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INTRODUCTION

Inuleae familiar to North American botanists are mostly herbs, some of them among the most diminutive of annuals. As in so many dicot families, however, related woody genera occur in tropical and subtropical regions. Botanists who have not encountered woody Inuleae may be surprised to learn that wood of *Brachylaena merana* has been used for carpentry and for railroad ties in Madagascar (Lecomte, 1922), that of *Tarchonanthus camphoratus* for musical instruments in Africa (Hoffmann, 1889-1894) and that the wood of *Brachylaena (Synchodendrum) ramiflorum* is described as "resistant to rot, hard and dense, known to be of great durability" (Lecomte, 1922). In Argentina, the relatively soft wood of *Tessaria integrifolia* is used "in paper making and also in the construction of ranchos" (Cabrera, 1939). All of these species are trees. *Tessaria* and *Brachylaena* also contain shrubs as well. Most other species included in this study could be considered shrubs *(Pluchea, Cassinia)* or woody herbs.

The geographical distribution of Inuleae roughly reflects the relative woodiness of genera and species, because there is a tendency for the more woody species to occur in tropical regions, shrubby species in subtropical areas, and herbs in temperate or montane situations. The genus *Pluchea,* for example, is represented by one woody species in the southern United States, *P. sericea,* which extends from southern California to Texas and Baja California. Other North American species are markedly herbaceous. The somewhat more woody species of *Pluchea* studied here are native to warm, dry parts of Indomalaysia. *Pluchea indica,* although native to India, has been carried as a weed as far west as the Hawaiian Islands, source of the specimen studied here. Likewise, *P. odorata,* native to South America, is an introduced weed as far north as the Florida Keys and the Hawaiian Islands. These two localities are the sources of the specimens studied. *Pluchea scabrida* is a native of the Philippine Islands. Other shrubby species representing other genera in this study include *Cassinia longifolia* (Australia), *Gnaphalium californicum* (Oregon to southern California), *Helichrysum petiolatum* (South Africa), and *Inula viscosa* (Mediterranean coast). Among the arborescent species, *Anaphalis sordida* is native to Java. *Brachylaena* (including *Synchodendrum*) occurs in the forests of central and northwest Madagascar (Humbert, 1923) as well as in forested regions of South Africa (e.g., *B. discolor*). *Tarchonanthus camphoratus* grows in South Africa and the east African coast, and the arborescent species of *Tessaria* occur in southern Brazil and northern Argentina. Curiously, two diminutive shrubs studied here, *Stoebe kilimandscharica* and *Loricaria thuyoides,* occur in alpine regions near the equator. *Stoebe kilimandscharica* grows in subalpine and alpine stations in eastern Africa (Hedberg, 1957), whereas *Loricaria thuyoides* is characteristic of the elevations above timberline from Chile to Colombia (Cuatrecasas, 1954).

The tribe Inuleae is of especial interest from a taxonomic point of view. Species now recognized as belonging to Inuleae have at one time or another been included in such diverse tribes as Vernonieae and Astereae. Is Inuleae an unnatural assemblage or has our understanding of the composition of this tribe merely been slow? If it is a natural group, to which of the other major groups of Compositae is Inuleae related? The data of the present paper may be considered a contribution toward solution of some of these questions. Further commentary on taxonomic relationships, as suggested by wood anatomy, will be found in the section entitled "Taxonomic Conclusions" near the end of this paper. A more complete assessment of these questions will also be attempted in a final installment to this series of papers on wood anatomy of Compositae, of which the present paper is one.

MATERIALS AND ACKNOWLEDGEMENTS

Without the relatively many samples of woody Inuleae obtained from the Samuel J. Record wood collection of Yale University, this study would have been impossible. Thanks for providing these samples are due Dr. William L. Stern, formerly of that institution. These samples are indicated in table 1 by the designation "Yw", in accordance with the wood-collection abbreviations offered by Stern and Chambers (1960). Other samples were collected by the writer from natively-growing or cultivated specimens. Herbarium specimens, where known, which document collections of wood samples are given in table 1 and are followed by herbarium abbreviations according to Lanjouw and Stafleu (1959). A set of duplicate slides representing the species used in this study has been deposited at the Division of Woods, Smithsonian Institution, Washington, D.C. The assistance of Mr. Alfred G. Diboll and Mr. Charles F. Quibell, who sectioned many of the woods studied, is gratefully acknowledged.

METHODS

The methods for sectioning and staining of woods are the same as outlined earlier by the writer (1958a). In the accompanying photographs, wood transections show the most recently formed elements above (at left in fig. 25).

ANATOMICAL DESCRIPTIONS

Table 1 contains a summary of qualitative and quantitative features, much the same as those given in earlier papers by the writer, which appear best to express differences as well as points of agreement among the taxa of Inuleae studied. Those characters which cannot be expressed conveniently in chart form are discussed below under the appropriate headings. A question mark or absence of a figure (i.e., uniseriate rays) indicates that few or no such structures are present, and are, for all practical purposes, absent in the wood, or else that they are virtually impossible to measure.

Explanation of symbols in table 1:

$$cb = \text{coarse bands on vessel walls}$$
$$cg = \text{grooves interconnecting many pits in a helix}$$
$$f = \text{libriform fibers}$$
$$fb = \text{fine bands on vessel walls}$$
$$ff = \text{a few fibers}$$
$$g = \text{grooves interconnecting two or several pits in}$$
$$\text{a helix on a vessel wall.}$$
$$mv = \text{more numerous vessels}$$
$$p = \text{axial parenchyma}$$
$$r = \text{vascular rays}$$
$$tf = \text{thin-walled libriform fibers}$$
$$v = \text{vessel elements}$$

vt = vascular tracheids
wv = wider vessels
+ = presence of characteristic
O = absence of characteristic

VESSELS

Dimensions, shapes, types.—Narrow vessels are the rule, rather than the exception, in Inuleae. Of the taxa studied, only four genera—*Brachylaena* (fig. 19, 21), *Helichrysum, Pluchea* (fig. 1) and *Tessaria* (fig. 7)— had vessels the average diameter of which exceeds 50μ. Among these genera, average diameter exceeding 50 μ occurred in all species in only one—*Tessaria.* Metcalfe and Chalk (1950) indicate vessels averaging less than 50 μ for *Brachylaena hutchinsii, Inula,* and *Stoebe.* Several of the collections in the genus *Pluchea* studied here likewise do not exceed 50 μ in average vessel diameter. Interestingly, narrowness of vessels is highly characteristic of the two alpine species, *Stoebe kilimandscharica* (fig. 15) and *Loricaria thuyoides* (fig. 27). Because narrow vessels grade into vascular tracheids (imperforate vessel elements) in *Loricaria thuyoides,* calculation of average vessel diameter was impossible, but the fact that the widest vessel measured was 27 μ in diameter speaks for itself. A sort of vessel dimorphism is visible in *Inula viscosa* (fig. 9). As noted for *"Inula"* by Metcalfe and Chalk (1950), numerous narrow angular vessels and vascular tracheids are formed in patches adjacent to larger vessels.

How can one explain the marked tendency toward narrowness of vessels in Inuleae, as compared with other groups? The only other tribe in which vessels are so frequently narrow is Helenieae (Carlquist, 1959), in which 51 μ was the widest average vessel diameter observed. To be sure, a number of Astereae (Carlquist, 1960) have such narrow vessels although that tribe is by no means uniform in this respect. This tendency toward narrow vessels appears related to increasingly dry habits, in general. This would by no means be an unprecendented suggestion, for increasing xeromorphy has been related to narrowness of vessels in a number of groups. The narrowness of vessels in the alpine species *Tetramolopium humile* of Astereae (Carlquist, 1960), as well as *Loricaria thuyoides* and *Stoebe kilimandscharica* of the present study appear to bear this out, since alpine situations must often be said to be physiologically xeric. Curiously, an increasing abundance of vessels is related to vessel diameter: the narrower the vessel element, the more abundant vessels appear to be. Thus, in *Tetramolopium humile* (Carlquist, 1960), vessels and vascular tracheids are present almost to the exclusion of libriform fibers. Complete exclusion of libriform fibers has, in fact, been achieved in *Loricaria thuyoides* (fig. 27, 28). In this peculiar wood, the axial portion of the xylem consists wholly of vessel elements, vascular tracheids, and axial parenchyma cells. Thus the wood has an almost homoxylous or pseudo-gymnospermous quality, owing to the total emphasis on conducting rather than mechanical cells, and must be rated as one of the most specialized of all composite woods. Additional discussion of vessel diameter is given below under "Growth Rings."

Comparison of vessel-element lengths in Inuleae reveals nothing of major importance, although note might be made of the fact that the species with average length of less than 200 μ would all fall in the category of shrubs or herbs. This is shown photographically by comparison of fig. 8, 19, and 21 (trees) with fig. 14, 16, 21, and 28 (shrubs or herbs). If vessel-element length were interpretable as a criterion of phylogenetic advancement within Inuleae, the trees would be more primitive. Within a limited group of woods, interpretations of this sort are not advisable, however. Markedly caudate vessel elements were observed in all of the collections of *Tessaria* and in *Pluchea odorata,* but no special importance—other than as a characteristic of these species—need be given to this feature.

Lateral-Wall Pitting.—Alternate circular bordered pits are characteristic of Inuleae. Occasionally, as in *Anaphalis sordida* (fig. 17), *Pluchea scabrida* (fig. 5) and the species

TABLE 1. *Wood Characteristics of Inuleae.*

SPECIES	COLLECTION
Anaphalis sordida Boerl.	Yw-31140
Brachylaena discolor DC.	Yw-50252
Brachylaena meran (Baker) Humbert	Yw-10767
Cassinia longifolia R. Br.	Yw-15909
Gnaphalium californicum DC.	Carlquist 498 (RSA)
Helichrysum petiolatum DC.	Carlquist 633 (RSA)
Inula viscosa Ait.	Yw-33837
Loricaria thuyoides (Lam.) Sch. Bip.	Yw-20733
Pluchea indica (L.) Less.	Carlquist 501 (RSA)
Pluchea odorata (L.) Cass.	Carlquist 500 (RSA)
Pluchea odorata (L.) Cass.	Stern & Brizicky 249 (Y. RSA)
Pluchea scabrida DC.	Yw-34265
Pluchea sericea (Nutt.) Cov.	Detweiler 37 (F), Yw-26692
Pluchea sericea (Nutt.) Cov.	Balls 23598 (RSA), RSA no. 9117
Stoebe kilimandscharica O. Hoffm.	Schlieben 4805, Yw-29436
Tarchonanthus camphoratus L.	Yw-43544
Tessaria integrifolia R. & P.	Ducke 319 (Y), Yw-34083
Tessaria integrifolia R. & P.	Rimbach 186 (Y), Yw-28540
Tessaria mucronata DC.	Dugand 621, Yw-27139

of *Tessaria* (e.g., fig. 11) pit cavities may be angular in outline. As table 1 and comparison of photographs showing enlarged portions of vessel walls indicate, intervascular pitting shows a great range in size. Although the average pit diameter in Compositae is about 5 μ, most Inuleae have pits of this size or smaller. Exceptions to this include *Brachylaena discolor* (fig. 23) and *Tessaria integrifolia*. Examples of species with pits about 5 μ diameter are shown here: *Pluchea scabrida* (fig. 5), *Tessaria mucronata* (fig. 11) and *Anaphalis sordida* (fig. 17). Markedly smaller pits occur in *Pluchea sericea* (fig. 6), *Tarchonanthus camphoratus* (fig. 12), and *Brachylaena discolor* (fig. 24). The reader will have noted that within two genera—*Brachylaena* and *Pluchea*—pit size differs greatly among species. Minute intervascular pitting and variation in pit size within a single genus are both unusual features. They may, however, be found elsewhere in Compositae in the Vernonieae, particularly in the genus *Vernonia*.

Helical Sculpture.—As the data for this feature given in table 1 indicate, Inuleae differ from some other tribes to a certain degree. Although types of helical sculpture were not observed in a few taxa, the majority of Inuleae studied possess grooves which interconnect apertures of either a few or many pits adjacent in a helix on the vessel wall. These grooves

TABLE 1. *Wood Characteristics of Inuleae.*

DIAMETER WIDEST VESSEL, μ	DIAMETER VESSELS, AVERAGE, μ	VESSELS PER GROUP, AVERAGE	LENGTH VESSEL ELEMENTS, AVERAGE, μ	LENGTH LIBRIFORM FIBERS, AVERAGE, μ	MAXIMUM WIDTH LIBRIFORM FIBERS, AVERAGE, μ	WALL THICKNESS FIBERS, μ	PIT DIAMETER, μ	HELICAL SCUPTURE ON VESSELS	ELEMENTS DISTINGUISHING RINGS	STORIED ELEMENTS	HEIGHT MULTISERIATE RAYS, AVERAGE, MM.	HEIGHT UNISERIATE RAYS, AVERAGE, μ	MAXIMUM WIDTH MULTISERIATE RAYS, CELLS, AVERAGE	RAY CELLS ISODIAMETRIC TO PROCUMBENT	RAY CELLS ISODIAMETRIC TO ERECT
84	36.4	2.53	260	360	25.5	2–3	4	g	0	0	3.45		4.80	0	+
144	89.4	2.09	238	312	21.7	3–4	6	g	0	0	.16	66	2.84	+	0
108	62.2	1.73	257	420	22.3	4–5	2–3	cg	0	v, p, r	.17	125	2.26	+	0
79	49.2	3.60	185	239	25.1	3–4	5	cb	0	v, f, p	.51		5.96	+	0
60	36.8	2.37	127	190	19.5	.5–1	3–4	0	0	0	1.39		5.18	0	+
126	56.2	1.87	163	300	21.9	2–3	4	cg	0	0	3.0+		5.25	0	+
82	29.2	00	177	275	22.2	3–4	4	0	wv, p	0	1.46		5.93	0	+
27	?	00	162	?	?	?	5	cb	0	v, vt	1.82		5.80	+	+
105	57.3	1.71	191	380	24.6	2–4	5	g	0	0	.94		5.36	0	+
84	45.9	2.41	235	420	18.5	3–4	3–4	cg	wv	0	1.55		4.56	0	+
110	61.4	2.00	229	385	26.6	3–4	4	cg	wv	0	1.36		5.68	0	+
98	45.5	2.87	190	420	20.6	3–4	5	g	0	ff	1.68		6.12	0	+
70	43.7	2.71	225	265	18.7	2–3	2–3	cg	f	0	.94		3.29	0	+
68	32.0	2.51	246	300	21.8	3	2–3	cg	f	0	1.70	96	2.67	0	+
54	24.8	13.8	121	275	21.6	2–3	4	cb, fb	p	0				0	0
72	48.0	3.22	234	232	19.0	3–6	2	cg	tf	f, v, p, r	.20	63	3.09	+	0
136	89.9	1.55	297	470	25.9	1–2	5–7	cg	0	0	1.32		4.93	+	+
114	70.3	1.87	334	480	27.8	1–2	5	g	mv	0	1.17	194	2.75	+	+
90	55.2	1.29	274	360	32.8	.5–1	5	0	0	0	.81	164	3.61	+	+

were figured for *Pluchea odorata* earlier by the writer (1958b), in connection with a description of wood of that species. They may also be seen here in *Pluchea sericea* (fig. 6), *Tarchonanthus camphoratus* (fig. 12, lower left), and two species of *Brachylaena* (fig. 23, 24). The only species in which a more prominent form of helical sculpture, that of fine raised bands on either side of the grooves interconnecting pits, was observed in *Stoebe kilimandscharica* (fig. 18). The report of spiral thickenings in *Anaphalis sordida* (Janssonius, 1906-1936) may be attributable to the aforementioned grooves. Other tribes of Compositae are not so richly provided with the groove type of sculpture, with the possible exception of Vernonieae. Many Astereae show such grooves (Carlquist, 1960), but the tribe has a greater abundance of the more prominent types of sculpture: fine and coarse helical bands or thickenings. Fine bands are also fairly frequent in Vernonieae.

Vessel Grouping.—A figure for number of vessels per group is given in table 1. These aggregations most often take the form of radial chains, a condition prominent in *Pluchea odorata* (fig. 1) and *P. sericea,* and less conspicuous in transections of other woods shown in the photographic plates. The high degree of vessel aggregation in *Stoebe kilimandscharica* may not be readily apparent because the smaller vessels and vascular tracheids appear like
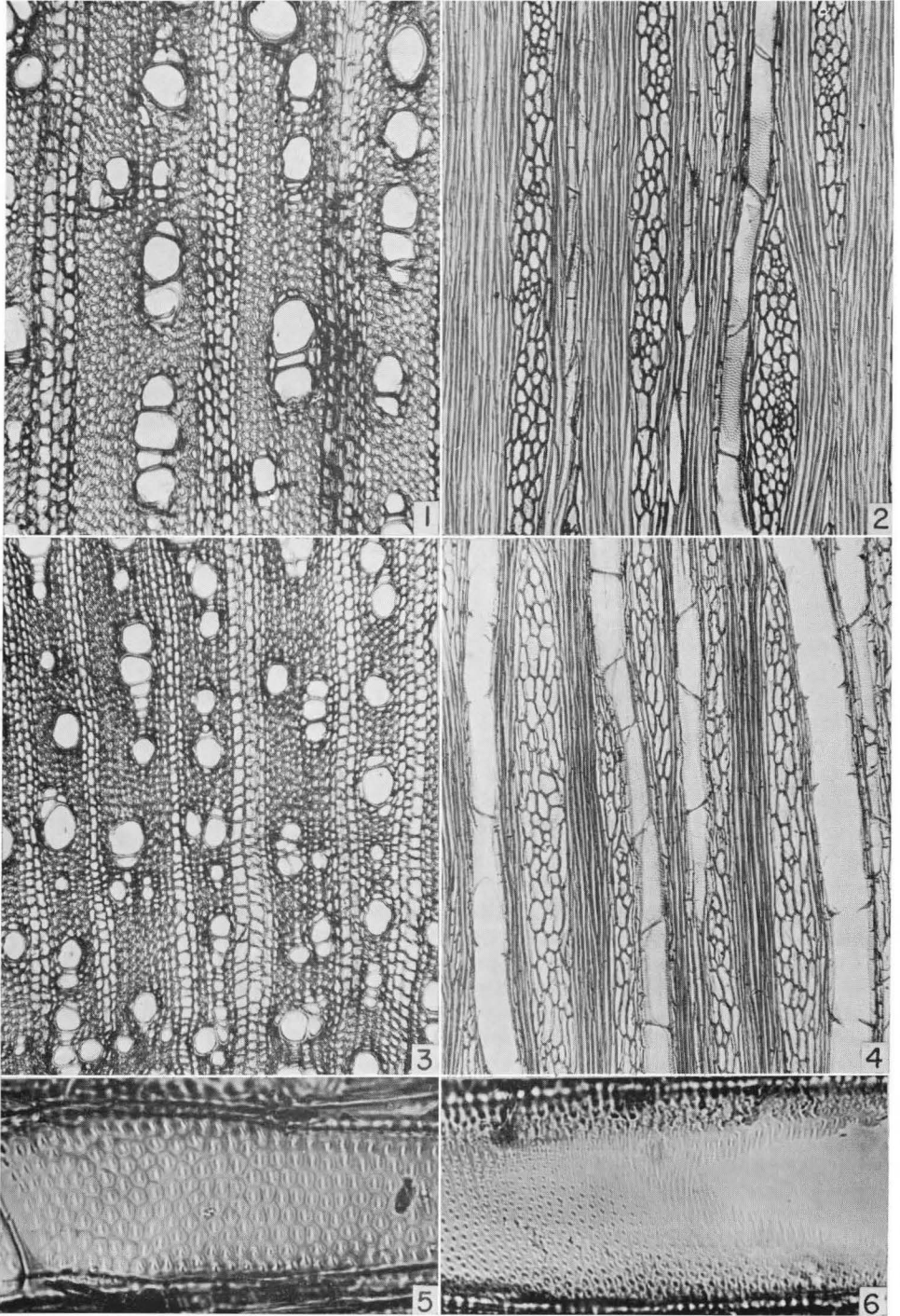
FIGURES 1–6

fibers and parenchyma cells (fig. 15), and can be identified only by careful study. Large clusters of vessels, not particularly radial in orientation, are seen in *Cassinia longifolia* (fig. 25). A peculiar and prominent form of radial aggregation of vessels can be seen for *Inula viscosa* in fig. 9. Internal to each of the larger vessels or vessel groups, there are chains of very narrow vessels and vascular tracheids. These may also be seen in the tangential section (fig. 10, left). The vessel and vascular-tracheid aggregation of *Loricaria thuyoides* (fig. 27) is well-nigh infinite. Elements which might be identified as fibers in transection all proved to be narrow vessels or vascular tracheids when tangential and radial sections were studied. The genera in the present study which show the least degree of vessel aggrgation are *Pluchea* (fig. 1, 3), *Tessaria* (fig. 7), and *Brachylaena* (fig. 19, 21). Radial grouping of vessels in Inuleae has been figured for *Brachylaena hutchinsii* by Metcalfe and Chalk (1950), who also note the peculiar situation in *Inula*. The occurrence of tangential bands of vessels in *Anaphalis sordida* (Janssonius, 1906-1936) and *Stoebe* (Metcalf and Chalk, 1950) cannot be confirmed on the basis of materials in the present study (cf. fig. 13, 15).

LIBRIFORM FIBERS

Figures for average length, average width (at the widest point) and wall thickness of libriform fibers are given in table 1. As expected, libriform fibers are longer than vessel elements in any given species. Exceptionally short fibers occur in the woody herbs *Gnaphalium californicum, Inula viscosa* (fig. 10), *Pluchea sericea.* and *Stoebe kilimandscharica* (fig. 16, right half of photograph). Interestingly, fiber width bears no relation to wall thickness. The widest fibers occur in *Tessaria* (fig. 7, 8). This genus also possess markedly thin-walled fibers, which probably accounts for the use of woods of *Tessaria integrifolia* in paper-making (Cabrera, 1939). Exceptionally thick-walled fibers occur in the various species of *Brachylaena* (fig. 19–22) and *Tarchonanthus camphoratus,* and probably account for the economic uses of these woods, mentioned earlier. The occurrence of both very thin and very thick-walled fibers in the tribe Inuleae is probably not as strange as it would at first appear, although the thick-walled fibers all occur in members of the subtribe Tarchonanthinae. Because thick-walled fibers have been reported for Tarchonanthinae not studied here, *Brachylaena hutchinsii* (Metcalfe and Chalk, 1950) and *Brachylaena (Synchodendrum) ramiflorum,* (Lecomte, 1922), this feature may well be a characteristic of this subtribe. Fibers which are radially flattened as seen in transection were observed in *Brachylaena discolor*. This feature may also be seen in some Vernonieae. Septate fibers occur with some frequency in *Pluchea indica* and *P. scabrida.* Differentiation into long and short fibers, located in particular portions of the xylem, a phenomenon termed "fiber dimorphism" by the writer (1958a), could be observed in *Tarchonanthus camphoratus.*

AXIAL PARENCHYMA

Apotracheal Parenchyma.—Despite the tendency toward fiber dimorphism in *Tarchonanthus camphoratus,* the shorter fibers in this species cannot be termed apotracheal parenchyma cells. The apotracheal parenchyma in *Stoebe kilimandscharica* is a special case, and is discussed below under "Anomalous Secondary Growth". In the remaining species, some apotracheal parenchyma can be seen in *Brachylaena discolor* and *B. merana* (fig. 19, 21). This takes the form of occasional axial parenchyma cells which are not adjacent to a vessel

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Fig. 1–6. Fig. 1, 2. *Pluchea odorata.*—Fig. 1. Transection, showing large vessels.—Fig. 2. Tangential section. Note abundant fibers.—Fig. 3–5. *Pluchea scabrida.*—Fig. 3. Transection. Note smaller vessels; a moderate change in vessel diameter occurs with relation to growth rings.—Fig. 4. Tangential section. Ray tissue is abundant in comparison to axial xylem.—Fig. 5. Lateral-wall pitting of vessel. Pits are fairly large, pit cavities are angular in outline.—Fig. 6. *Pluchea sericea,* lateral-wall pitting of vessel. Pits are small, grooves interconnect apertures (evident near cut portion of wall). Fig. 1–4, × 85. Fig. 5, 6, × 555.
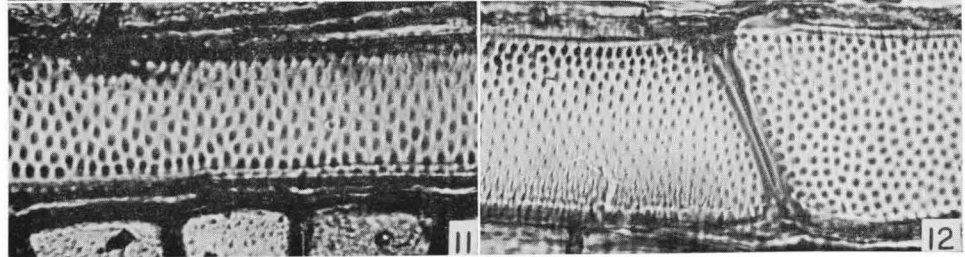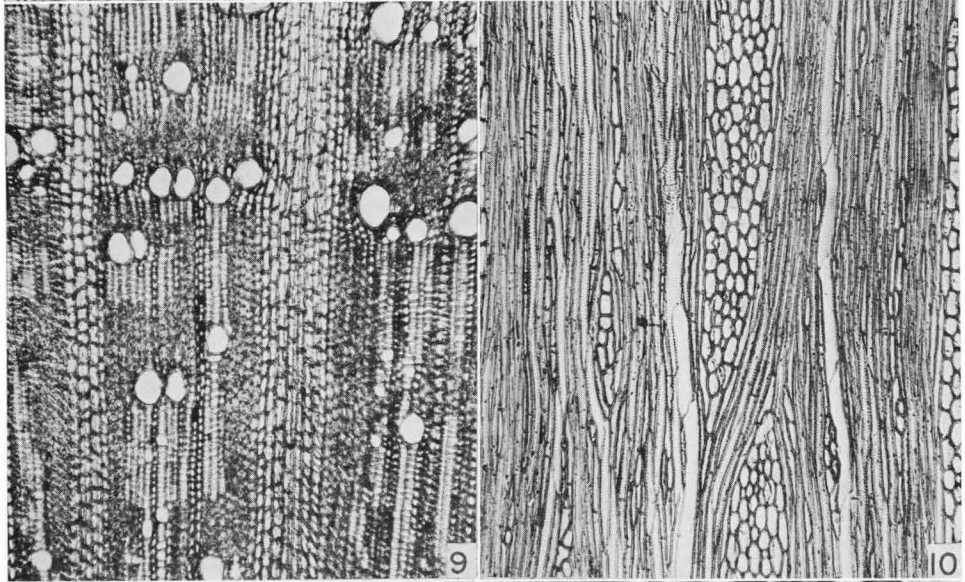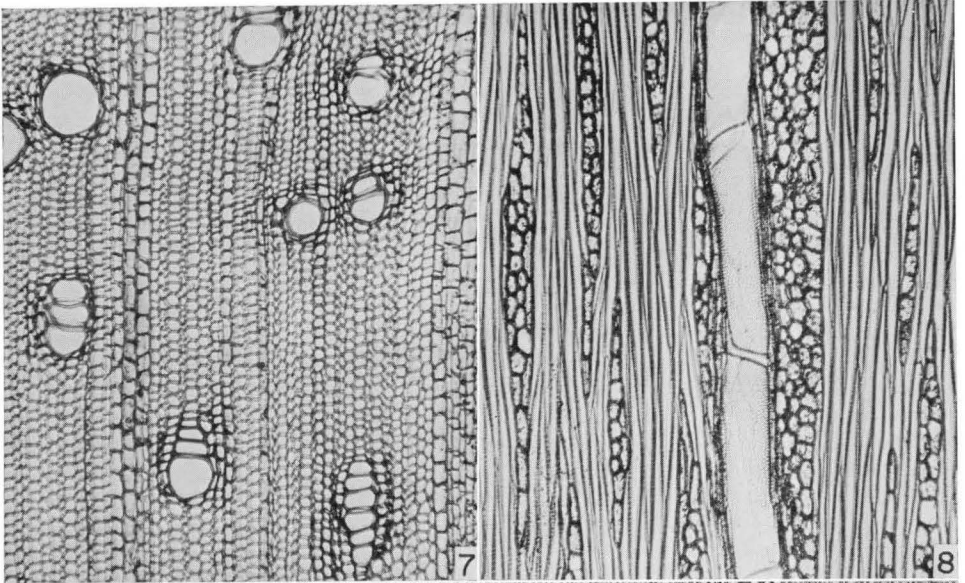
or vessel group, and which are surrounded by fibers. Such scattered axial parenchyma cells have been note for *Brachylaena merana* by Perrot (1922) and are suggested in *B. hutchinsii* by the figure given by Metcalfe and Chalk (1950). Scattered axial parenchyma cells of this sort also occur in two genera of Astereae, *Baccharis* and *Olearia* (Carlquist, 1961). As suggested in that reference, scattered parenchyma cells are probably not, in Compositae, related to major trends of parenchyma evolution (e.g., Kribs, 1937), but represent a special case. In addition, very narrow partial bands of apotracheal parenchyma may be seen in *Brachylaena merana* (fig. 21), as the photograph of Lecomte (1922) shows.

Vasicentric Parenchyma.—As in other Compositae, Inuleae have scanty vasicentric parenchyma. The only possible exceptions to this are in *Brachylaena discolor* (fig. 19) and *B. hutchinsii* (Metcalfe and Chalk, 1950), where at least some vessel groups have a relatively abundant sheath of parenchyma. This is not true, however, in *B. merana* (fig. 21; Lecomte, 1922) and *B. (Synchodendrum) ramiflorum* (Lecomte, 1922). *Tessaria* may have a sheath two cells in thickness around some vessels and vessel groups, but this could be considered abundant only in relation to the scanty parenchyma characteristic of most Compositae. If the two species of *Brachylaena* with more abundant vasicentric parenchyma could be interpreted according to the general evolutionary trends of Kribs (1937), they would be more specialized. Because of other specializations in *Brachylaena* (e.g., storied structure), this interpretation is possible.

VASCULAR RAYS

Among the Inuleae, uniseriate rays are very scarce. They could be said to be frequent only in *Brachylaena* (fig. 20) and *Tarchonanthus*. They are occasional in *Tessaria* (fig. 8), and are rare or absent in the other Inuleae studied. However, *Brachylaena hutchinsii* (Metcalfe and Chalk, 1950) is reported to have only uniseriate and biseriate rays, and those authors claim that uniseriate rays are more frequent than multiseriate rays in *Inula*. This is not true in the writer's material of *Inula viscosa* (fig. 10). Uniseriate wings on multiseriate rays are frequent in *Tessaria* (fig. 8). Inuleae other than *Brachylaena* have relatively wide multiseriate rays. The average multiseriate ray widths given in table 1 do not give an idea of the extremes, but the prominent width of some multiseriate rays can be seen in fig. 2, 4, 8, 10, 26, and 28. Metcalfe and Chalk (1950) report rays "up to 18 cells wide" in *Inula*. The figures for multiseriate ray height in table 1 indicate the extremely short rays in *Brachylaena* and the related genus, *Tarchonanthus*. The only other genus in which short rays are present is *Cassinia* (fig. 26). Rays are so high in *Anaphalis sordida* (fig. 14) and *Helichrysum petiolatum* that only a few can be measured on any given section.

With regard to shape of ray cells, only *Brachylaena, Cassinia,* and *Tarchonanthus* have cells within the range of square to procumbent exclusively. In *Brachylaena* and *Tarchonanthus*, in fact, all ray cells are procumbent, and add another feature by which these two genera are allied. The reverse condition, that of predominance of erect cells and absence of procumbent cells, is much more common, as table 1 indicates. Even in *Tessaria*, where both procumbent and erect cells are present, erect cells are more common. This tendency toward erectness is quite marked in *Anaphalis sordida* (fig. 14), in which rays are difficult to define because erect ray cells approximate the shape, size, and wall characteristics of adjacent libriform fibers so closely. The strong tendencies, in Inuleae, toward marked

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Fig. 7–12. Fig. 7, 8. *Tessaria mucronata.*—Fig. 7. Transection. Fibers are extremely thin-walled, paratracheal parenchyma fairly abundant.—Fig. 8. Tangential section.—Fig. 9, 10. *Inula viscosa.*—Fig. 9, transection. In addition to prominent vessels, large bands of narrow vessels and vascular tracheids (light) are present.—Fig. 10. Tangential section. A zone of narrow vessels and vascular tracheids may be seen at left.—Fig. 11, 12. Lateral walls of vessels, showing pitting.—Fig. 11. *Tessaria mucronata.*—Fig. 12. *Tarchonanthus camphoratus,* showing small size of pits, grooves. Fig. 7–10, × 85. Fig. 11, 12, × 555.
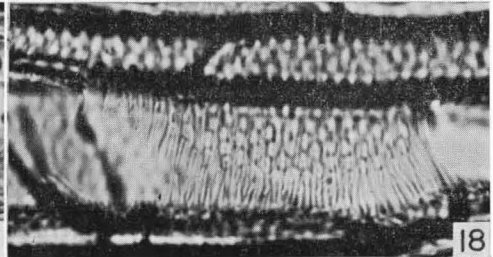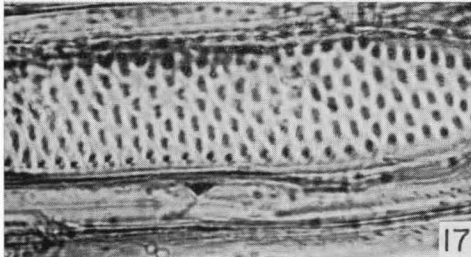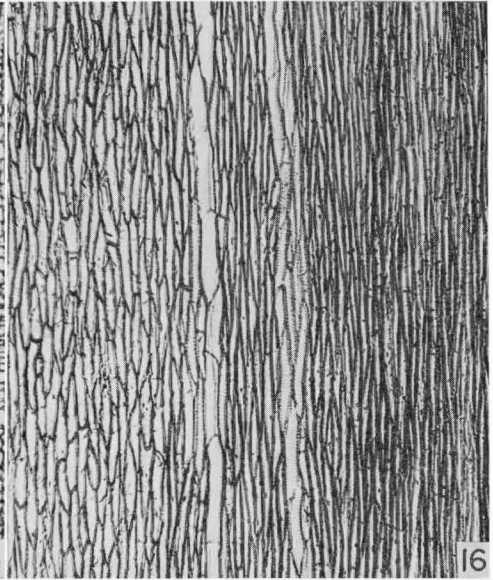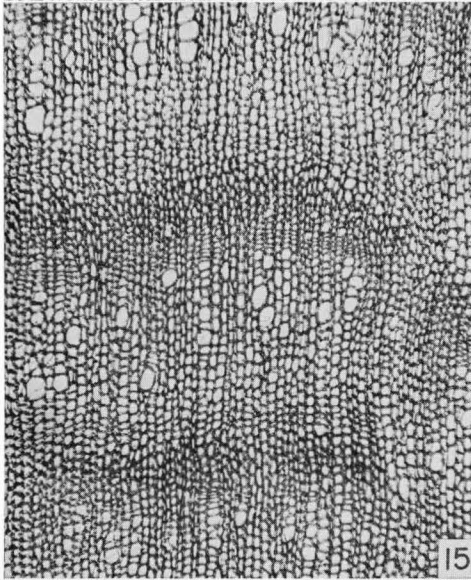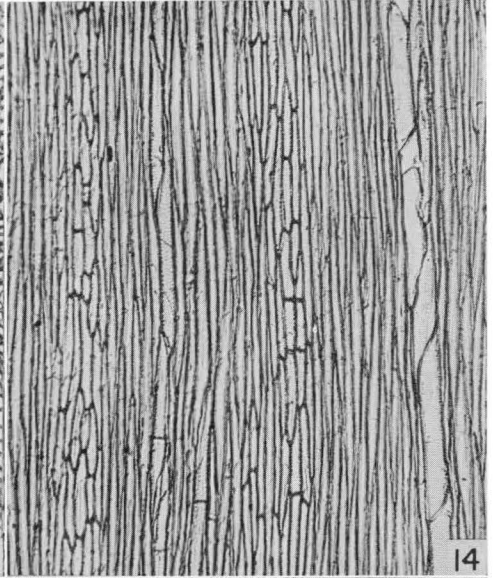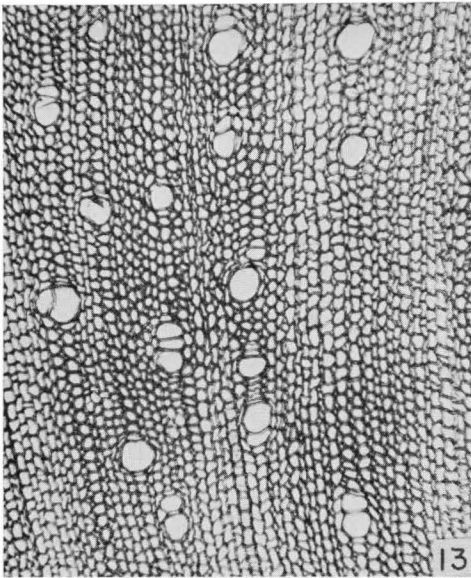
FIGURES 13–18

erectness of ray cells on the one hand and procumbency on the other must be counted as indications of the relative specialization of most woods in this tribe, according to the hypotheses of Kribs (1935). Only *Tessaria* retains a clearly heterocellular condition, and even in woods of this genus, erect ray cells are much more common than procumbent cells.

On account of the fact that *Stoebe kilimandscharica* has a wood structure influenced by anomalous cambial activity, one cannot cite it as an example of a rayless wood in the same sense as rayless woods which result from normal cambial activity. However, there is no evidence of rays in this wood despite a continous radial sequence of all derivatives from cambial initials. In woods where successive cambia form successive new radial patterns, one might not expect rays at all. The cambial activity of *Stoebe kilimandscharica,* in other words, does not deviate so much from normal patterns that the rayless condition can be wholly attributed to anomalous conditions.

Subtle differences among species, in addition to those mentioned above for the several species of *Brachylaena,* are evident in rays. The two species of *Pluchea* illustrated in fig. 2 and 4, respectively, differ in relative abundance of rays. That illustrated below, *P. scabrida,* shows much greater abundance of rays, with proportionately less axial xylem.

TYLOSES

No tyloses were observed in the Inuleae studied.

GROWTH RINGS

Corresponding to the tropical or subtropical nature of the areas in which they grow, relatively few of the Inuleae studied show any great tendency toward formation of growth rings. The column headed "Elements Distinguishing Rings" in table 1 lists those elements which are present in early wood of a ring and contrast with elements in late wood. Wider vessels distinguish the early wood of most of those species which do show growth rings. Thus, for example *Inula viscosa* (fig. 9; early wood is at top third of photograph) has a tendency toward ring porosity. In *Tarchonanthus camphoratus,* the shorter, more thin-walled fibers, characterize early wood.

ANOMALOUS SECONDARY GROWTH

Although few Compositae show anomalous secondary growth, those which have been studied fall in Inuleae with rare exceptions (e.g., *Osteospermum* of Calenduleae; Adamson, 1937). Such anomalous conditions have been reported in stems of the inuloid genera *Lachnospermum, Elytropappus, Disparago, Stoebe, Perotriche,* and *Phaenocoma* (Adamson, 1934). Adamson investigated four species of *Stoebe,* of which only one *(S. cinerea)* is identified by name. The general descriptions for woods of *Stoebe* given by Adamson seem to apply to the present findings for *S. kilimandscharica,* although the writer could not identify, either because of the nature of preservation (dried wood sample) or because of true absence, any sieve-tube elements within the xylem. Features of the wood of *Stoebe kilimandscharica* which can be established are as follows. The wood does have, in agreement with Adamson's descriptions for the genus, successive bands of various tangential width. These bands (fig. 15) appear as follows: external to the fibers of a preceding band, parenchyma cells are formed, followed by vessels, which in turn are followed by narrow lignified cells and then the darker-appearing thick-walled fibers. Observation of the cambial

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Fig. 13–18. Fig. 13, 14, 17, *Anaphalis sordida.*—Fig. 13. Transection. Vessels are few.—Fig. 14. Tangential section. Two rays (near center; at left) are present; height of ray cells is only slightly less than that of fibers.—Fig. 15, 16, 18. *Stoebe kilimandscharica.*—Fig. 15. Transection. Note zonate appearance due to peculiar growth rings. Darker portions are fibers. Further explanation in text.—Fig. 16. Tangential section. A ray-like area of parenchyma, left, appears very similar to fibers, right.—Fig. 17. Lateral-wall pitting, showing moderate-sized pits, lack of spirals.—Fig. 18. Lateral-wall pitting, showing paired small spirals and grooves. Fig. 13–16. × 85. Fig. 17, 18, × 555.
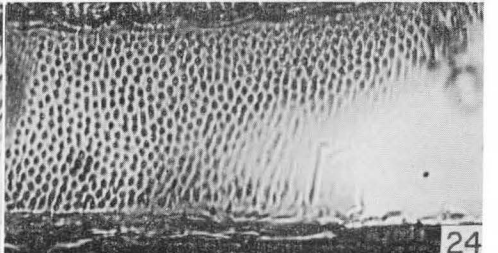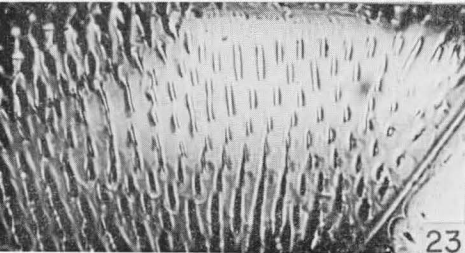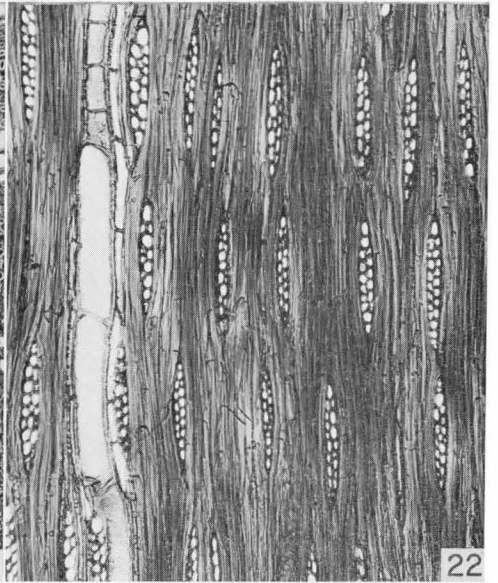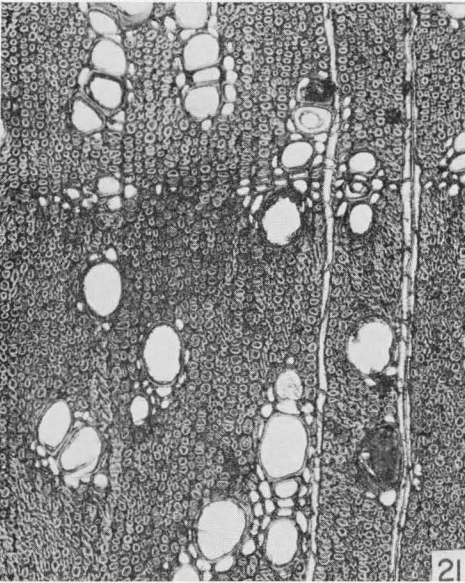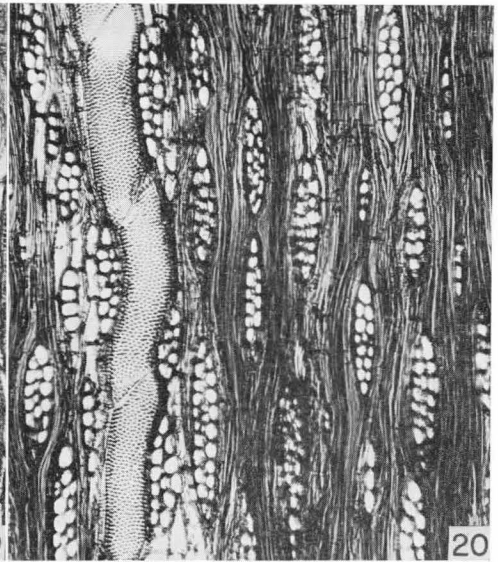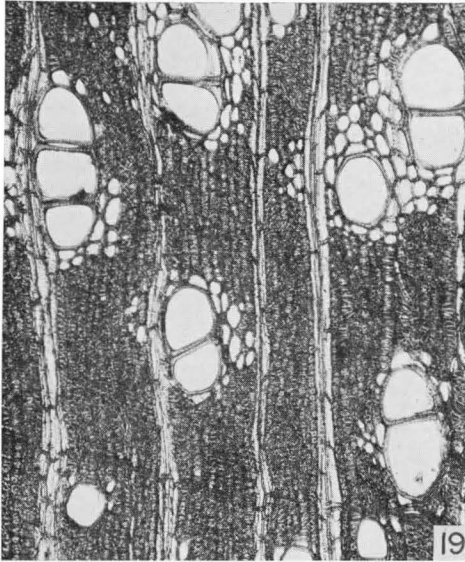
FIGURES 19–24

zone and newly-formed xylem of the sample available showed that the cambium produces elements in a normal radial sequence. However, there is a residual cambium in each band. The action of this residual cambium is fairly short-lived, but it does produce the radially-narrowed relatively thin-walled lignified elements external to vessels and internal to thick-walled fibers in each band. This type of cambial action, which was clearly visible in the specimen studied, is not mentioned by Adamson, nor has it been suggested in the review of Chalk and Chattaway (1937). If the area of thick-walled fibers does, in each band, contain sieve-tubes, the occurrence of a residual cambial region between vessels and phloem-bearing fiber areas would be logical if the bands were considered as tangentially widened bundles.

STORIED WOOD STRUCTURE

Although relatively few Inuleae have storied structure of secondary xylem, storying is quite marked in those which possess it. For example, in *Brachylaena merana* (fig. 22) and *B. ramiflorum* (Lecomte, 1922) all axial elements conform to the storied pattern. *Brachylaena discolor* (fig. 20) does not have storied rays. All axial elements except rays are storied in *Cassinia longifolia* (fig. 26), *Loricaria thuyoides* (fig. 28) and *Tarchonanthus camphoratus*. In these species, presence of storied wood structure seems a good indication of specialization. There are only a few other genera of Compositae *(Hecastocleis, Olearia)* in which a species has been observed to have rays, as well as vertical elements, storied.

RESINOUS DEPOSITS

Only a few species of Inuleae *(Anaphalis sordida, Gnaphalium californicum, Pluchea sericea, Stoebe kilimandscharica,* and *Tarchonanthus camphoratus)* were observed to lack droplets of resin-like materials. The remainder of Inuleae studied proved to have droplets of such substances in ray and axial parenchyma cells. In addition, droplets in vessels were noted in *Brachylaena discolor, B. merana,* and the species of *Pluchea* other than *P. sericea.* Massive deposits of resin-like materials were observed in *Brachylaena merana* (note occlusion of vessels in fig. 21). Resinous deposits have been noted previously in *Tessaria* by Williams (1936) and in *Brachylaena* by Metcalfe and Chalk (1950).

TAXONOMIC CONCLUSIONS

SPECIES CHARACTERISTICS

Wood anatomy aids in defining several of the species in genera for which material of more than one species was available. In *Brachylaena,* for example, *B. discolor* is distinctive on account of its non-storied rays and large pits in vessels. *Brachylaena hutchinsii* is separable specifically because of its narrow vessel diameter and frequency of uniseriate rays. *Brachylaena merana* and *B. ramiflorum* are very close in wood anatomy, judging from present material and the descriptions of Lecomte (1922). Segregation of *B. ramiflorum* as *Synchodendrum* is certainly not supported on these grounds.

Within *Pluchea,* a much larger genus than *Brachylaena,* four species were studied. These four species show close resemblances to each other, but a few species characteristics may be found in such respects as: prominent radial rows of vessels, minute pitting on vessels, and absence of resin-like deposits in *P. sericea;* abundance of ray tissue as compared with axial xylem in *P. scabrida.*

Fig. 19–24. Fig. 19, 20, 23. *Brachylaena discolor.*—Fig. 19. Transection, showing relatively abundant vasicentric parenchyma.—Fig. 20. Tangential section. Fibers and rays are twisted in orientation.—Fig. 21, 22, 24. *Brachylaena merana.*—Fig. 21. Transection. End of a growth ring is above center.—Fig. 22. Tangential section. Note storied condition of rays.—Fig. 23. Lateral-wall pitting of vessel, showing elongate apertures and grooves interconnecting apertures.—Fig. 24. Lateral-wall pitting. Features are similar to those of fig. 23, but pitting is much more minute. Fig. 19–22, ×85. Fig. 23, 24, ×555.
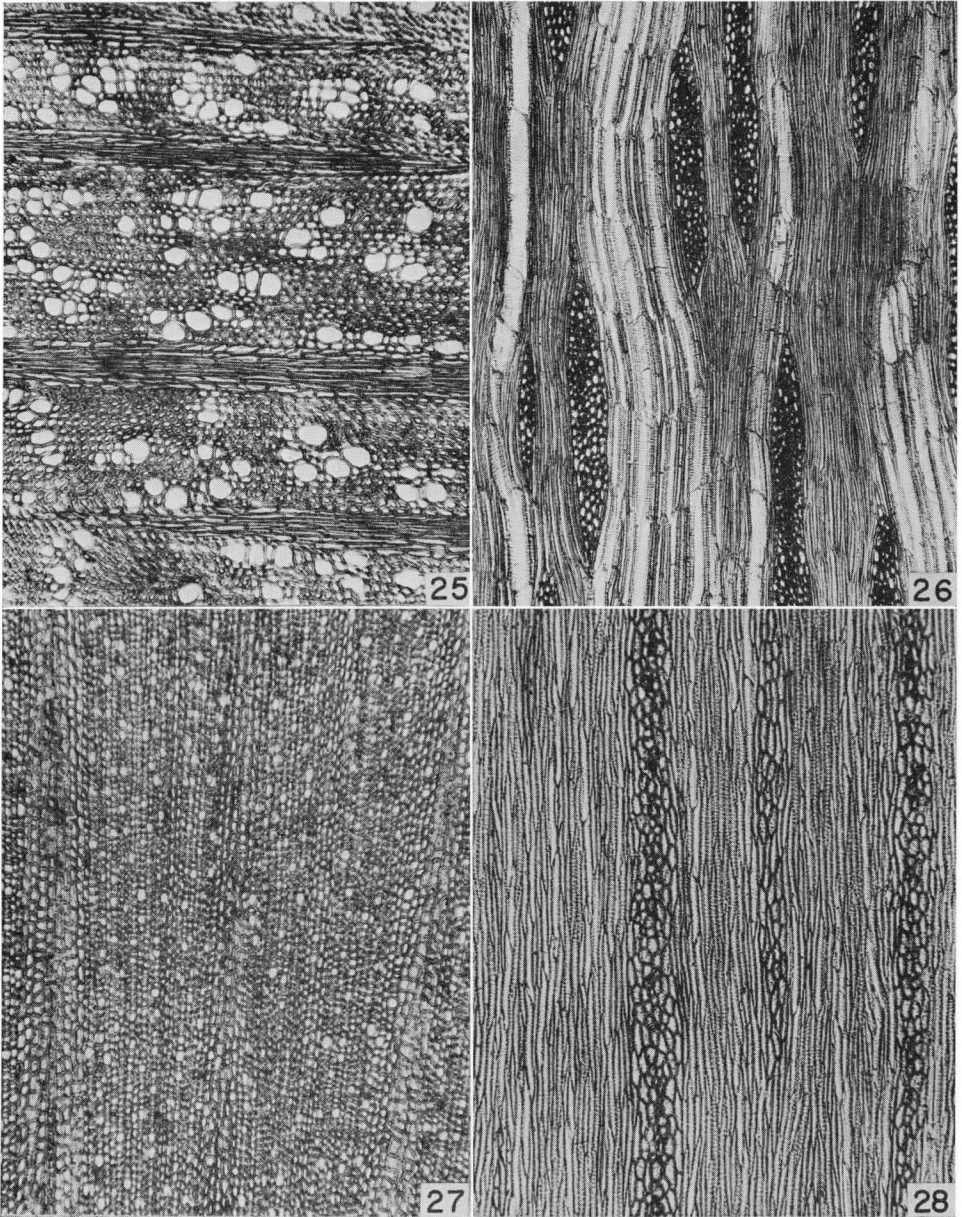
Fig. 25–28. Fig. 25, 26. *Cassinia longifolia.*—Fig. 25. Transection. Note grouping of vessels and vascular tracheids.—Fig. 26. Tangential section. Tracheary elements are prominently storied, uniseriate rays are absent.—Fig. 27, 28. *Loricaria thuyoides.*—Fig. 27. Transection. Note extremely narrow vessels and vascular tracheids.—Fig. 28. Tangential section. All tracheary elements are vessel elements or vascular tracheids. Axial elements are storied. All, × 85.

In the genus *Tessaria*, Cabrera (1939) considers *T. mucronatum* a sysnonym of *T. integrifolia*. This may be a defensible taxonomic decision, but attention should be called to the fact that the collection identified as *T. mucronatum* in the present study differed from the two collections of *T. integrifolium* in the following respects; absence of grooves on vessel walls, narrower vessels, smaller pits on vessels, wider, shorter fibers, and shorter multiseriate rays. Although these respects are probably not very major ones, they could be used in addition to other characteristics to recognize *T. mucronatum* as a distinct species.

GENUS CHARACTERISTICS

Of the genera in which more than one species were studied, several possess excellent xylary features by which genera can be characterized. For example, *Brachylaena* can be recognized anatomically by virtue of the libriform fibers and narrow (rarely wider than 2 cells), short rays. The relationship of *Tarchonanthus* to *Brachylaena* is suggested by such features as presence of procumbent cells exclusively in rays, shortness and narrowness of multiseriate rays, presence of uniseriate rays, and the similarity (to one or more species of *Brachylaena*) in storied structure and minute pitting. A thorough study of wood anatomy in *Brachylaena* is needed to show if all the Madagascar species of this genus have storied structure, as opposed to lack of storying in the mainland species.

Generic characteristics of *Pluchea* would seem to accrue from a lack of particular specializations (e.g., storying), but such features as absence of uniseriate rays, erectness of cells in the relatively wide multiseriate rays, and thin-walled fibers could be used to define woods of this genus as know thus far.

Likewise, the three collections of *Tessaria* all agree in long, wide, vessel elements, often with caudate or oblique ends, wide thin-walled fibers, and presence of both erect and procumbent cells in the multiseriate rays.

SUBTRIBAL CHARACTERISTICS

The representation of genera and species within Inuleae is really not sufficient to justify comparison to any given system of subtribes for the family. The close relationship of *Brachylaena* and *Tarchonanthus*, noted above, and the differences of these genera from other Inuleae, would seem to justify recognition of these two genera as a separate subtribe, Tarchonanthinae (e.g., Hoffman, 1889-1894). Adamson (1934) notes that all the Inuleae with anomalous secondary growth which he has studied belong to the subtribe Relhaniinae, with the single exception of *Phaenocoma*.

DEFINITION AND RELATIONSHIPS OF INULEAE

Before consideration of what evidence wood anatomy has to offer with relation to this problem, we may examine the various theories which taxonomists have advanced. As noted by Bentham (1873), Inuleae are defined by virtue of their imbricate involucres, tailed anthers, and the shape of stigmatic branches. Other features, such as cyanic corollas, sexual differentiation of disk flowers within a head, and woolly vesture of the plant may characterize many, but not all, of the genera of the tribe as it is currently recognized. Curiously, Bentham (1873) finds bonds of relationship with such diverse groups as Senecioneae and Mutisieae, but also notes resemblances between the genus *Buphthalmum* and certain Helantheae. The relationships sought by other authors seem to depend in a remarkable way upon what tribe they consider to have been primitive. In evolutionary logic, there can never be any such thing as a primitive family, or genus, etc. Only characteristics can be primitive, and retention of primitive characteristics in one genus or tribe only is highly unlikely. Indeed, my experience in Compositae has suggested that various primitive characteristics may be found in most tribes of Compositae, although some tribes (but not one in particular) do show a greater abundance of features best regarded as primitive than others. Various authors, however, seem to have sought the "primitive tribe" in Compositae. We find that

Small (1919), who has chosen Senecioneae as the primitive tribe, derives Inuleae directly from that assemblage. Leonhardt (1949), who regards Cynareae as primitive for the family, derives a portion of Inuleae ("Filagininae") from Astereae, the remainder ("Helichrysinae") from Cynareae. Augier and du Merac (1951) consider Vernonieae the primitive tribe, and find Inuleae closely allied to Vernonieae. Cronquist (1955) has selected Heliantheae as the primitive tribe of Compositae, and so it is not surprising that he regards Inuleae as a direct derivative of Heliantheae. Cronquist mentions the resemblances, noted earlier by Bentham, between *Buphthalmum* of Inuleae and certain Heliantheae.

The taxonomic history of individual genera is even more revealing of the confused situation Inuleae presents. Species of *Brachylaena* were originally described in the genus *Vernonia* (Vernonieae), species of *Loricaria* were first named as *Baccharis* (Astereae), and the above-noted genus, *Buphthalmum,* was regarded as possessing species which now reside in *Borrichia* (Heliantheae). Undoubtedly more examples of intertribal confusion involving Inuleae could be cited.

The most charitable conclusion would seem to be that Inuleae is not a natural tribe. It might, in fact, be a far more heterogeneous assemblage than Helenieae, and more in need of solution, if the divergent views of the various workers in this tribe are to be credited. Obviously, the problem of the limits and relationships of Inuleae are insoluble in terms of the data we now have.

Nevertheless, wood anatomy of the Inuleae studied here does suggest certain affinities. Caution should be applied in using the features listed below as criteria of relationship, because Compositae is a family in which the most primitive woods are already quite specialized, and advancement from this point occurs in a parallel fashion within various tribes. Thus, a particular wood, whether primitive or advanced, could be within the variation pattern of any of several tribes. However, the writer has noted that certain features of the majority of Inuleae studied are similar to those of many Vernonieae. The basis for data in the latter tribe is the writer's collection of wood slides in this tribe, and studies on these slides will be published in the near future. Features in which many woods of the two tribes agree are: minute pitting (rare in tribes other than Vernonieae and Inuleae), presence of grooves connecting pits in a helix on a vessel wall (other tribes show few such grooves or an abundance, as in Astereae, of spiral bands), and few or no uniseriate rays. Individual species of genera show some additional resemblances. *Oliganthes* and *Lychnophora* (Vernonieae) resemble *Brachylaena* in their thick-walled, sometimes radially-flattened, libriform fibers, their narrow rays, and their frequently grooved vessel walls. The genera with extremely thin-walled fibers, such as *Anaphalis, Pluchea,* and *Tessaria,* find counterparts in such species of *Vernonia* as *V. arborea.* One feature by which the two tribes differ, in general, is the narrower vessel diameter which characterizes Inuleae. Many members of the genus *Vernonia* have extremely wide vessels.

Such generalities do suggest that many inuloid genera have affinities to Vernonieae and are thus referable to that portion of the family which includes Vernonieae, Eupatorieae, Mutisieae, Cynareae, and Cichorieae. These tribes share, in whole or in part, such features as imbricate involucral bracts, cyanic flowers, lack of a prominent ring of collecting hairs on the stigmatic branches, and tailed anthers. Nevertheless, individual genera now placed in Inuleae may have affinities elsewhere. *Buphthalmum,* for example, represents a genus which needs further investigation in this regard. Even supposing that such investigation demonstrates that *Buphthalmum* is helianthoid in affinities, this would not mean that the entire contents of Inuleae are allied to Heliantheae. In *Loricaria,* Cuatrecasas (1954) reaches the paradoxical conclusion that this genus "belongs to Gnaphalinae [Inuleae]", but ironically, "doubtless has genetic connections to *Baccharis* [Astereae]." From the standpoint of wood anatomy, *Loricaria* could be regarded as the end-product of increasingly abundant and narrow vessels, with concomitantly less abundant fibers, a trend evident in

Baccharis or *Tetramolopium* (Astereae). These two examples represent two of the many opportunities for study of phylogenetic problems in Inuleae. Until such problems have been given a satisfactory solution, we cannot speak with any certainty about the relationships of Inuleae or even the limits of the tribe itself.

LITERATURE CITED

Adamson, R. S. 1934. Anomalous secondary thickening in Compositae. Ann. Botan. 48: 505–514.
———. 1937. Anomalous secondary growth in *Osteospermum*. Trans. Roy. Soc. S. Afr. 24: 303–312.
Augier, J., and Marie-Louise du-Merac. 1951. La phylogénie des Composées. La Revue Sci. 89: 67–182.
Bentham, G. 1873. Notes on the classification, history, and geographical distribution of Compositae. J. Linn. Soc., Botan. 13: 335–577.
Cabrera, A. L. 1939. Les especies argentinas del genero "*Tessaria*". Lilloa 4: 181–189.
Carlquist, S. 1958a. Wood anatomy of Heliantheae (Compositae). Trop. Woods 108: 1–30.
———. 1958b. The woods and flora of the Florida Keys. Compositae. Trop. Woods 109: 1–37.
———. 1959. Wood anatomy of Helenieae (Compositae). Trop. Woods 111: 19–39.
———. 1960. Wood anatomy of Astereae (Compositae). Trop. Woods 113: 54–84.
Chalk, L., and M. Margaret Chattaway. 1937. Identification of woods with included phloem. Trop. Woods 50: 1–31.
Cronquist, A. 1955. Phylogeny and taxonomy of the Compositae. Am. Midland Naturalist. 53: 478–511.
Cuatrecasas, J. 1954. Synopsis der Gattung *Loricaria* Wedd. Feddes Repert. 56: 149–172.
Hedberg, O. 1957. Afroalpine vascular plants. Symb. Botan. Upsalienses 15(1): 1–411.
Hoffmann, O. 1889–1894. Compositae. *In,* Engler & Prantl, Die natürlichen pflanzenfamilien 4(5): 87–391.
Humbert, H. 1923. Les composées de Madagascar. E. Lanier. Caen.
Janssonius, H. H. 1906–1936. Mikrographie des Holzes der auf Java vorkommenden Baumarten. 6 vols. Leiden.
Kribs, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. Botan. Gaz. 96: 547–557.
———. 1937. Salient lines of structural specialization in the wood parenchyma of dicotyledons. Bull. Torrey Botan. Club 64: 177–186.
Lanjouw, J., and F. Stafleu. 1959. Index herbariorum. Part. I. The herbaria of the world. ed. 4 International Bureau for plant taxonomy and nomenclature. Utrecht.
Lecomte, H. 1922. Les bois de la forêt d'Analamazaotra. Augustin Challonel. Paris.
Leonhardt, R. 1949. Phylogenetisch-systematische Betrachtungen. I. Betrachtungen zur Systematik der Compositen. Ost. Botan. Zeitschr. 96: 293–324.
Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Vol. 2. Clarendon Press. Oxford.
Perrot, E. 1922. Los bois de Madagascar. Augustin Challonel. Paris.
Small, J. 1919. The origin and development of Compositae. (New Phytologist Reprint No. 11). William Wesley & Son. London.
Stern, W. L., and K. Chambers. 1960. The citation of wood specimens and herbarium vouchers in anatomical research. Taxon 9: 7–13.
Williams, L. 1936. Woods of northeastern Peru. Field Musuem. Chicago.