. Transection. Note narrow vessels.—Fig. 2. Tangential section. Both multiseriate and uniseriate rays may be seen. Predominance of erect cells in rays makes them difficult to delimit from adjacent libriform fibers.

dominance of erect cells in most Cynareae can be interpreted as a criterion of their premanent juvenility. Absence of procumbent cells in the sample studied of *Warionia saharae* may be related to the fact that only a thin cylinder of wood was present, so the pattern would be expected to be highly juvenile. Procumbent cells occur only in the central portions of multiseriate rays in Cynareae. Erect cells on the tips and sides of rays intergrade in shape and length with libriform fibers, making the precise limits of rays sometimes difficult to define (fig. 2, 4). In *Centaurea melitensis* this condition was particularly notable, and the sample studied could be said to be close to raylessness on account of the abundance of erect ray cells which simulated libriform fibers in length and morphology.

Unusually wide rays characterized *Centaurea cineraria*, *Centaurodendron palmiforme*, *Cirsium arvense*, *C. californicum*, *C. subcoriaceum* (fig. 6) and *Cnicus benedictus*. Relatively short (vertically) multiseriate rays occur with frequency only in a few Cynareae, such as *Centaurea cineraria* (fig. 4), whereas most species, as illustrated here by *Cirsium subcoriaceum* (fig. 6) have multiseriate rays which average more than a millimeter in height. As might be expected in wood of herbs, rather active breakup of large multiseriate rays into shorter segments could be observed in Cynareae. This phenomenon appears to be related, as suggested by Chalk and Chattaway (1933), to a high frequency of perforated ray cells (vessel elements derived from ray initials). Perforated ray cells were frequent in the material of *Silybum marianum* studied, but at least a few were seen in other Cynareae.

Ray cells of Cynareae typically have lignified secondary walls. Ray cells with thin primary walls occur, however, in *Centaurea cineraria* (central portion of rays only) and *Centaurea ragusina* (nearly all ray cells).

STORIED WOOD STRUCTURE

As shown in table 1, storied elements were observed only in the three species of Juan Fernandez Cynareae. This fact may derive from the more extensive xylem of these species. Storied elements are derived from storied fusiform cambial initials, which are in turn the result of a phylogenetically specialized type of division, radial longitudinal, during increase in girth of the cambium. Storied wood structure is rather common in Compositae, but in a stem in which the cambium has not markedly increased in girth, the storied condition may develop slowly, lacking the girth-increasing divisions which lead to storied structure. Thus the woody Juan Fernandez Cynareae are the most logical species of the tribe to possess storied elements.

RESINOUS DEPOSITS

Deposits of resin-like materials which are commonly encountered in woods of Compositae were observed in several Cynareae, such as *Cirsium arvense*. Cortical secretory canals containing such substances are quite common in Cynareae, so that merely during the process of cutting and killing a small

—Fig. 3. *Centaurea cineraria*. Transection. Successive bands of pore multiples may be seen. These bands do not correspond to annual growth rings.—Fig. 4. *Centaurea solstitialis*. Tangential section. Both multiseriate and uniseriate rays are present.—All, × 62.

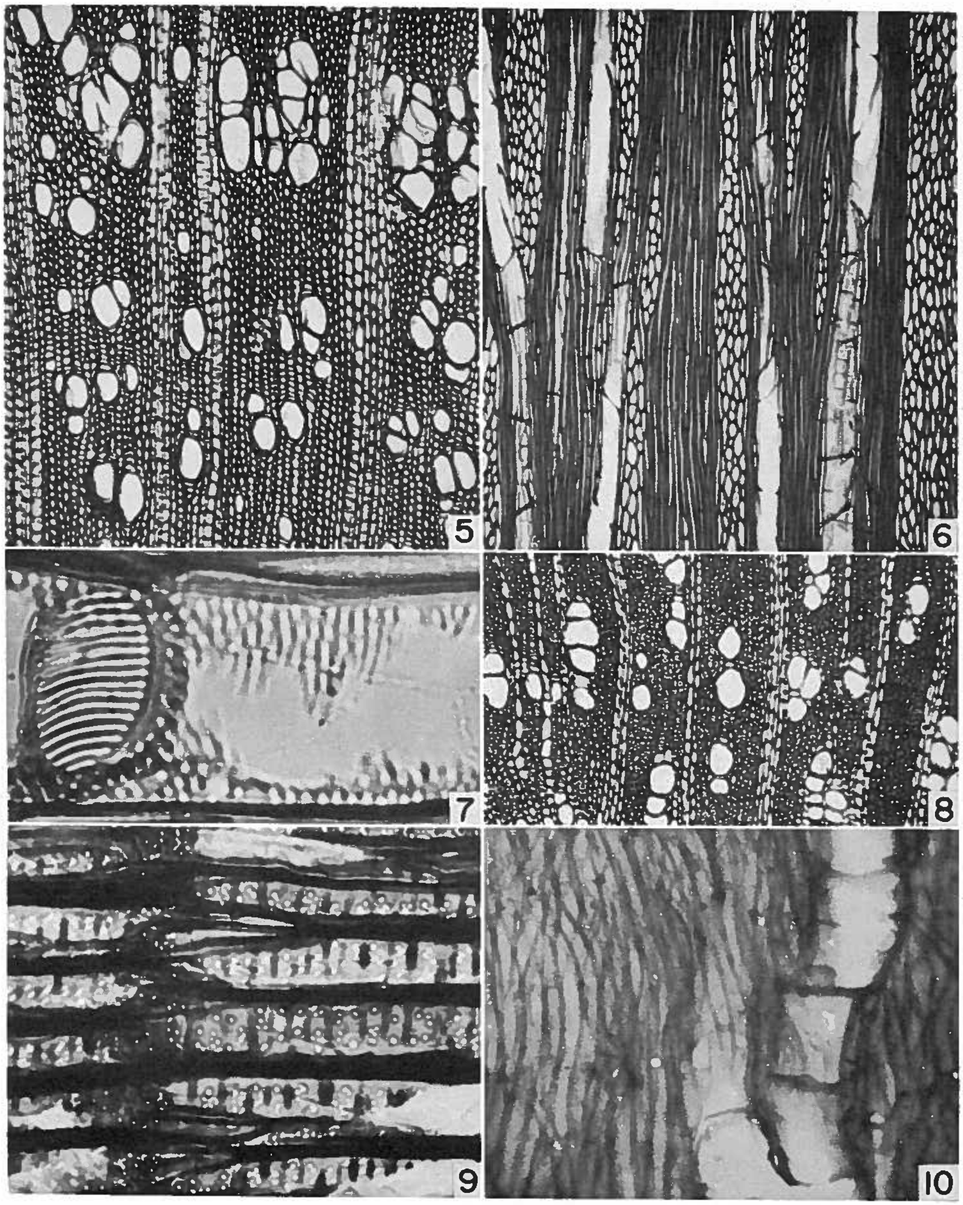

Fig. 5–10. Wood sections.—Fig. 5–7. *Cirsium subcoriaceum.*—Fig. 5. Transection. A band in which numerous wide vessels are aggregated may be seen, above.—Fig. 6. Tangential section. Multiseriate rays are notably wide and high.—Fig. 7. Portion of a vessel from radial section, showing a multiperforate perforation plate.—Fig. 8. *Warionia saharae.* Transection. Note

wood sample, the resin-like materials might infiltrate into the xylem. Consequently, presence of these compounds in woods of Cynareae was not considered a reliable and diagnostic characteristic. In other tribes, where continual deposition over a period of years in large wood samples can be seen, resinous deposits can be a useful identifying feature.

DISCUSSION

Relation of Wood to Habit.—Because of the herbaceous habit and limited accumulation of secondary xylem of most Cynareae, one would expect juvenile characteristics in their woods. This appears to be observed, in fact. Presence of large primary rays with various stages in breakup into smaller rays, change in vessel diameter (*Centaurea americana*), predominance of erect cells in ray cells and decrease in length of vessel elements seem manifestations of immature wood patterns. Possibly interpretable in this fashion are radially widened fibers, presence of multiperforate perforation plates, and strong radial alignment (like that in primary xylem) of vessels.

The specialized rosette-herb habit of most Cynareae may be related to the relatively short vessel elements observed in many species. Species with the longest vessel elements are plants with less extreme habits: shrubs, rosette trees, or otherwise robust growth forms.

Phylogenetic and Taxonomic Considerations.—As stressed earlier (Carlquist, 1962), woods of herbs and herb-like plants are not readily comparable within a systematic group because they may merely reflect different degrees of juvenilism rather than constant expression of distinctive assemblages of characters. Also, Compositae have a tendency for rapid and sensitive evolutionary adjustment to specialized ecological conditions. The wood of an annual is not comparable in many respects to wood of a tree, because the annual will have immature wood patterns. The wood of a species which shows, in wood anatomy, adaptation to xeric conditions should not be overstressed in making taxonomic distinctions. For the above reasons, as well as the fact that only a fraction of the species of Cynareae have been studied here, no purpose would be served by attempting to correlate wood anatomy with, for example, the subtribal groupings of Hoffmann.

Nevertheless, certain Cynareae have wood characteristics which do not seem related directly to ecological factors or juvenilism. The thin-walled ray cells and thick-walled fibers of *Centaurea ragusina* seem distinctive in its genus, for example. Contrasts among *Centaurodendron dracaenoides*, *C. palmiforme* and the closely-related *Yunquea tenzii* have been offered earlier (Carlquist, 1958b). In that paper, no woods of mainland Cynareae were compared with the Juan Fernandez species. The data of the present study show that although—as one would expect—no mainland Cynareae match exactly the woods of *Centaurodendron* and *Yunquea*, there is great similarity, especially in qualitative char-

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thick-walled fibers.—Fig. 9. *Centaurodendron dracaenoides*. Portion of radial section, showing walls of libriform fibers. Between groups of pits, prominent crassulae are visible.—Fig. 10. *Silybum marianum*. Portion of radial section, showing wavy shapes of libriform fibers and vessels.—Fig. 5, 6, 8: × 62; Fig. 7, 9: × 280; Fig. 10: × 120.

acters. Wood anatomy seems to support the possibility, proposed earlier (Carlquist, 1958b) that the Juan Fernandez genera are related to *Centaurea.*

Similarities between Cynareae and Vernonieae or Mutisieae were noted by Bentham (1873). The facts of wood anatomy do not contradict such relationships. All three tribes contain woods of a relatively low degree of specialization, with comparable helical sculpture on pitted vessels and similar ray types and histology. Wood anatomy, however, is not the best basis for establishing a scheme of relationships among these tribes, although it may prove useful when added to other types of information.

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