WOOD ANATOMY OF CICHORIEAE
(COMPOSITAE)

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INTRODUCTION

The tribe Cichorieae is distinctive among Compositae in possessing a high proportion of herbaceous genera, with very few that could be termed woody at all. The woody members of the tribe take on a special significance both because of the localities in which they occur and because of the current controversy over their mode of origin. Either the woody Cichorieae represent vestiges of ancestrally woody Cichorieae, or they represent instances in which herbs have increased production of secondary xylem. The reader must keep in mind that these hypotheses bear no relation to the primitive condition for Compositae as a whole. From the writer's various studies in Compositae, a primitively woody condition for the family as a whole seems more in accord with known observations than does an herbaceous ancestry. Nevertheless, certain groups of Compositae could have evolved from woody to herbaceous, and these herbs could have secondarily acquired increased production of secondary xylem.

Skottsberg (personal communication) believes that the woody Cichorieae of the Juan Fernandez Islands are best interpreted as vestiges of now-extinct mainland woody ancestors. His reasons for this belief seem to stem largely from phytogeographical considerations. This ancestry has been questioned by Stebbins (personal communication), who claims that the Juan Fernandez Cichorieae are best designated, in fact, as herbs. The Juan Fernandez Cichorieae seem relatively advanced in terms of gross morphology.

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(Stebbins, 1953), pollen structure (Erdtman, 1952), chromosome number (Stebbins, Jenkins, and Walters, 1953), and floral anatomy. The most primitive floral anatomy described for the tribe occurs in the herbaceous Asiatic genera *Dubyaea* and *Soroseris* (Stebbins, 1940). The writer, on the basis of independent study in other tribes (1957b, 1957c) arrived at the same general concepts as Stebbins in regard to primitive features of floral anatomy in Compositae.

With respect to Cichorieae at large, the hypothesis that woody Cichorieae are secondarily woody at least in part might be more satisfying because: (1) woody Cichorieae on islands possess many characteristics of herbs (succulence, large pith and cortical regions); (2) woodiness is not present in the genera now regarded as primitive for the tribe, but rather in various relatively advanced genera which are not taxonomically close to each other; (3) woodiness, even in a single genus, is quite different in different species (e.g., *Stephanomeria guadalupensis* acquires secondary xylem in a mode entirely different from that of *S. virgata*); and (4) woody Cichorieae on islands resemble herbs which have been able to continue growth by virtue of release from marked annual cycles in moisture, temperature, or day-length. Nevertheless, the writer does not feel that any interpretation of the mode, or modes, of origin of woody Cichorieae has as yet been supported by decisive evidence. Characteristics of wood anatomy may, however, be examined with regard to this question, and the present paper may be considered a contribution toward resolution of such questions. In addition, wood anatomy of Cichorieae offers a number of features which are of importance to the taxonomic system.

Fourteen species of Cichorieae have been studied here. Additional species of continental herbs, such as several more species of *Lactuca*, could have been included, but the present materials encompass all the "woody" genera of Cichorieae and probably give a representative picture of the gamut of wood characters to be found in the tribe.

Examples of herbs in the present study are species basically annual which, by virtue of a long growing season, may
acquire a woody base. Such species include *Lactuca Serriola*, *Stephanomeria exigua*, and *S. virgata*. *Stephanomeria virgata*, for example, is ideally adapted to the long growing season of southern California, because it germinates and forms a leafy rosette during the winter months, then, as moisture becomes less available, forms a tall (up to 10 feet) inflorescence stem before dying, usually in September.

The two perennial species of *Malacothrix* studied here are distinctive in their maritime habit. *Malacothrix Blairii* is endemic to San Clemente Island, California, whereas *M. saxatilis* occurs on maritime bluffs of southern California and on the southern California islands (Williams, 1957). Most species of *Malacothrix* are annuals, and the perennial habit of the two species may be related to the relatively even maritime climate which they enjoy. The same principle may account for the perennial habit of *Stephanomeria guadalupensis*, an endemic of Guadalupe Island, Mexico. This species possesses a very woody base which annually innovates shoots which terminate in inflorescences.

For whatever reason, predominantly herbaceous families of dicots often include woody insular representatives. This phenomenon is clearly illustrated by the tribe Cichorieae. For example, the Juan Fernandez Cichorieae, represented by *Dendroseris* and its segregates *Phoenicoseris*, *Rea*, and *Hesperoseris*, are rosette-trees or rosette-shrubs. For taxonomic descriptions and illustrations of these remarkable genera, the reader is referred to the studies of Skottsberg (1922, 1928, 1951, 1953). Information concerning distribution and ecology of the Juan Fernandez Cichorieae is also offered by Kunkel (1957a, 1957b). Although these species may develop a xylem cylinder up to an inch or more in thickness in some instances, they are characterized by relatively wide cortical and pith regions.

The genus *Thamnososeris*, with two species, grows on the low, dry, and thoroughly desolate Desventuradas Islands, located west of northern Chile. *Thamnososeris* is a succulent subshrub, much like *Malacothrix Blairii* (which grows in similar habitats) in habit. For illustrations, taxonomic dis-
cussions, and ecological information, the reader is referred to the works of Skottsberg (1937, 1947) and Johnston (1935).

*Sonchus* is represented by several species (section *Dendrosonchus*) on the Canary Islands. These subshrubs are similar to *Thamnoseris* or *Malacothrix Blairii* in habit, and this habit again may be related to the dry, temperate to subtropical climate of the Canary Islands. For illustrations and phytogeographical discussions, the work of Schenck (1907) on the *Dendrosonchus* species may be consulted. These species are represented in the present investigation by *S. leptocephalus*.

Finally, note should be taken of a group of oriental insular representatives of Cichorieae, the subgenus *Crepidiastrum* of *Ixeris* (Stebbins, 1937), which is not represented in this study. Species of *Crepidiastrum* are notably woodier than other species of *Ixeris*.

Although the Cichorieae are, at least in many genera, well known taxonomically, just as they are cytologically (Stebbins, Jenkins, and Walters, 1953), anatomical studies are relatively few. In addition to this study of wood anatomy in the tribe, the writer is undertaking anatomical studies of other portions of insular Cichorieae to aid in elucidating the problems outlined above. Because wood anatomy represents only one element of such investigation, few conclusions concerning evolutionary and systematic problems can be reached in the present study.

**Materials and Acknowledgments**

Because woody Cichorieae occur in such remote localities, the cooperation of a number of individuals was necessary before sufficient material for this study could be accumulated. The writer wishes especially to acknowledge Dr. Carl Skottsberg for sending samples which he and his party collected in the Juan Fernandez Islands in 1955. Wood samples from Dr. Skottsberg’s 1917 expedition, located in the Samuel J. Record Memorial Collection at Yale, were made available through the courtesy of Dr. William L. Stern. Thanks are extended to Dr. Reid Moran, of the San Diego Natural His-
Fig. 1–4.—Fig. 1–2. *Dendroseris litoralis.*—Fig. 1. Transection. Fig. 2. Tangential section. Fig. 3–4. *Dendroseris macrophylla* (Yw-27420).—Fig. 3. Transection. Fig. 4. Tangential section. All, × 65.
tory Museum, and to the Scripps Institute of Oceanography, for enabling the writer to visit Guadalupe Island in 1958. Gratitude is expressed to Dr. Roxana S. Ferris of the Dudley Herbarium, Stanford, and to Dr. David D. Keck, formerly of the New York Botanical Garden, for wood samples from herbarium specimens in those institutions, respectively. Dr. William L. Stern and Dr. Carl Skottsberg read the manuscript and offered helpful suggestions. Finally, thanks are due Mr. Alfred G. Diboll for his services in sectioning many of the woods used in this study. Herbarium specimens documenting wood samples, or specimens from which wood samples were taken, are listed in table 1. Herbarium abbreviations are according to Lanjouw and Stafleu (1959). Taxonomic treatment of species collected in California follows that of Munz (1959). Names of the Juan Fernandez Cichorieae are according to Skottsberg (1951).

**Methods**

Wood samples collected by the writer were fixed in formalin-acetic-alcohol. All other wood samples were dried. For both types of samples the typical methods, described earlier by the writer (1958) were used. In the photographs of wood transections, more recently formed xylem is toward the top of the illustrations.
Table 1. Wood Characters in Cichorieae

<table>
<thead>
<tr>
<th>Species</th>
<th>Collection</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dendroseris litoralis</em> Skottsb.</td>
<td>Skottsberg 20-XII-1954 (SBT)</td>
</tr>
<tr>
<td><em>D. macrophylla</em> D. Don</td>
<td>Kunkel II-1955 (SBT)</td>
</tr>
<tr>
<td><em>D. macrophylla</em> D. Don</td>
<td>Skottsberg, 1917 (NY) (Yw-27420)</td>
</tr>
<tr>
<td><em>Lactuca Serriola</em> L.</td>
<td>Carlquist 617 (RSA)</td>
</tr>
<tr>
<td><em>Malacothrix Blairii</em> (Munz &amp; Jtn.) Munz</td>
<td>Blair, 1923 (Type, POM)</td>
</tr>
<tr>
<td><em>M. saxatilis</em> (Nutt.) T. &amp; G.</td>
<td>Carlquist 496 (RSA)</td>
</tr>
<tr>
<td><em>Phoenicoseris Berteriana</em> (Dcne.) Skottsb.</td>
<td>Sparre 5-III-1955 (SBT)</td>
</tr>
<tr>
<td><em>P. pinnata</em> (Bert. ex Dcne.) Skottsb.</td>
<td>Skottsberg, 1917 (NY) (Yw-27423)</td>
</tr>
<tr>
<td><em>P. regia</em> (Skottsb.) Skottsb.</td>
<td>Skottsberg, 1917 (NY) (Yw-27424)</td>
</tr>
<tr>
<td><em>Rea micrantha</em> Bert. &amp; Dcne.</td>
<td>Skottsberg, 1955 (SBT)</td>
</tr>
<tr>
<td><em>R. micrantha</em> Bert. &amp; Dcne.</td>
<td>Skottsberg, 1917 (NY) (Yw-27421)</td>
</tr>
<tr>
<td><em>Sonchus leptosephalus</em> Cass.</td>
<td>Kuntze 6-I-1888 (NY)</td>
</tr>
<tr>
<td><em>Stephanomeria exigua</em> Nutt.</td>
<td>Munz &amp; Johnston 11258 (POM)</td>
</tr>
<tr>
<td><em>S. guadalupensis</em> Brandegee</td>
<td>Carlquist 457 (RSA)</td>
</tr>
<tr>
<td><em>S. virgata</em> Benth.</td>
<td>Carlquist 616 (RSA)</td>
</tr>
<tr>
<td><em>Thamnoseris lobata</em> Jtn.</td>
<td>Willis 1 (Type, DS)</td>
</tr>
<tr>
<td>DIAMETER WIDEST VESSEL, μ</td>
<td>DIAMETER VESSELS, AVERAGE, μ</td>
</tr>
<tr>
<td>--------------------------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td>93 58 2.62 195 377 26.6 2-4 ap</td>
<td>.59 126  +  +</td>
</tr>
<tr>
<td>169 79 2.24 338 357 27.5 3-6 vv fff</td>
<td>.63 85  +  +</td>
</tr>
</tbody>
</table>
ANATOMICAL DESCRIPTIONS

Table 1 contains a summary of characters considered to be significant in comparing species of Cichorieae with each other and with other Compositae. Characteristics which are not easily summarized in chart form, or which occur in a limited number of species, are discussed under appropriate headings below.

Explanation of symbols in table 1:

- **ap** = apotracheal parenchyma
- **f** = fibers
- **ff** = a few, or some, fibers
- **mv** = more numerous vessels
- **nv** = narrow vessels
- **sf** = short fibers
- **tf** = thin-walled fibers
- **v** = vessel elements
- **vp** = vasicentric parenchyma
- **vt** = vascular tracheids
- **wv** = wide vessels
- **+** = presence of characteristic
- **—** = presence of characteristic to a limited extent
- **blank space** = absence of characteristic

VESSELS

Dimensions, shapes, types.—Columns 1, 3, and 4 of table 1 give dimensions of vessel elements in woods of Cichorieae. Although species where more than one collection was studied (Dendroseris macrophylla, Rea micrantha) show that figures for these dimensions are by no means constant, there are some good differences among the taxa. The species which occur in California all have vessels the average diameter of which is 45μ or less. *Sonchus leptoccephalus*, with similarly narrow vessel elements (fig. 17), grows in a similar warm, dry, climate. These species with narrow vessels also have relatively short vessel elements (fig. 15, 18, 20). Notably long vessel elements occur in the close pair of species Phoenicoseris pinnata and *P. Berteriana*. This fact may be significant in relation to the tall, single-stemmed, rosette-
Fig. 5—10.—Fig. 5—8. *Phoenicoseris regia*.—Fig. 5, 7, Transections.—Fig. 6, 8, Tangential sections.—Fig. 5–6 show xylem between specialized bands; fig. 7–8 show bands composed largely of narrow vessels and vascular tracheids.—Fig. 9–10. *Phoenicoseris pinnata*.—Fig. 9. Transection.—Fig. 10. Tangential section.—Fig. 5–8, × 65; Fig. 9–10, × 70.
tree form of these species. *Phoenicoseris regia*, which has shorter vessel elements, develops a shorter stem. Some variations in vessel-element dimensions may be attributed to relative maturity of wood samples. In the stem of *Stephanomeria virgata* studied, vessels become narrower in later-formed wood (possibly in response to decreasing moisture). The last-formed xylem in the stem of *Malacothrix Blairii* studied contained narrow vessels, some of which, by virtue of their imperforate nature, are vascular tracheids. Such a ring of vascular tracheids may be related to the closing of a season's growth, as seemed to be the case in an annual composite, *Blepharizonia plumosa* (Carlquist, 1958). In *Thamnoseris lobata*, on the contrary, wider vessels appear to be formed in the outer portions of a stem.

Markedly caudate vessel elements were observed in *Stephanomeria exigua*. Some tendency toward caudate vessel elements was seen in *S. virgata* and *Thamnoseris lobata*.

**Lateral wall pitting.**—Typical alternate bordered pits, circular in outline, were observed in wood of the annual or near-annual species *Lactuca Serriola*, *Stephanomeria exigua*, and *S. virgata*. All the other Cichorieae studied differed to various degrees from this pattern. Although alternate circular bordered pits may be presumed to be basic to the group, all other species possessed at least some pits which were elliptical (elongate tangentially) in outline (fig. 23, 25, 31). Transitions between pits of this shape and decidedly scalariform pits were not infrequent in these species. Three species, *Dendroseris litoralis*, *Phoenicoseris regia*, and *Sonchus leptosephalus*, possessed more scalariform than elliptical pits in vessels. Such pitting is illustrated for *Phoenicoseris regia* in figure 27.

The writer believes that the possession of this type of pitting is of considerable significance. It has been reported in other genera of Compositae, such as the mutisioids *Chimantaea mirabilis*, *Quelchia × grandiflora*, and *Wunderlichia mirabilis*, as well as a number of Heliantheae, such as *Coreopsis gigantea* and three species of *Espeletia* (Carlquist, 1957a, 1958). The curious fact about all the species mentioned, as well as all the Cichorieae which have abundant
scalariform pitting, is that these species have a growth form which could be termed “rosette tree” or “megaphyte.” The writer (1958) has interpreted the occurrence of such pitting in secondary xylem as perhaps being indicative of retention of metaxylem pitting patterns throughout the life of the plant. This may appear to the reader to be merely a form of words, but there can be no doubt, with evidence from three tribes of Compositae, that there is some correlation between growth form and pitting type. Such a correlation might be usable—when more is known about wood anatomy of rosette trees—as a possible indication of derivation from herbaceous ancestry rather than woody. Such pitting, however, should not yet be regarded as the sole criterion for such an evolutionary history in certain groups of Compositae, but it should not be overlooked as having such a possible significance.

Spiral bands or grooves are notably absent in vessels of Cichorieae. The only instance in which this phenomenon was observed to any degree was *Malacothrix saxatilis*. In this species, narrow short grooves extend on either side of apertures in areas where pits are relatively sparse.

*Perforation plates.*—Simple circular or slightly elliptical perforation plates are characteristic of the vast majority of Compositae. There are occasional reports of multiperforate plates in Compositae. A resumé of such occurrences has been given by the writer (46–47. 1957b) and additional instances may be found in subsequent papers (Carlquist, 1958, 1959b). The Cichorieae studied here exhibit a wide variety of such multiperforate plates. However, only the Juan Fernandez species exhibited these plates with any degree of abundance. Plates of *Phoenicoseris Berteriana* (fig. 23–26) show a number of thin bars. In smaller plates, the arrangement of these bars is transverse with relation to the stem, although larger plates (fig. 24, 25) may have bars arranged vertically. If numerous bars are present, many of them are forked. Anastamoses of the bars may be present, so that, as in figure 24, a “fingerprint”-like arrangement is often achieved. In *Phoenicoseris regia* (fig. 28–31), on the contrary, multiperforate plates most frequently give the appearance of round-
ed perforations separated by wider bands of wall material (fig. 29–31). Another interesting phenomenon in this species is the marked elongation of pits surrounding the perforation plate, so that the margin of the plate may appear as an isolated ring (fig. 28). Perforation plates like those illustrated for Phoenicoseris Berteriana were observed in small numbers in P. pinnata and both collections of Rea micrantha. In Cichorieae studied other than the Juan Fernandez species, multiperforate plates were found to be quite uncomplicated and very infrequent. In Lactuca Serriola, a single one-bar plate was observed, and in Stephanomeria virgata, one two-bar plate was seen. Thus, although multiperforate plates—which are apparently present in only a fraction of the vessels in any wood section of Compositae—cannot definitely be said to be absent in any of the species not mentioned, they are far more abundant in woods of the Juan Fernandez Cichorieae. Interestingly, Sanio (1863) has figured a variety of perforation plates for Hieracium vulgatum (Cichorieae), including both the type shown for Phoenicoseris Berteriana and that of P. regia. Thus there may be no significance in the fact that divergent types were found in the two species.

One fact which does appear to be of some significance—at least morphogenetically—is that in Phoenicoseris Berteriana and P. regia, which have relatively numerous multiperforate plates, such plates occurred not at random but in radial series. Thus, a cambial initial tends to produce a series of vessels with multiperforate plates, whereas others give rise to vessel elements with simple plates. The writer has not encountered any mention of this mode of occurrence of multiperforate plates in the literature.

Grouping.—As in the writer's previous studies on woods of Compositae, a figure is given for number of vessels per group. This figure seems to be significant for the mainland species of Cichorieae, all of which are annuals and have a figure of 3.00 or greater (see fig. 19). The insular species all have an average of fewer than 3.00 vessels per group. The cause of this difference is not readily apparent to the writer. The Cichorieae studied show a strong tendency toward formation of radial rows of vessels (e.g., fig. 3). This tend-
ency is not apparent in some of the species with a very low number of vessels per group, such as Sonchus leptocephalus (fig. 17) or Thamnosseris lobata (fig. 13).

**LIBRIFORM FIBERS**

The figure for fiber length given in table 1 shows that in most species, libriform fibers are between 300 and 435 μ in length. The upper extreme is found in Phoenicoseris Berteriana, a species which also has relatively long vessel elements. Notably short fibers occur in Lactuca Serriola. The lowest average fiber-length, however, occurs in Sonchus leptocephalus (fig. 18). In this species, moreover, a fiber dimorphism occurs. As indicated in table 1, the average fiber length is 204 μ. Shorter fibers (fig. 18, right) occur in bands. Such fibers average 175 μ in length, whereas fibers between bands average 234 μ in length. The two types of fibers are otherwise alike in all histological characteristics, and thus the shorter ones do not qualify as apotracheal parenchyma cells. In one collection of Rea micrantha, several concentric bands of thin-walled fibers were present (fig. 11, just above center). Because the thinness of walls is the only variation in histology of fibers of this specimen, such fibers cannot be termed apotracheal parenchyma cells. The other collection of Rea micrantha showed a single band of only slightly more thin-walled fibers. In both Sonchus leptoce-
phalus and Rea micrantha, such variation in fiber characteristics is probably related to duration of certain climatic conditions.

In table 1, a figure for range in thickness of fiber walls is given. These figures are intended to demonstrate the relatively thin-walled condition of fibers in almost all of the Cichorieae studied. The only notable exception is Thamnosseris lobata (fig. 13), in which some rather thick-walled fibers occur.

An interesting tendency which appears in all of the taxa studied is the radially-widened nature of fibers, as seen in transection.
Fig. 11–14.—Fig. 11–12. *Rea micrantha* (Yw-27421). Fig. 11. Transsection.—Fig. 12. Tangential section. Fig. 13–14. *Thamnosera loba*- *tata.*—Fig. 13. Transsection. Fig. 14. Tangential section. All, $\times 65$. 
AXIAL PARENCHYMA

Anotracheal parenchyma.—The fact that some fiber dimorphism, mentioned above, is present in certain Cichorieae, may be a similar expression to the presence of actual concentric bands of apotracheal parenchyma cells. Such parenchyma cells are shorter, more thin-walled, and generally richer in latex droplets than are fibers. Examples of such bands may be seen in *Thamnoseras lobata* (fig. 13, just below center) and *Stephanomeria guadalupensis* (fig. 21, two successive bands on lower half of photograph) and, to a lesser extent, *Dendroseris litoralis* (fig. 1, center). In the last-named species, apotracheal parenchyma cells are shorter (ca. 250μ) than fibers. These bands are doubtless related to durations of certain climatic conditions. Such bands have been described in other Compositae, such as *Hemizonia clementina* (Carlquist, 1959a), an insular endemic of southern California. The presence, in the rather short succulent stem of *Thamnoseras lobata*, of wide apotracheal parenchyma bands alternating with thick-walled fibers is curious. Another example of this type of construction may be found in the similar stem of *Wunderlichia mirabilis* (Carlquist, 1957a), however.

Vasicentric parenchyma.—The Cichorieae studied here show marked differences with regard to presence of vasicentric parenchyma. Relatively abundant parenchyma, forming a sheath 1-2 cells in width around vessels or vessel groups, occurs in the Juan Fernandez species as well as in *Thamnoseras lobata* and *Sonchus leptoccephalus*. Vasicentric parenchyma in *Stephanomeria guadalupensis* is less abundant. It may be present as a sheath, a single layer of cells wide, which is not continuous around a vessel or vessel group, although it may be more abundant, forming a sheath that is two cells in thickness at certain points around the periphery of a vessel or vessel group. *Malacotrix Blairii* has a condition typical for composites: an incomplete sheath, never more than a single layer of cells thick. The three mainland species, *Lactuca Serriola*, *Stephanomeria exigua*, and *S. virgata*, show a minimum of vasicentric parenchyma. In these species, only one or two parenchyma strands may
be present adjacent to a vessel or vessel group. Kribs (1937) has suggested that both loss of vertical parenchyma and abundant vasicentric parenchyma are derived conditions. If this is true, the Juan Fernandez Compositae, together with Thamnoseras lobata and Sonchus leptoccephalus form one extreme of specialization, while the mainland Cichorieae mentioned form another extreme. Vasicentric parenchyma in the former group could not be termed “abundant” compared with that in dicotyledons at large, but it is abundant when compared to that of other Compositae.

Because the Juan Fernandez Cichorieae form such relatively abundant vasicentric parenchyma, the writer decided to determine the number of cells per strand for each species of Cichorieae. Lactuca Serriola, with minimal parenchyma, has mostly two cells per strand. The same number of cells per strand is typical of the two species of Malacothrix, Sonchus leptoccephalus, and Stephanomeria guadalupensis. The Juan Fernandez species and Thamnoseras have a range of from two to four or five cells per strand. In Dendroseris macrophylla four cells were more common, whereas in Raimicrantha, two or three cells predominated. In Phoenicoseras Berteriana and P. pinnata, four or five cells per strand is most frequent, although in P. regia, a single cell, rarely two or three, is present per strand.

TYLOSES

The only instance of tyloses was seen in Dendroseris macrophylla, where thin-walled tyloses were observed in one portion of a transection. As in other groups of Compositae, tyloses are thus of infrequent and sporadic occurrence.

VASCULAR RAYS

Types.—In comparison with Heliantheae, Cichorieae are distinctive in possessing uniseriate rays in comparative abundance. The only species in which uniseriate rays are absent or nearly so is Thamnoseras lobata; they are rare in Phoenicoseras regia.

Dimensions.—Ray dimensions may be computed in units or in terms of cells. Table 1 gives average ray height for
both multiseriate and uniseriate rays. Notably high rays occur in *Phoenicoseris regia* (fig. 6) and one collection of *Dendroseris macrophylla* (fig. 4). The relatively high rays of *Thamnoseris lobata* (fig. 14) are related to the fact that little alteration of pith rays occurs during secondary growth. Some breakup of rays, as seen in transection, may be observed in this species, however. Relatively short multiseriate rays occur in *Lactuca Serriola*, *Malacothrix Blairii* (fig. 15), *M. saxatilis* (fig. 16), *Rea micrantha* (fig. 12), and the three species of *Stephanomeria* (fig. 20, 22). As measured in number of cells, there is wide variation in width of multiseriate rays among Cichorieae. Juan Fernandez species (fig. 2, 4, 6, 10, 12) and *Thamnoseris lobata* (fig. 14) have notably wide rays, numerous cells in width. In some of these species (e.g., *Rea micrantha*, fig. 12; *Dendroseris litoralis*, fig. 2, upper left) the cells in the central portion of the ray (procumbent cells) are much smaller in diameter than those of the ray margin. Relatively narrow multiseriate rays, rarely more than three and often only two cells in width, occur in *Malacothrix* (fig. 15, 16), *Sonchus leptoccephalus* (fig. 18), and *Stephanomeria* (fig. 20, 22). This distinction is certainly a noteworthy one for separating these groups of species. Often, in the latter group of species, multiseriate rays have long uniseriate wings. This character in these species is not related to primitiveness in ray structure but is more likely related to the abundance of uniseriate rays and the narrowness (in number of cells) of the multiseriate rays. Certainly there seems to be a relation, in *Malacothrix*, *Lactuca*, and *Stephanomeria*, between the height of uniseriate rays (note the rather great height of such rays in these taxa) and the fact that they have narrow multiseriate rays. These species also have tall uniseriate rays as measured by number of cells. This correlation is due to the fact that multiseriate rays, which are few cells in width, with uniseriate portions, are closer in construction to uniseriate rays than is the case with species possessing wide multiseriate rays, and thus more numerous and taller uniseriate rays may be expected in species with narrow multiseriate rays. Mention should be made of the fact that uniseriate rays in *Dendroseris macro-
phylla are often three or more cells in height. Two to three cells is the most common condition in uniseriate rays of the species of Stephanomeria. In Phoenicoseris, Rea (fig. 12, center), and Sonchus leptoccephalus, uniseriate rays are most frequently only a single cell in height.

Histology.—Table 1 shows the occurrence of erect and procumbent cells among the various taxa. Cells nearly isodiametric, as seen in radial section, occur in all taxa. These distinctions in pattern of ray-cell shapes are interesting ones, and may be interpreted, in part, as indications of differentiation among the taxa. Erect cells on the margins of rays may be similar to libriform fibers and render precise limits of rays difficult to define in some species, such as Thanmoseris lobata (fig. 14).

Relative thickness of cell walls varies in rays of Cichorieae. Thin-walled, non-lignified rays occur in Phoenicoseris regia. In the regions where bands of narrow vessels and vascular tracheids occur (fig. 7, 8) all ray cells are non-lignified and thin-walled. In regions between these bands (fig. 5, 6) only the central portion of multiseriate rays consists of such cells. Relatively thick-walled ray cells occur in Dendroseris (fig. 2, 4) and Rea (fig. 12). Because of this thickness of cell walls in these genera, pits, which are rounded in face view, appear prominently. Ray cells of Phoenicoseris are thinner, and pitting, consisting of circular to fusiform areas, is less conspicuous. Relatively thin-walled ray cells with inconspicuous pitting occur in the three species of Stephanomeria as well as in Sonchus leptoccephalus, Thanmoseris, and Malacothrix (fig. 15–16). Pitting on the ray cells of Lactuca Serriola is relatively prominent, however, despite a thin-walled condition.

Phoenicoseris Berteriana and P. pinnata are notable in that the ratio of the area of fibers to the area of rays, as seen in transection, is high in comparison with that of the other Cichorieae studied.

GROWTH RINGS; RING POROSITY

Variation in the type or nature of elements produced has been mentioned above in relation to fibers and apotracheal
Fig. 15—18. Fig. 15. *Malacothrix Blairii*, tangential section. Fig. 16. *Malacothrix saxatilis*, tangential section. Fig. 17—18. *Sonchus leptocephalus*.—Fig. 17. Transection. Fig. 18. Tangential section. All, × 65.
parenchyma. Thus characteristics of these two cell types are summarized under the heading "ELEMENTS DISTINGUISHING RINGS" in table 1. Vertical elements of the band shown for Phoenicoseris regia in figures 7 and 8 are notable because they are narrow vessels and vascular tracheids, with fibers absent. A similar condition was present in the terminal band of the stem examined of Malacothrix Blairii. Because variation in vessel diameter and relative abundance characterized bands in these two species, they might be termed ring-porous, or having a ring-porous tendency. Likewise, the presence of wider vessels in a band in Phoenicoseris pinnata (fig. 9) or more numerous vessels, combined with presence of shorter fibers in bands in wood of Sonchus leptoccephalus (fig. 17, just above center) or the combination of apotracheal parenchyma with narrower vessels in Stephanomeria guadalupensis (fig. 21, two bands in lower half of photograph) would render these instances also examples of ring-porous tendencies.

STORIED STRUCTURE

Despite the presence of patches of obscurely-storied fibers in Phoenicoseris pinnata (fig. 10, left), P. regia, and Rea micrantha, the only prominently and consistently storied condition in the tribe was observed in Sonchus leptoccephalus (fig. 18), in which all elements except rays conform to the storied pattern. Elements in the terminal band described for Malacothrix Blairii are also storied. Examples of storied structure are not infrequent in Compositae and they have been reported in Mutisieae, Heliantheae, and Heleneieae (Carlquist, 1957a, 1958, 1959b).

LATEX DEPOSISTS

Identification of latex deposits in woods of Cichorieae was, to be sure, circumstantial, because no microchemical tests were applied. Such supposed latex deposits, however, do not have the same staining reactions as resin-like deposits in other Compositae. None of the Cichorieae in this study has secretory cavities or canals, whereas the writer's sections of vegetative structures other than wood revealed laticifers clearly in many of the taxa. Indeed, laticifers are considered
a universal feature within Cichorieae. Therefore, the deposition of droplets of latex within xylem elements of Cichorieae is not at all unexpected. The writer does believe, however, that although the presence of numerous small droplets in xylem elements is a genuine characteristic of certain cichoriean woods, latex may be infiltrated or soaked into vessels or other elements when a wood sample is cut from a stem. Therefore, the reports below are data the writer believes to represent normal occurrences only. Examples of latex deposition are most apparent in the accompanying photographs as darkish clotted appearances, as for example in figure 1 (center), figure 17 (upper left) and figure 18 (lower left).

*Dendroseris litoralis*: droplets present especially in axial and ray parenchyma, also in fibers and in vessels.

*D. macrophylla* (*Kunkel 1955*): droplets in rays, tyloses, and especially vasicentric parenchyma.

*D. macrophylla* (*Skottsberg 1917*): droplets in rays and axial parenchyma.

*Lactuca Serriola*: no appreciable deposits.

*Malacothrix Blairii*: deposits in ray cells (fig. 15); fewer in other cells.

*M. saxatilis*: no appreciable deposits.

*Phoenicoseris Berteriana*: droplets in parenchyma, fibers.

*P. pinnata*: droplets in axial and ray parenchyma.

*P. regia*: droplets in rays, fibers.

*Rea micrantha*: scattered droplets in all cell types.

*Sonchus leptocephalus*: prominent deposits in axial parenchyma; a few droplets in other cell types.

*Stephanomeria exigua*: a few droplets, especially in rays.

*S. guadalupensis*: abundant in apotracheal parenchyma and vasicentric parenchyma, droplets somewhat less abundant in fibers, rays, and axial parenchyma.

*S. virgata*: latex deposits virtually absent.

*Thamnoseris lobata*: scattered droplets in all cells.

The above summary of occurrence shows that latex appears to be more abundant in parenchyma cells than in tracheary
elements. Probably latex in tracheary elements is formed as
the element matures and remains when the element dies.
The relative abundance of latex in insular species and rela-
tive absence in species collected in mainland southern Cali-
ifornian may be at least in part attributed to the lack of paren-
chyma cells in the latter species. The difference, in any case,
is a rather sharp one.

**DISCUSSION AND CONCLUSIONS**

Analysis of the variation patterns outlined above inevit-
ably involves numerous references to the taxonomic system,
to geographical, and to ecological considerations. Summation
of relationships of wood anatomy to these factors may be
considered under the following headings.

*Variation within a species.*—Two collections were avail-
able for two species, *Dendroseris macrophylla* and *Rea*
*micrantha*. Comparison of collections in each of these two
species showed a number of differences of a quantitative
nature. In *Dendroseris macrophylla*, the collection *Kunkel*
1955 showed narrower, longer vessel elements, fewer vessels
per group, and markedly shorter multiseriate rays than the
wood sample *Skottsberg 1917*. These differences might be
attributed to greater maturity of wood characters in the
former sample, but the stem from which this was taken did,
in fact, show less xylem accumulation. Variations of this sort
may be correlated with origin of sample within the stem, or
normal variation. No qualitative differences separate the two
collections, however.

Comparison of the two collections of *Rea micrantha* re-
veals that the collection *Skottsberg 1955* possesses narrower,
shorter vessels, narrower, longer rays, and lack of the promi-
nent bands of thin-walled fibers which characterize the
wood sample *Skottsberg 1917*. These characteristics may
indicate a greater maturity in the latter sample, which was
obtained from a larger stem. In neither species is there any
reason to believe that there was any misidentification.
Rather, different growing conditions and different ages of a
stem may account for these differences. Such differences,
however, do emphasize the unreliability of quantitative char-
acters where source of samples may vary, in agreement with the evidence on this point presented by Stern and Greene (1958).

Correlations of habit and ecology with anatomy.—The data presented in this paper suggest that a number of differences exist between the mainland herbs (*Lactuca Serriola*, *Malacothrix saxatilis*, *Stephanomeria exigua*, *S. virgata*) and the insular species. The following contrasts can be offered. These features are not entirely without exception, as reference to the above data will show, but they are generally true.

<table>
<thead>
<tr>
<th>Mainland Species</th>
<th>Insular Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Many vessels per group, in radial rows</td>
<td>Fewer vessels per group</td>
</tr>
<tr>
<td>Relatively narrow vessels</td>
<td>Relatively wide vessels</td>
</tr>
<tr>
<td>Near-circular, alternate pits on vessel walls</td>
<td>Vessel-wall pits elliptical to scalariform</td>
</tr>
<tr>
<td>Vasicentric parenchyma scanty</td>
<td>Vasicentric parenchyma more abundant</td>
</tr>
<tr>
<td>Multiseriate rays fewer cells in width</td>
<td>Multiseriate rays often four or more cells wide</td>
</tr>
<tr>
<td>No bands formed in xylem</td>
<td>Bands of various types formed in xylem</td>
</tr>
<tr>
<td>Latex deposits scanty or absent</td>
<td>Latex droplets abundant in parenchyma, other cells</td>
</tr>
</tbody>
</table>

These differences may be attributed at least in part to the rosette-shrub or rosette-tree habit of the insular species, which in turn may have evolved in relation to certain climatic factors characteristic of temperate-zone islands. In addition, these differences may reflect other factors inherent in insular floras. The reader should note that all the "mainland species" are from southern California, and this location may account for some of the differences, although two of the insular species are from the same region.

The peculiar features of rosette-shrubs and rosette-trees are not unique among Compositae. There are parallels in other tribes of Compositae, as well as in other families. For example, xylem of *Thamnoseris lobata* shows similarities to
Fig. 19–22.—Fig. 19–20. *Stephanomeria exigua.* Fig. 19. Transection.—Fig. 20. Tangential section.—Fig. 21–22. *Stephanomeria guadalupensis.* Fig. 21. Transection.—Fig 22. Tangential section. All, × 65.
that of *Hemizonia clementina* (Heliantheae, subtribe Madinae) or *Wunderlichia mirabilis*, as mentioned above. Similar parallels may be found for other Cichorieae. The significance of scalariform pitting of vessels in relation to the rosette-shrub or rosette-tree habit, discussed earlier, has been entertained earlier by the writer (1958). The relatively long vessels in *Phoenicoseris Berteriana* and *P. pinnata* may be related to the peculiar palmiform habit of these species.

The possibility must be noted that the mainland species of Cichorieae may represent just as much adaptation to their locations as insular species do, so that the characteristics of insular species need not be regarded as necessarily derived from the characters listed for the particular mainland species studied.

**Comparisons with the taxonomic system.**—The recent system offered by Stebbins (1953) for the tribe is based on Stebbins' morphological and cytological (Stebbins, Jenkins, and Walters, 1953) studies of that tribe and doubtless represents the best expression of subdivisions within the tribe to date. According to Stebbins' system, the taxa studied here would fall into the following groups:

Subtribe 4. Stephanomerinae: *Thamnoseris, Stephanomeria, Malacothrix*

Subtribe 5. Dendroserinae: *Dendroseris* and the segregate genera *Phoenicoseris* and *Rea*

Subtribe 6. Crepidinae:

- *Launaea-Sonchus* line: *Sonchus*
- *Prenanthes-Lactuca* line: *Lactuca*

The genus *Thamnoseris*, on account of its peculiar growth form, geographic location, and certain features of gross morphology, has proved a genuinely anomalous genus within Cichorieae. Skottsberg (1937, 1947) has maintained that the totality of features, including anatomical ones, indicate a relationship to the Juan Fernandez genera of Cichorieae. If this relationship is valid, it perhaps should be placed in the same subtribe. Johnston (1935) was skeptical of this relationship, and Stebbins (1953) has questioned this disposition. Stebbins emphasizes contrasts between *Thamnoseris* and the
Juan Fernandez genera in achene morphology, but Skottsberg (1947), in a paper not cited by Stebbins, seems to have offered close similarities as well as contrasts between the two in respect to achene morphology. Stebbins does not detail his grounds for suggesting affinity between *Stephanomeria* and its allies and *Thamnoseris*. The writer is developing additional anatomical information concerning *Thamnoseris* and the Juan Fernandez Cichorieae, and such data may prove of significance in furthering comparisons and attempting a more definitive statement on the relationships of this genus. At any rate, the present study shows that the secondary xylem, which seems closely related to the peculiar growth form of *Thamnoseris*, offers no close similarities to the secondary xylem of the other taxa considered here.

The grouping by Stebbins of *Stephanomeria* in the same subtribe with *Malacothrix* would seem to be justified on the basis of wood anatomy, although some of these similarities may in fact be due to similar climate and growth form. *Lactuca*, for example, shows much the same features although it is in another subtribe. This accounts for the grouping of *Lactuca* with *Malacothrix saxatilis*, *Stephanomeria exigua*, and *S. virgata* in the *Mainland Species* category above. From the anatomical features which the *Mainland Species* have in common, *Malacothrix Blairii* and *Stephanomeria guadalupensis*, both insular species, depart in similar ways. Such parallelisms need not necessarily indicate any close relationship between these species. Interestingly, *Malacothrix Blairii* was first described by Munz and Johnston (1924) as a species of *Stephanomeria* and later transferred by Munz (1935) to *Malacothrix*. Williams (1957) in a monograph of *Malacothrix* retains the species in that genus, without commenting on the placement, as does Munz (1959). In the opinion of the writer, the affinities of *M. Blairii* have not yet been thoroughly explored, and consideration of other anatomical characteristics is needed to find if more criteria for its placement exist. The chromosome number (Stebbins, Jenkins, and Walters, 1953) of *M. Blairii* is exceptional in the genus *Malacothrix*, but characteristic of
Stephanomeria, and on this and other grounds the species has been regarded as a Stephanomeria in the paper just cited. The great similarity of Stephanomeria exigua and S. virgata in respect to secondary xylem characters is noteworthy, and probably indicates a close relationship.

The placement of the Juan Fernandez genera in subtribe Dendroseridinae, which includes no other genera, was originated by Hoffmann (1890) and seems to have been accepted. Skottsberg, after considering all the Juan Fernandez species as Dendroseris (1922) recognized four genera in the group (1951), largely persuaded by evidence from pollen morphology developed by Erdtman (see Erdtman, 1952). Stebbins, Jenkins, and Walters (1953) note that two species of Juan Fernandez Cichorieae, placed in separate genera by Skottsberg, have the same distinctive chromosome number and size, and they discount the value of generic distinctions.

The Juan Fernandez Cichorieae could be said to have the following characteristics in common: abundant vasicentric parenchyma, vasicentric parenchyma strands often consisting of four or more cells, relatively wide (four or more cells in width) multiseriate rays, lateral-wall vessel pitting elliptical to scalariform, and relatively frequent, often large multiperforate perforation plates in vessels. These similarities may not seem to be particularly substantial, but attempts to find distinctions corresponding to the segregate genera yielded fewer characteristics. Dendroseris (sensu stricto) and Rea both possess relatively thick-walled ray cells with fairly prominent pits, whereas in Phoenicoseris, the cell walls are thinner, with less conspicuous pitting. Both Dendroseris (sensu stricto) and Rea have relatively short, wide rays, with narrow procumbent cells in the central portion of the ray. In Phoenicoseris, multiseriate rays are somewhat narrower, without smaller cells, and occupy a smaller area in a tangential section, in comparison to fibers, than is the case in Dendroseris (sensu stricto) or Rea.

The writer has in progress anatomical studies to illumine further degrees of similarity or difference among the groups
of Juan Fernandez species. Meanwhile, the names of segregate genera have been used provisionally.

The wood of *Sonchus leptocephalus* is easily the most distinctive of the Cichorieae studied on account of the short, storied fibers which are shorter in the occasional bands which occur. The xylem of *Lactuca Serriola*, as mentioned above, shows similarity, possibly because of similar ecological conditions, to the mainland species of *Stephanomeria* rather than to *Sonchus leptocephalus*, despite the fact that both *Lactuca* and *Sonchus* are placed in the same subtribe.

**Characteristics and evolution of wood in Cichorieae.—** Relatively few features can be cited as being characteristic of Cichorieae rather than species of tribes studied earlier by the writer. The presence of relatively numerous uniseriate rays and, at least in some species, relatively narrow multiseriate rays is like *Mutisieae* but unlike *Heliantheae* and *Helenieae*. Spirals and grooves in vessels (with the exception of *Malacothrix saxatilis*) are notably absent in Cichorieae, unlike a number of Heliantheae, Helenieae, and Astereae. The tendency toward elliptic to scalariform pitting in vessels and the possession of thin-walled fibers, wider radially than tangentially, are characteristics of many Cichorieae but comparatively few species in other tribes.

The gamut of specialization of characteristics in Cichorieae is small, but certainly, as in other Compositae, the possession of very short, storied fibers (*Sonchus leptocephalus*), large grouping of vessels and very scanty vasicentric parenchyma (*Lactuca, Malacothrix saxatilis, Stephanomeria exigua, S. virgata*) or relatively abundant vasicentric parenchyma (Juan Fernandez species, *Thamnoseras*) seem advanced characteristics.

Certainly some Cichorieae show anatomical adjustment to particular growth forms or ecology. The xylem of *Thamnoseras* seems exemplary of this, as does the formation of bands in this species and others. The species with narrow, short vessel elements and narrow multiseriate rays all occur in Mediterranean-type climates. Thus, suppositions concerning patterns of wood evolution in Cichorieae must untangle the
Fig. 23–31. — Fig. 23–26. Phoenicoseris Berteriana, perforation plates of vessels from radial sections.—Fig. 27–31. Phoenicoseris regia.—Fig. 27. Scalariform lateral-wall pitting from section shown in fig. 8.—Fig. 28–31. Perforation plates of vessels; fig. 28, 31, from radial sections; fig. 29, 30, dislodged plates from tangential sections.—Fig. 23, × 310; fig. 24, × 305; fig. 25, × 347; fig. 26, × 320; fig. 27, × 330; fig. 28–31, × 355.
over-all phylogenetic trends in wood anatomy from changes which may be induced by particular climates or peculiar growth forms. The possibility that these latter considerations might play a relatively important role in attainment of particular wood configurations was explored in Helenieae (Carlquist, 1959b), and this possibility seems equally valid in Cichorieae. If special climatic or ecological factors underlie wood patterns in Cichorieae, the fact that such patterns are different from those described in Helenieae is readily understandable, considering the different habits and habitats occupied by members of the two tribes.

If one were to cite characteristics which could be used in assessing whether or not woody Cichorieae originated from herbaceous ancestors, several might be mentioned. The high proportion of genera with elliptic to scalariform pitting on lateral walls of vessels in Cichorieae seems significant. The presence of thin-walled, radially widened fibers may also be noteworthy in this regard. Woodiness, if it is derived from herbaceousness in Cichorieae, could have originated more than once in Cichorieae. Intensive examination of wood (and other features) of rosette trees throughout Compositae, as well as in other families, is needed before the mode, or modes of origin of such growth forms can be clarified. Cichorieae will undoubtedly prove significant in such further comparisons, however, because of the decidedly herbaceous nature of the tribe, and the striking relation between woodiness and insular habitats.

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