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WOOD ANATOMY OF EUPATORIEAE (COMPOSITAE)

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INTRODUCTION

The tribe Eupatorieae, a tribe almost exclusively American in distribution, has been thought to be related to Vernonieae by various authorities (Bentham, 1873; Hoffmann, 1890). Eupatorieae possess only a few characters which differentiate the tribe from Vernonieae; chief among these are the blunt style branches and lack of basal anther appendages. A degree of resemblance between Eupatorieae and tribes other than Vernonieae has also been noted (Bentham, 1873). However, the view which would probably command the widest support from students of Compositae is that Eupatorieae is derived from ancestors like Vernonieae and has undergone considerable radiation throughout the New World. The tribe consists of one large genus, *Eupatorium*, and about 50 other genera which seem closely related to *Eupatorium* and to each other.

Eupatorieae which occur outside the New World are the monotypic *Adenostyles* in Europe and Asia minor, several species of *Eupatorium*, and one cosmopolitan species in each of the genera *Adenostemma*, *Ageratum* and *Mikania*. These distributions seem more likely the result of chance long-distance dispersal than vestiges of a once-greater distribution of the tribe. The Madagascar genus *Apodocephala*, the wood of which was described by Lecomte (1922), was once placed by Hoffmann (1890) in Eupatorieae, but later (1894) he acknowledged that it belongs in Vernonieae. There seems little doubt that *Apodocephala* is, in fact, a member of Vernonieae, as Lecomte (1922) and Humbert (1923) agree.

Brickellia, with about 90 species, is a genus of shrubs and herbs characteristic of drier areas of the southwestern United States and Mexico (Robinson, 1917). A few species range into Central America, the West Indies, and northern South America. Three species, collected in California, were utilized in the present study. *Eupatorium*, with more than 500 species, is one of the larger genera of Compositae. Ranging from herbs to shrubs and a few small trees, Eupatoriums are most abundant in Mexico and southern South America (Record and Hess, 1943). The species studied here are distributed as follows: *E. billbergianum* (Panama); *E. celtidifolium* (Colombia); *E. dalea* (Jamaica and Cuba); *E. daleoides* (Mexico); *E. frustratum* (S. Florida); *E. hiemale* (Argentina); *E. itatiayense* (northwestern South America); *E. morifolium* (Mexico); *E. odoratum* (Florida to South America), *E. oersteditianum* (Cen-

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tral America); *E. pittieri* (Venezuela); *E. portoricensis* (Puerto Rico); *E. sordidum* (Mexico); *E. theaeifolium* (Colombia). Species of *Eupatorium* in the present study which have been regarded by some taxonomists under segregate genera are *E. frustratum* and *E. odoratum* (Osmia) and *E. portoricensis* (Crittoria). Allied closely to *Eupatorium* is the genus *Mikania*, which consists of about 150 species of lianoid and vining herbs from tropical America. *Mikania cordifolia* is native to Brazil. By error, data on this species were included in an earlier study (Carlquist, 1962a). *Piqueria*, which is represented here by the Peruvian species *P. peruviana*, consists of about 15 species of shrubs or herbs, and ranges from Mexico to Bolivia.

Literature on wood anatomy of Eupatorieae is very scanty. Solereder (1885, 1908) and Metcalfe and Chalk (1950) have offered scattered observations on certain species of *Eupatorium* and *Ageratum*. In a study of Compositae native to the Florida Keys, the wood anatomy of two species of *Eupatorium* was described (Carlquist, 1958).

MATERIALS, METHODS AND ACKNOWLEDGMENTS

The wood samples studied here and specimens documenting them are listed in table 1. Some wood samples (*Brickellia californica*, *B. nevinii*, *Eupatorium sordidum*) were collected from living plants. Others were obtained from wood collections. For these, appreciation is expressed to the curators of wood collections at Harvard University (Arnold Arboretum Wood Collection), Yale University (Samuel J. Record Collection) and Chicago Museum of Natural History. Wood accession numbers are listed in table 1 according to the wood-collection abbreviations of Stern and Chambers (1960), and herbarium vouchers follow the citation system of Lanjouw and Stafleu (1964). Dr. Peter Raven provided the sample of *Brickellia nevinii*. Acknowledgement is expressed to Dr. I. W. Bailey and Dr. William L. Stern for their help in securing wood samples and their interest in these studies.

Woods were sectioned by means of a sliding microtome, stained with safranin and mounted in Canada Balsam according to the usually-employed techniques. Wide vessels and thin walled fibers in certain Eupatorieae provided difficulties in sectioning which were in part overcome by cutting somewhat thicker sections. Some sections used in this study were prepared by Dr. Loran G. Anderson, Mr. James S. Henrickson, and Mr. Charles F. Quibell. More numerous wood samples, particularly in the genera *Eupatorium*, *Brickellia* and *Mikania* could have been added had a more intensive survey of Eupatorieae woods been desired, and had travel toward this end been undertaken. The focus of this series of papers, however, is not on synoptical study of woods of Compositae but on sources of variability and patterns of evolution in the family. Not only are comparable materials difficult to obtain where so many species are involved, the value of such comparison over large areas of a family is doubtful. This does not, however, rule out the possibility that wood anatomy can be a useful systematic tool within particular genera of Eupatorieae and other tribes.

ANATOMICAL DESCRIPTIONS

Table 1 provides a summary of quantitative and qualitative wood characteristics in Eupatorieae. The features listed cover some of the most significant and easily-condensed data. Additional descriptions are provided in the text under headings below. Conventions and symbols used in table 1 are as follows:

- cg = continuous grooves which interconnect apertures of numerous pits adjacent in a helix on a vessel wall
- f = libriform fibers
- fb = fine bands which usually form pairs beside grooves on walls of pitted vessels
- ff = a few libriform fibers
- fv = fewer vessels
- p = paratracheal parenchyma
- sg = short grooves interconnecting apertures of two or several pits adjacent in a helix on a vessel wall
- tf = thin-walled libriform fibers
- v = vessel elements
- wv = wider vessels
- + = presence of character
- = presence of character to a limited extent
- 0 = absence of character

Absence of figures for uniseriate rays indicates that uniseriates are so scarce that meaningful figures cannot be obtained.

VESSEL ELEMENTS

Dimensions, Shapes, Types.—In average diameter, vessels of Eupatorieae fall within a range median for Compositae. Exceptionally wide vessels are frequent in *Mikania cordifolia*, and are related to the lianoid habit of this genus. The vessels of *Eupatorium frustratum* and *E. odoratum* are relatively narrow, as are those of *Brickellia* (fig. 1), on the average. In the case of *Brickellia*, adaptation to xeric conditions may be causal in narrowness of vessels. Exceptionally long vessel elements characterize many species of *Eupatorium*: *E. dalea*, *E. daleoides*, *E. hiemale* (fig. 22), *E. itatiayense* (fig. 20), *E. oerstedtianum*, *E. pittieri*, *E. portoricensis*, *E. sordidum* (fig. 14) and *E. theaeifolium* (fig. 16). In part, this long vessel-element length would seem to indicate a lack of specialization. This situation is quite comparable to that of many Vernonieae (Carlquist, 1964). The shortness of vessel elements in *Mikania cordifolia* is directly related to its liana habit. Short, wide vessels of this sort are hallmarks of vines and lianas. Short vessel elements in *Brickellia* (fig. 2) are, on the other hand, probably indicative of the aridity of sites favored by species in this genus. This may also apply to *Piqueria peruviana* (fig. 8) as well.

As in other Compositae, simple perforation plates characterize Eupatorieae. In *Eupatorium billbergianum*, *E. sordidum* and *E. theaeifolium*, a few near-scalariform perforation plates were seen. As with Cynareae (Carlquist, 1965),

these cannot be interpreted as true vestiges of a primitive wood condition. A very interesting type of multiperforate plate was observed in some vessels of *Brickellia multiflora* (fig. 3-6). In these, a few very narrow strands of wall material traverse otherwise simple perforation plates. These strands are often loop-like or organized into network-like patterns. Strands of wall material are always irregular in orientation, like some figured for Cichorieae (Carlquist, 1960). Such multiperforate plates are definitely not remnants of a truly scalariform pattern. Why they should occur sporadically in a particular species is

TABLE 1. *Wood Characteristics of Eupatorieae*

SPECIES	COLLECTION	DIAMETER WIDEST VESSEL, μ	DIAMETER VESSELS, AVERAGE, μ
<i>Brickellia californica</i> Gray	Balls 21441 (RSA)	122	44.4
<i>Brickellia multiflora</i> Kellogg	Wolf 2576 (RSA)	98	55.6
<i>Brickellia nevinii</i> Gray	Raven 16757 (RSA)	88	53.0
<i>Eupatorium billbergianum</i> Beurl.	Smith 146 (Y), Yw35420	104	76.4
<i>Eupatorium celtidifolium</i> Lam.	Williams 10307 (F)	100	57.4
<i>Eupatorium dalea</i> L.	USw5913	92	54.1
<i>Eupatorium daleoides</i> Hemsl.	Bailey 1 (A), Aw27275	123	86.0
<i>Eupatorium frustratum</i> Rob.	Stern & Chambers 277 (RSA)	42	24.1
<i>Eupatorium hiemale</i> Lillo	Venturi 17 (A), Aw20197	112	77.3
<i>Eupatorium itatiayense</i> Hieron.	Fw622866	172	80.1
<i>Eupatorium morifolium</i> Mill.	Williams 9113 (F)	110	76.4
<i>Eupatorium odoratum</i> L.	Stern & Chambers 257 (RSA)	81	48.1
<i>Eupatorium oerstedtianum</i> Benth.	Edwards 445 (A)	82	59.1
<i>Eupatorium pittieri</i> Klatt	Skutch 1983 (A), Aw22953	94	71.2
<i>Eupatorium portoricensis</i> Urban	Aw3078	101	64.9
<i>Eupatorium sordidum</i> Less.	Carlquist 112 (RSA)	80	46.1
<i>Eupatorium theaeifolium</i> Benth.	Cuatrecasas 43-46, Aw20566	96	69.9
<i>Mikania cordifolia</i> (L.E.) Willd.	Rimbach 797 (Y), Yw34199	270	65.5
<i>Piqueria peruviana</i> (Gmel.) Rob.	Rimbach 855 (Y), Yw34200	110	65.5

not easily explained, however. Multiperforate perforation plates were reported in Eupatorieae in the genus *Ageratum* by Metcalfe and Chalk (1950).

Lateral-Wall Pitting.—Alternate bordered pits, circular in outline and between 2 and 6 μ in diameter, may be found on intervacular walls in woods of Eupatorieae (fig. 17, 18). The presence of rather small as well as medium-sized pits is characteristic of Inuleae (Carlquist, 1961) and Vernonieae (Carlquist, 1964) as well as Eupatorieae. The unusually large pits of *Mikania cordifolia* are probably a feature to be associated with the liana habit. The intervacular pits in this species are crowded and polygonal in outline as seen in face view.

VESSELS PER GROUP, AVERAGE	LENGTH VESSEL ELEMENTS, AVERAGE, μ	LENGTH LIBRIFORM FIBERS, AVERAGE, μ	MAXIMUM WIDTH LIBRIFORM FIBERS, AVERAGE, μ	WALL THICKNESS FIBERS, μ	DIAMETER INTERVASCULAR PITS, μ	HELICAL SCULPTURE ON VESSELS	ELEMENTS DISTINGUISHING EARLY WOOD OF RINGS	STORIED ELEMENTS	HEIGHT MULTISERiate RAYS, AVERAGE, mm.	HEIGHT UNISERiate RAYS, AVERAGE, μ	MAXIMUM WIDTH MULTISERiate RAYS, AVERAGE, CELLS	RAY CELLS ISODIAMETRIC TO PROCUMBENT	RAY CELLS ISODIAMETRIC TO ERECT
1.00	155	387	22.7	3	5	cg	wv,fv	ff	.89	136	5.48	+	+
1.52	163	222	16.1	3	5	cg	wv,fv	ff	.45	123	3.93	+	+
1.94	183	251	21.7	3	5	cg	wv,fv	f,v,p	2.90	—	4.56	+	+
1.97	289	445	21.0	4	3	cg	tf	ff	.89	—	6.59	+	+
2.70	287	370	24.5	3	3	cg		ff	.39	139	3.29	+	+
1.87	380	497	18.4	3	2	cg,fb		ff	3.23	—	4.12	0	+
1.43	338	505	26.0	3	3	cg		f	4.08	—	5.87	+	+
1.80	157	350	20.0	3	3	sg	wv		.54	—	3.71	0	+
2.47	316	394	25.1	3	4	cg		f,v,p	1.13	—	7.62	+	+
2.92	309	428	20.8	3	5	cg,fb		ff	1.00	—	3.82	+	+
2.07	289	478	24.2	3	5	cg		ff	1.75	—	9.94	—	+
1.93	278	700	26.2	4	2	cg,fb	wv		1.90	—	5.19	—	+
1.65	415	810	21.8	3	3	cg			1.41	—	4.75	—	+
1.87	383	514	24.7	4	2	cg,fb	tf		1.36	—	3.81	+	+
2.17	377	700	24.0	3	4	cg	tf		2.77	—	4.88	—	+
1.89	341	816	31.7	3	3	sg			.62	—	3.45	0	+
2.31	398	623	27.7	5	5	sg		ff	1.01	—	3.96	—	+
6.17	230	296	29.3	3	6			f,v,p	>10	—	?	+	0
2.40	226	367	23.5	3	5	cg		f	.72	—	4.59	+	+

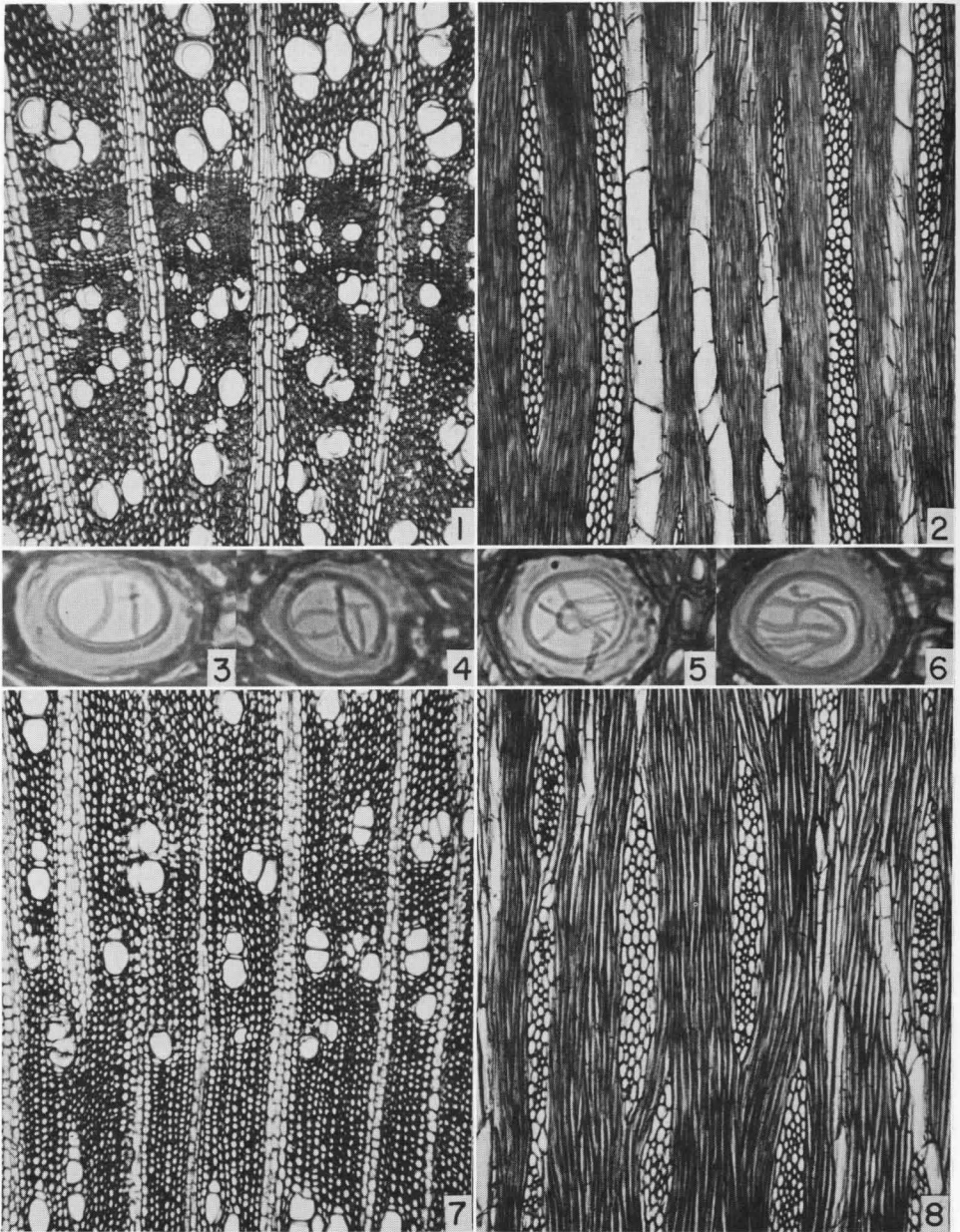


Fig. 1-8. Wood sections.—Fig. 1-2. *Brickellia californica*.—Fig. 1 Transverse. The boundary between adjacent growth rings shows narrow vessels and thick-walled fibers, below, and wider vessels with thinner-walled fibers, above.—Fig. 2. Tangential section.—Fig. 3-6. *Brick-*

Vessel-parenchyma pitting consists of laterally widened pits and appears virtually scalariform in *Eupatorium billbergianum* and *Mikania cordifolia*. In the latter, such pits have unusually wide apertures and are like those figured for *Vernonia baccharoides* (Carlquist, 1964).

Vessels of Eupatorieae are almost uniformly provided with grooves which interconnect pit apertures in a helix (table 1; fig. 17, 18). Grooves of this sort were observed in all Eupatorieae studied except *Mikania cordifolia*. Where these grooves are most prominent, their margins may be slightly raised, forming a pair of fine bands paralleling each groove. This was observed in *Eupatorium itatiayense* (fig. 21), *E. pittieri* and *E. odoratum* (Carlquist, 1958). In these species, walls of vessels facing parenchyma may be sparsely pitted, and on such walls fine bands or striae occur in places where pits are absent or rare. Notably wide grooves were observed in *Eupatorium hiemale*. The only tribes which are provided with grooves like those of Eupatorieae in abundance and low level of specialization are Vernonieae (Carlquist, 1964), Inuleae (Carlquist, 1961) and Cynareae (Carlquist, 1965). This feature may be a clue to relationships among these groups. Spirals (presumably of the sort described) were reported in Eupatorieae by Solereder (1885) in the case of *Ageratum* sp. and *Eupatorium petiolare*.

Vessel Grouping.—Relatively small groups of vessels, as seen in transection, characterize most Eupatorieae. These take the form of pore multiples in some species (fig. 1, 7, 19), although radial chains are the form of vessel aggregation most commonly encountered in the tribe (fig. 9, 11, 13, 15). Exceptionally large groups of vessels occur in *Mikania cordifolia*. In this species, large vessels tend to be surrounded by a circle of smaller vessels which are flattened, as though compressed by the large vessel. Radial chains of vessels also occur in *Mikania cordifolia*. The exceptionally large groups of vessels in *Brickellia californica* and other species of *Brickellia* are related to growth-ring phenomena, because the end of each year's growth features production of large numbers of narrow vessels and vascular tracheids.

LIBRIFORM FIBERS

The average lengths of libriform fibers in Eupatorieae parallel those of vessel elements. A notable feature in morphology of libriform fibers is the tendency for septation. Septate fibers were observed in *Eupatorium dalea*, *E. daleoides*, *E. hiemale* (fig. 22), *E. morifolium* (fig. 12), *E. pittieri*, *E. portoricensis*, *E. sordidum* (fig. 14) and *Piqueria peruviana* (fig. 8). Septate fibers are reported for species (unlisted) of *Eupatorium* by Metcalfe and Chalk (1950) and for *Eupatorium petiolare* by Solereder (1885). Fibers of *Eupatorium oerstedianum* appear to have gelatinous walls by virtue of the wavy shrinkage patterns observed in longitudinal sections.

ellia multiflora. Multiperforate perforation plates as seen in transections of wood. Various degrees of complexity in the number and arrangement of the narrow bars are seen.—Fig. 7–8. *Piqueria peruviana*.—Fig. 7. Transection. Vessels are scattered in arrangement, but with some tendency toward tangential bands.—Fig. 8. Tangential section. Libriform fibers are clearly storied in most portions of this section.—Fig. 1, 2, 7, 8: $\times 62$; fig. 3–6, $\times 280$.

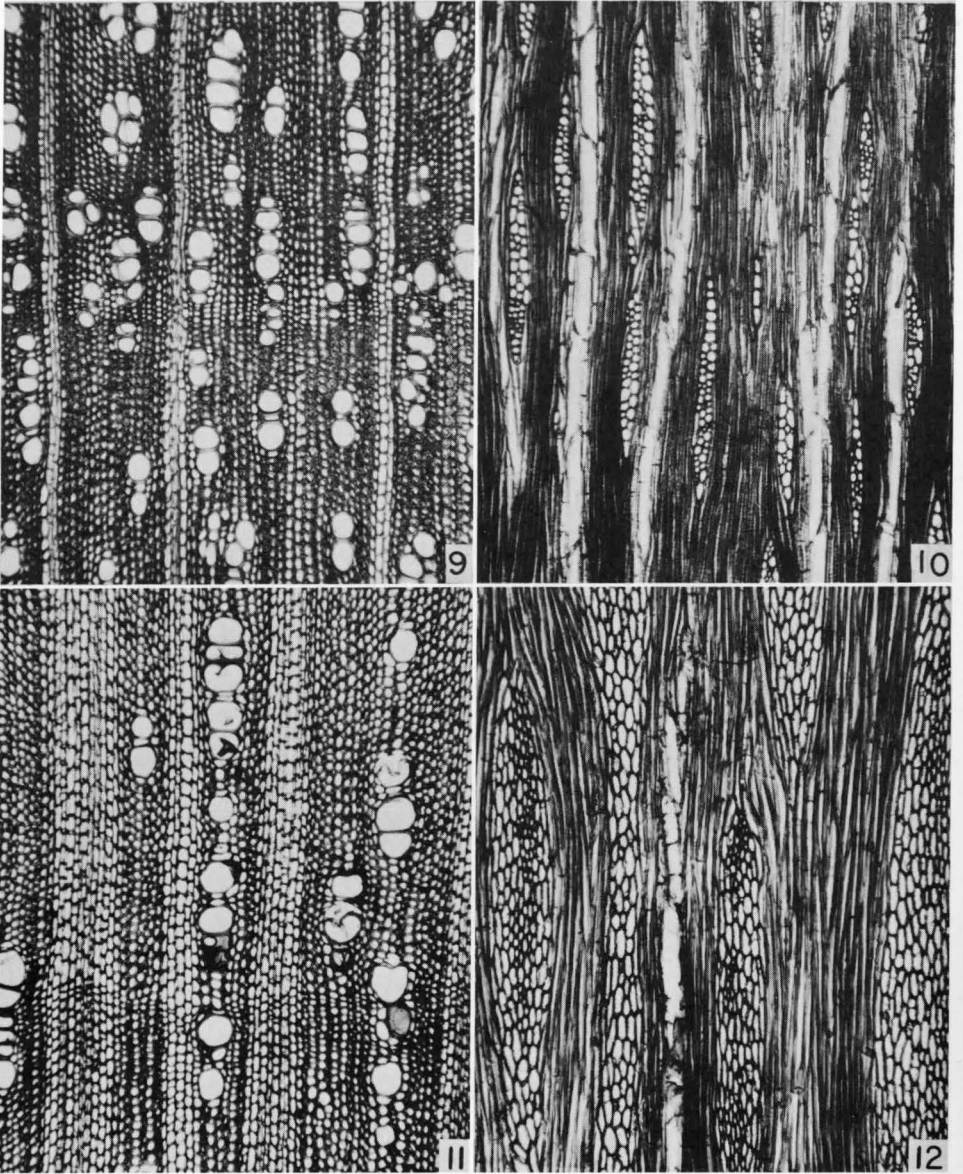


Fig. 9-12. Wood sections.—Fig. 9-10. *Eupatorium celtidifolium*.—Fig. 9. Transection. Vessels are prominently aggregated into radial chains.—Fig. 10. Tangential section. Many fibers are storied; rays are short, discrete, and procumbent cells are relatively abundant.—Fig. 11-12. *Eupatorium morifolium*.—Fig. 11. Transection. Vessels are wide; some are filled with resin-like deposits.—Fig. 12. Tangential section. Libriform fibers are not frequently storied. Rays are tall, wide, and composed predominantly of erect cells.—All, $\times 62$.

Variation in fiber-wall width was noted in *Eupatorium billbergianum*, *E. pittieri* and *E. portoricensis*. In these woods, thin-walled fibers could be seen at the beginning of growth rings. This can be seen in the illustration of *Eupatorium celtidifolium* (fig. 9). Variation in fiber-wall thickness is especially prominent in *Brickellia* in relation to the well-marked growth rings in that genus (fig. 1). The thick-walled fibers of *B. nevini* are especially prominent because the fibers are so narrow, whereas notably wide, thin-walled fibers occur in *Eupatorium sordidum* (fig. 13, 14). This variation of fiber-wall thickness does not constitute fiber dimorphism, such as has been seen in other Compositae, and no bands of apotracheal parenchyma originating from fiber dimorphism or other means can be said to be present.

AXIAL PARENCHYMA

Paratracheal parenchyma in Eupatorieae takes the form of incomplete sheaths, a single cell layer in thickness, of vasicentric cells. Occasionally vasicentric parenchyma can be seen prominently, as in *Eupatorium theae-folium* (fig. 15). Longitudinal sections of *Mikania cordifolia* show especially conspicuous vasicentric parenchyma, probably because of the wideness of the vessels which are clothed with parenchyma. In this species, parenchyma strands form arcuate patterns along the vessel walls; cells in these strands are as wide as they are long, and thus are unusual among Compositae in that they appear predominantly square as seen in longitudinal sections. Other Eupatorieae have strands of 2-6 elongate cells. Strands of two were common in *Eupatorium billbergianum* and *E. hiemale*, whereas strands of three to four were observed in *E. pittieri* and *E. portoricensis*. Strands varied from two to five cells in *E. oerstedianum*. Metcalfe and Chalk (1950) report strands of two to four or occasionally six in *Eupatorium*.

VASCULAR RAYS

Rays vary widely in size and histology in Eupatorieae, forming a major source of diversity among woods in the tribe. In no species, however, were uniseriate rays abundant. Absence of uniseriate rays characterizes a larger segment of Eupatorieae than of any other tribe. If absence of uniseriate rays is a specialized characteristic, as hypothesized by Kribs (1935), Eupatorieae may be said to be relatively specialized. In very few Compositae, however, are uniseriate rays as numerous as, or more numerous than, multiseriate rays.

Multiseriate rays vary considerably in height. The extremely high rays of *Mikania cordifolia* probably represent minimal alteration of the primary rays. Active breakup of rays could be seen in some wood samples. This accounts for presence of perforated ray cells, as in *Brickellia californica* and *Eupatorium morifolium*. Multiseriate rays which average less than a millimeter in height occur, among species of the present study, only in *Brickellia californica* (fig. 2), *B. multiflora*, *Eupatorium billbergianum*, *E. celtidifolium* (fig. 10), *E. frustratum*, *E. sordidum* (fig. 14) and *Piqueria peruviana* (fig. 8). Rays are relatively wide in *Brickellia californica* (fig. 2), *Eupatorium billbergianum*, *E. hiemale* (fig. 22) and *E. morifolium* (fig. 12).

Ray cells have lignified secondary walls in all Eupatorieae studied except *Mikania cordifolia*, in which thin-walled ray cells collapsed and ray width

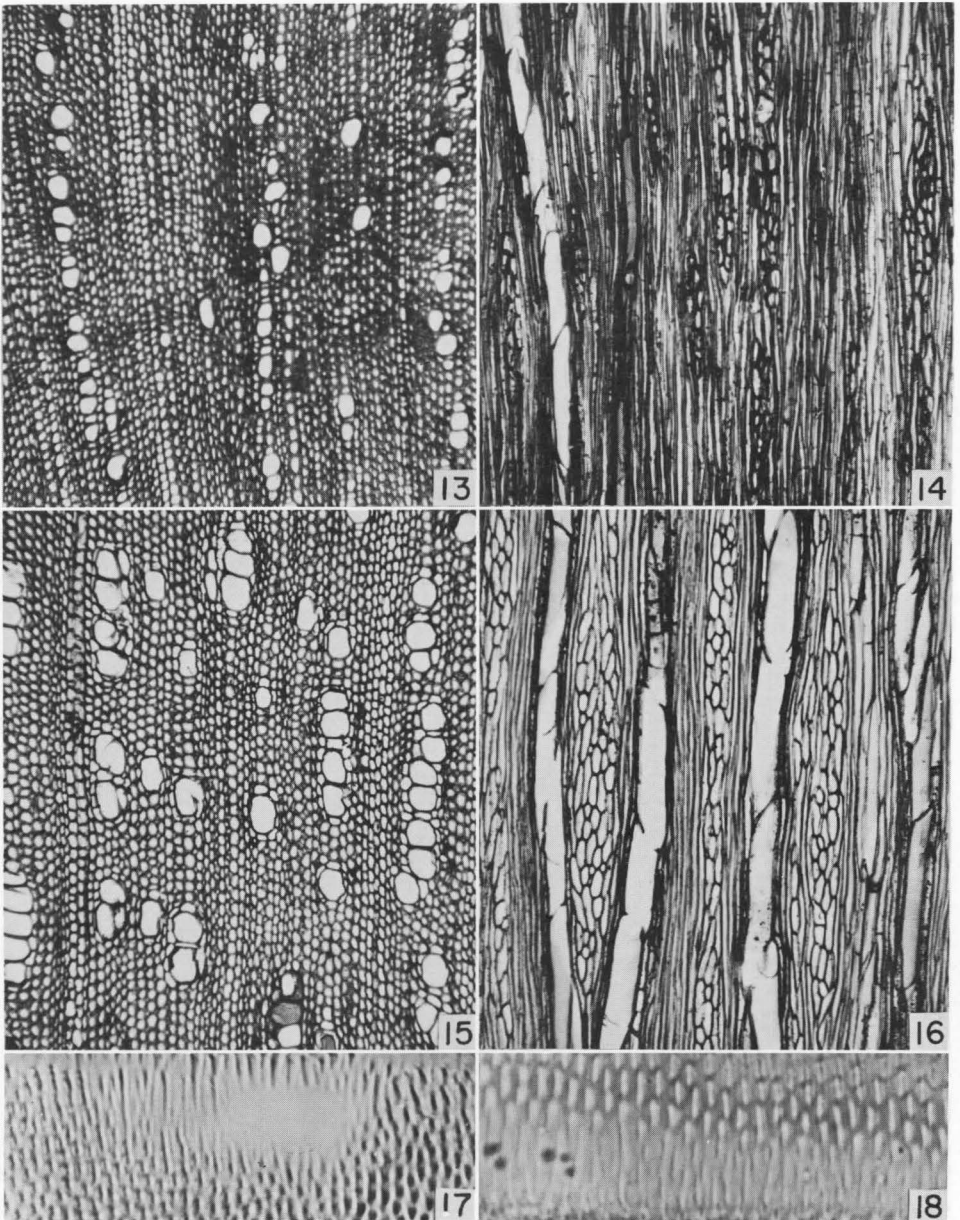


Fig. 13-18. Wood sections.—Fig. 13-14. *Eupatorium sordidum*.—Fig. 13. Transection. Note narrow vessels; dark areas of xylem are filled with deposits of resin-like materials.—Fig. 14. Tangential section. Rays are narrow; droplets of resin-like materials may be seen in all cell types.—Fig. 15-17. *Eupatorium theaeifolium*.—Fig. 15. Transection. Parenchyma cells adja-

in cells could not be measured. *Mikania cordifolia* also proved exceptional among Eupatorieae in the presence of procumbent to square cells exclusively. Most Eupatorieae have many fewer procumbent cells than erect cells in rays. Where procumbent cells do occur, they are always in the central portion of multiseriate rays. *Eupatorium sordidum* (fig. 14) and *E. theaeifolium* (fig. 16) are particularly notable for erectness of ray cells. In these species multiseriate rays appear to fade into the axial portion of the secondary xylem because erect ray cells on ray margins so closely approximate libriform fibers in shape and wall characteristics. This strong tendency toward erectness of ray cells results from lack of change, ontogenetically, to a greater proportion of procumbent cells by subdivision of ray initials, and is a phenomenon probably referable to paedomorphosis (Carlquist, 1962b). With this tendency present in Eupatorieae, one would expect raylessness in at least a few species of the tribe. Exhaustive studies of woods, especially of smaller woody herbs, would doubtless uncover several instances in Eupatorieae. That this is true is suggested by a report of a rayless condition in an unidentified species of *Ageratum* (Solereider, 1885).

GROWTH RINGS

Most Eupatorieae have relatively little alteration in wood histology related to seasonal alteration. Where such rings occur (table 1), they take the form of thinner-walled fibers or wider vessels, or both. An exception to this statement is provided only by *Brickellia*, which has much more marked rings (fig. 1). Production of these growth rings is related to cessation of rainfall and commencement of a dry season. At the end of the growing season, vessels narrow markedly in width and become more numerous within a given transectional area. Progressive narrowing in vessel diameter is accompanied by narrowing of perforation plates, and in the narrowest, perforation plates are lacking, so that vascular tracheids result. Vascular tracheids were observed at the end of growth rings in all the species of *Brickellia* examined.

STORIED WOOD STRUCTURE

Marked storying can be found in only a few species of Eupatorieae (table 1). One such species is *Piqueria peruviana* (fig. 8), in which all fibers conform to a storied pattern, as sporadically do vessels and their associated vasicentric parenchyma cells. The same condition obtains in *Eupatorium dalea*, *E. hiemale* (fig. 22) and *Mikania cordifolia*. In the section of *E. itatiayense* illustrated (fig. 20), storying is apparent in some areas, not in others. In such a species, the fusiform cambial initials may be storied, but differential elongation of libriform fibers may mask the basically storied pattern. Several other Eupatoriums (*E. billbergianum*, *E. celtidifolium* and *E. theaeifolium*) fall into this category. The relatively low degree of storying in Eupatorieae is interest-

cent to vessels are wide, conspicuous.—Fig. 16. Tangential section. Erect cells are frequent in the tall rays.—Fig. 17. Portion of vessel wall from tangential section. Where wall is shaved away, grooves interconnecting pit apertures are evident.—Fig. 18. *Eupatorium billbergianum*. Portion of vessel wall from tangential section. Bordered pits are in focus, above, and the grooves which interconnect pit apertures are in focus, below.—Fig. 13–16: $\times 62$; fig. 17, 18: $\times 280$.

ing, for a very low degree of storying also characterizes Cynareae (Carlquist, 1965) and Vernoniaceae (Carlquist, 1964), in which relative primitiveness seems the best explanation for prevalence of the nonstoried condition.

ANOMALOUS GROWTH

No anomalous secondary growth was observed in the samples studied here, but Solereder (1908) reports "pericyclic" groups of xylem and phloem in *Mikania*. This may constitute a form of anomalous secondary growth, which would be expected in a liana.

RESINOUS DEPOSITS

Some woods of Eupatorieae characteristically have deposits of resin-like compounds. Where most abundant, these take the form of massive accumulations in vessel elements and in other types of cells. This was observed in *Eupatorium hiemale*, *E. morifolium* (fig. 11), *E. odoratum*, *E. sordidum* (fig. 13, 14) and *E. theaeifolium* (fig. 15). In these species, droplets also occur where more massive deposits are not present. In other species, resinous droplets were observed in parenchyma cells (*E. billbergianum*, *E. celtidifolium*, *E. oerstedtianum*, and *E. pittieri*) or fibers and parenchyma cells (*E. portoricensis*). Resin-like deposits between ray cells in *Brickellia nevinii* are carbonized in places.

CRYSTALS

Crystals were observed in pith cells of *Eupatorium sordidum*, where they take the form of small druses. They were not observed, however, in the wood of this species or in wood of other Eupatorieae.

DISCUSSION

Relation of Wood Anatomy to Habit and Ecology.—The diversity of habit which occurs within Eupatorieae is also expressed in terms of wood anatomy. In the liana *Mikania cordifolia*, high rays with soft-walled cells offer enhanced flexibility of stems, while wide short vessel elements with large pits maximize the conductivity of a stem with small transectional area. The prominent growth rings, the storied structure, and the short vessel elements observed in *Brickellia* are specializations referable to a strongly seasonal regime governed by temperature and alternating wet and dry seasons. Absence in most species of *Eupatorium* of marked specializations such as the above may be attributed in large degree to lacking adaptations to extreme habitat conditions or climatic fluctuations. In their wood anatomy Compositae as a whole show such sensitivity to local ecological conditions that specializations in wood anatomy can to a large extent be interpreted in this light.

Taxonomic Relationships.—Taking into account specializations in wood anatomy which are based rather directly upon ecological factors, one can find a number of features which can serve to distinguish species within the genera of Eupatorieae. The histology of rays offers several distinctions. Contrasting width of rays, presence or absence of procumbent cells in addition to erect ones

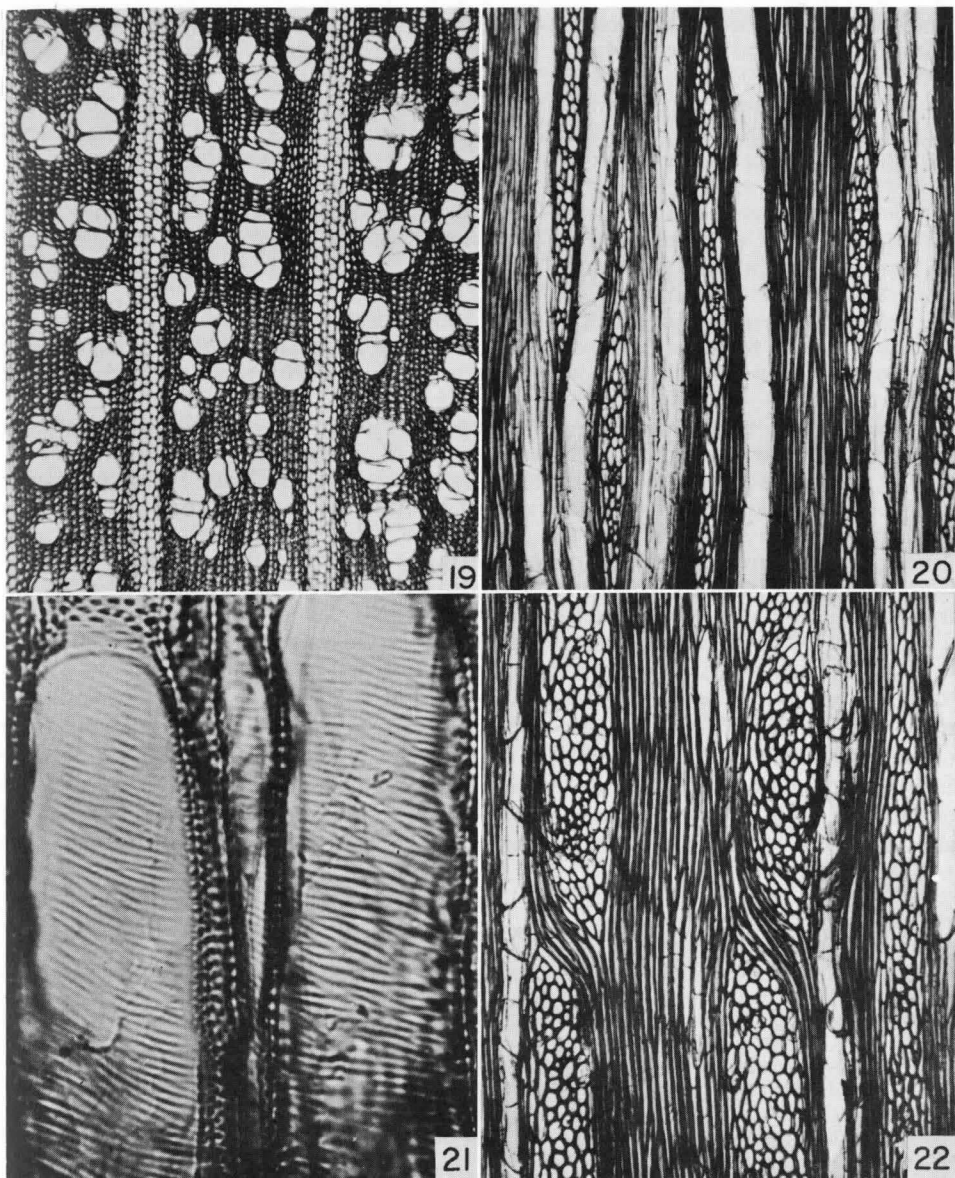


Fig. 19-22. Wood sections.—Fig. 19-21. *Eupatorium itaiyense*.—Fig. 19. Transection. The wide vessels are prominently aggregated into groups.—Fig. 20. Tangential section. Some degree of storieding is evident in the libriform fibers.—Fig. 21. Portions of the walls of vessels. On the areas shown, pits are sparse and the bands which accompany grooves can be seen.—Fig. 22. *Eupatorium hiemale*. Tangential section. The very wide rays are apparent, as well as the clearly storied libriform fibers, many of which are septate.—All, $\times 62$.

and relative height of rays could be used to differentiate species of *Eupatorium*. Notably short and narrow vessel elements (*Eupatorium frustratum*) or wide and long ones (*E. theaeefolium*) offer further distinctions. The narrow and thick-walled fibers and prominent grooves and fine bands on walls of pitted vessels in *E. itatiayense* might be useful taxonomically. The fact that some species of *Eupatorium* have storied wood structure whereas others do not might be useful as a specific criterion, as might the presence or absence of resin-like compounds. Some potential distinctions must be questioned because they may be expressions of different degrees of juvenilism. For example, differing heights of uniseriate rays may represent early or late stages in ontogenetic breakup of rays into smaller segments.

Piqueria, segregated by Hoffmann (1890) into the subtribe Piquerinae on account of such features as absence of anther-tip appendages, shows no features of wood anatomy which do not also occur in *Eupatorium*, on the basis of the present study.

With respect to relationship of Eupatorieae with other tribes, those which show the greatest number of resemblances in wood anatomy include Vernoniaeae, Cynareae, and to a somewhat lesser extent, Inuleae. Features which can be considered pertinent in this regard include the range of intervacular pits from medium to small in size, the presence of relatively inconspicuous grooves interconnecting pit apertures in vessels, the presence of fine bands in association with these grooves, the paucity of uniseriate rays, the absence of storying in the majority of species, and lack of apotracheal parenchyma in most species. The majority of these features suggest a relatively low degree of specialization, for Compositae. This is entirely appropriate, for such features of Eupatorieae, Cynareae and Vernoniaeae as absence of ray flowers, imbricate arrangement of involucre bracts, and relatively unspecialized style branches are often regarded as primitive within the family. In assessing the value of data from wood anatomy to the taxonomic system, however, one is faced with the possibility that the resemblances listed may be as much an indication of similar levels of specialization as a criterion for interrelationships among these tribes.

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