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WOOD ANATOMY OF ANTHEMIDEAE, AMBROSIEAE, CALENDULEAE, AND ARCTOTIDEAE (COMPOSITAE)

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INTRODUCTION

This study of wood anatomy in the four tribes Anthemideae, Ambrosieae, Calenduleae, and Arctotideae brings to completion the tribe-by-tribe survey of wood anatomy of Compositae. The four tribes named have been grouped here for convenience only. A summary of trends in wood structure within the entire family and an analysis of their significance is presented in a following paper.

In the tribe Anthemideae, the genus *Artemisia* is represented by many woody species, a number of which are centered in western North America. The majority of these are shrubs which have adapted to conditions of aridity. Of the species studied here, some are restricted to California: *A. pycnocephala* (coastal central California), *A. californica* (cismontane California), and *A. rothrockii* (Sierra Nevada, Panamint Mts., and San Bernardino Mts.). Others extend from California desert areas into the Great Basin: *A. arbuscula*, *A. cana*, *A. ludoviciana*, *A. spinescens*, and *A. tridentata*. *Artemisia filifolia* is a Great Basin species extending into Arizona and Mexico. *Artemisia abrotanum*, *A. absinthium*, and *A. arborescens* are European species; *A. arborescens* occurs in Mediterranean areas. Three species are endemic to the Hawaiian Islands: *A. australis*, *A. kauaiensis*, and *A. mauiensis*.

Among the other Anthemideae studied here, *Athanasia parviflora* is native to South Africa, while *Eriocephalus africanus* occurs in southwestern Africa. *Santolina* is a genus of Mediterranean shrubs. *Tanacetum canum* is native to montane areas in the western United States.

Ambrosieae are often considered as a subtribe, Ambrosiinae, of Heliantheae. Indeed, wood of one species, *Hymenoclea salsola*, was described under that tribe earlier (Carlquist, 1958a). A different collection of *H. salsola* is included in the present study. Wood of *Ambrosia hispida* was studied in connection with other Compositae native to the Florida Keys (Carlquist, 1958b). Of the Ambrosieae in the present study, most belong to the genus *Ambrosia*, which is interpreted here in the sense of Payne (1964), who combined the genus *Fran-*

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seria with it. *Ambrosia* contains annuals, short-lived perennials, and small shrubs. Of the species studied here, *A. acanthicarpa*, *A. dumosa*, *A. eriocentra*, and *A. psilostachya* extend eastward from California into the Great Basin, or beyond. *Ambrosia chenopodiifolia* ranges from southern California into Baja California, and *A. camphorata* is a Mexican species. *Ambrosia hispida* occurs in tropical America, reaching into Florida. *Ambrosia artemisiifolia* and *A. trifida* are species native to temperate North America, now widely distributed as weeds; this is also true of *Xanthium strumarium*. *Dicoria canescens* is a species of the Colorado Desert, extending from California to Sonora. The genus *Hymenoclea* has a similar but wider distribution which includes Utah and Texas. *Iva axillaris* ranges from eastern California to Canada and Nebraska, whereas *Oxytenia acerosa* occurs from eastern California into New Mexico.

The Calenduleae represented here are all natives of South Africa, although the material of *Chrysanthemoides monilifera* was collected in South Australia, where this shrub is a weed. The Arctotideae of the present study are native to South Africa.

Species belonging to the tribes represented here have been studied by several workers in a scattering of papers. Diettert (1939) analyzed the wood of *Artemisia tridentata*, while Moss (1940) surveyed occurrence and nature of interxylary cork rings in *Artemisia*. Webber (1936) gives data on vessels and rays for one species each of *Ambrosia*, *Hymenoclea*, and *Artemisia*. Anomalous secondary thickening in *Osteospermum* is the subject of a paper by Adamson (1937). Assorted data on species of Anthemideae, Calenduleae, and Arctotideae are offered by Metcalfe and Chalk (1950) and Solereder (1908).

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

The methods employed here are the same as in earlier papers of this series (e.g., Carlquist, 1965). Most wood samples were collected in the field. I wish to thank Dr. Loran C. Anderson, Dr. Peter H. Raven, and Dr. William L. Stern for samples they collected, listed in table 1. Additional specimens were available from cultivated plants through the courtesy of Mr. Myron Kimmach, Huntington Botanical Gardens, San Marino, California; Miss H. Gerber, National Botanical Institute, Pretoria, South Africa; and the Los Angeles State and County Arboretum, Arcadia, California. Herbarium specimens document all of these collections, and are listed in table 1, together with herbarium abbreviations according to Lanjouw and Stafleu (1964). Portions of wood samples of many of these collections have been retained in the wood collection of the Rancho Santa Ana Botanic Garden. Some samples (Yw numbers in table 1) were kindly made available by the Samuel J. Record collection of Yale University.

Woods were sectioned by methods outlined earlier (Carlquist, 1965). Thanks are due Dr. Loran C. Anderson, Mr. James S. Henrickson, and Mr. Charles F. Quibell for sectioning some of the samples.

While many of the truly woody specimen in the four tribes are included here, many others which would have been suitable for study were not examined because of lack of availability. The results of the present study must be considered not as a detailed systematic survey but as a reconnaissance into types of wood structure and their significance within species of Compositae which are at least somewhat woody.

ANATOMICAL DESCRIPTIONS

Quantitative and qualitative characters are summarized in table 1. In addition, facts not easily given in tabular form are added under various headings in the text below. Conventions and symbols used in table 1 are as follows:

- ap = axial parenchyma (paratracheal in the species reported here)
- c = interxylary cork bands
- cb = coarse bands on vessel walls
- cg = continuous grooves connecting a helical series of pits on a vessel wall
- fb = fine bands accompanying grooves on a vessel wall
- ff = a few libriform fibers
- mv = more numerous vessels
- nv = narrower vessels
- sf = shorter libriform fibers
- sg = short grooves interconnection two or several pits in a helix on a vessel wall
- tf = thin-walled libriform fibers
- v = vessels
- vt = vascular tracheids
- 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.—The average diameter of vessels in *Anthemideae* is rather small, owing in part to the fact that these shrubs show marked change in diameter within a growth ring. Many very narrow vessels often occur at the end of growth rings (fig. 5, 7, 13, 15). Some of these are so narrow that they lack perforation plates and are thus vascular tracheids. Some species without prominent growth rings have rather narrow vessels, however (fig. 1, 3, 9). Especially wide vessels occur in many species of *Ambrosia* and other *Ambrosieae* such as *Dicoria canescens*, *Oxytenia acerosa*, and *Xanthium strumarium*. The *Ambrosieae* with vessels such as these may be termed rapidly-growing herbs. This is also true of *Arctotis cuprea* (fig. 21) and *Chrysanthemoides monilifera* (fig. 19).

An exceptional condition is provided by *Dimorphotheca cuneata* (fig. 30-33). In this species, vessels are notably narrow. Although a transection (fig. 30, 32) suggests narrow vessels mixed with fibers, very few fibers are in fact present. The narrow fibriform elements are actually either very narrow vessels or vascular tracheids, as examination of tangential sections (fig. 31, 33) and

TABLE 1. Wood Characteristics of Anthemideae, Ambrosieae, Calenduleae, and Arctotideae

SPECIES	COLLECTION		
ANTHEMIDEAE			
<i>Artemisia abrotanum</i> L.	Yw-23345	61	30.0
<i>Artemisia abrotanum</i> L.	Anderson 2889 (KSC)	61	30.5
<i>Artemisia absinthium</i> L.	Carlquist 1818 (RSA)	69	34.6
<i>Artemisia arborescens</i> L.	Yw-33853	73	39.9
<i>Artemisia arbuscula</i> Nutt.	Rumpel s.n. (KSC)	68	26.3
<i>Artemisia australis</i> Less.	Carlquist 1721 (RSA)	94	36.2
<i>Artemisia californica</i> Less.	Carlquist 497 (RSA)	73	43.2
<i>Artemisia cana</i> Pursh ssp. <i>bolanderi</i> (Gray) Ward	Anderson 2932 (KSC)	57	31.0
<i>Artemisia filifolia</i> Torr.	Detweiler 23 (F), Yw-26678	82	28.5
<i>Artemisia kauaiensis</i> Skottsb.	Carlquist 1648 (RSA)	78	41.2
<i>Artemisia ludoviciana</i> Nutt.	Anderson 2980 (KSC)	49	29.3
<i>Artemisia mauiensis</i> (Gray) Skottsb.	Carlquist 545 (RSA)	69	34.1
<i>Artemisia pycnocephala</i> DC.	Balls 19499 (RSA)	65	32.3
<i>Artemisia rothrockii</i> Gray	Anderson 2933 (KSC)	73	29.9
<i>Artemisia spinescens</i> D. C. Eat.	Carlquist 533 (RSA)	34	13.0
<i>Artemisia tridentata</i> Nutt.	Carlquist 1701 (RSA)	61	28.4
<i>Athanasia parviflora</i> L.	L A S.C.A. 55-S-2542	86	49.4
<i>Eriocephalus africanus</i> L.	Carlquist 1813 (RSA)	65	33.5
<i>Santolina chamaecyparissus</i> L.	Carlquist 1817 (RSA)	102	37.6
<i>Santolina virens</i> Mill.	Carlquist 1819 (RSA)	73	44.5
<i>Tanacetum canum</i> DC.	Anderson 2925 (KSC)	65	28.6

radial sections shows. Narrow vessels grade into vascular tracheids, so that a figure for average vessel diameter is impossible to obtain (table 1). A notably similar condition was observed elsewhere in Compositae in the case of *Loricaria* of the tribe Inuleae (Carlquist, 1961).

The figure for average vessel-element length for species in the four tribes indicates few species which show exceptionally long or short vessel elements. Relatively short elements characterize *Tanacetum canum* and several species of *Artemisia*; this suggests adaptation to xeric conditions. Shortening of vessel elements appears hastened in drier habitats (Webber, 1936). Vessel elements averaging less than 160 μ in length were considered to exemplify this trend in Helenieae (Carlquist, 1959). If this arbitrary figure is applicable in Anthemideae, thirteen of the *Artemisia* species studied could be said to show this

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- ∞	181	420	15.5	3	5	cg,fb	wv,mv		.43	129	4.0	+	—
1- ∞	119	350	14.2	2	5	cg,fb			.33		3.9	+	0
1- ∞	119	310	20.1	3-4	5	cg,fb			.47		13.4	+	0
1.67	162	331	20.0	3-4	5	cg,fb	wv	ff	.54	90	3.2	+	+
1- ∞	116	245	15.8	4-5	4	cg,fb	c,etc.	v,vt,c,ff	.37		4.5	+	—
1.70	127	265	21.2	3-5	5	cg	wv,ap	v,ap,sf	.39	87	4.5	+	+
3.65	107	347	29.2	3-5	4	cg,fb		v,ap	.32	59	4.5	+	+
∞	115	333	18.7	3	5	cg,fb	wv,mv	v,ap	.55		7.5	+	0
1- ∞	138	265	14.2	3-4	5	cg,fb	wv	v,ap,ff	.58		4.6	+	0
1.62	145	284	21.9	3	5	cg		v,ap,sf	.41	102	4.5	—	+
1.39	152	309	19.0	3	5	cg			.77	106	3.8	+	+
4.07	146	369	19.4	3	5	cg,fb	wv	v,ap,sf	.44	73	3.5	+	+
2.37	182	367	26.4	1-2	6	sg,cg			nearly	rayless		(+)	
1- ∞	152	408	19.2	3-4	5	cg,fb,cb	c,wv	v,ap,c,ff	.58		9.8	+	—
1- ∞	128	416	17.8	4	6	cg,fb	c,etc.	v,vp	.65		3.7	0	+
1- ∞	140	340	17.2	3-4	5	cg,fb	c,etc.	v,vp	.36		5.8	+	—
3.26	206	469	22.8	1-3	4	cg	wv,tf		.35	139	2.4	+	—
2.90	208	319	23.4	5-6	5	cg,fb	mv	ff	.73	130	3.7	+	+
1- ∞	183	432	23.8	3-4	6	cg	wv	ff,nv	.48	55	3.5	—	+
3.75	123	258	26.4	2-4	6	cg			.49		5.0	—	+
2.04	100	265	13.5	3-4	5	cg,fb	c,etc.	c	.50		5.2	+	+

trend. In the other tribes studied here, *Ambrosia eriocentra*, *Hymenoclea salsola*, *Xanthium strumarium*, *Osteospermum* spp. and *Arctotis* spp. may be mentioned.

Simple perforation plates characterize Compositae, although occasional multiperforate plates may be observed. These do not represent derivatives of scalariform perforation plates. In cases where the plate appears scalariform, the bars often run tangentially, not radially, and forked and otherwise misshapen bars are not uncommon. In the four tribes studied, multiperforate plates were seen in *Artemisia filifolia*, *Ambrosia artemisiifolia* and *Ambrosia trifida*. Metcalfe and Chalk (1950) list multiperforate plates for *Berkheya* and *Cullumia* of Arctotideae and *Tripteris* of Calenduleae.

Lateral-Wall Pitting.—The tendency for pits on lateral walls of vessels to

TABLE 1. Wood Characteristics of Anthemideae, Ambrosieae, Calenduleae, and Arctotideae (continued)

SPECIES	COLLECTION		
AMBROSIEAE			
<i>Ambrosia acanthicarpa</i> Hook.	Wolf 1372 (RSA)	90	53.0
<i>Ambrosia artemisiifolia</i> L.	Anderson 2982 (KSC)	90	57.5
<i>Ambrosia camphorata</i> (Greene) Payne	Carlquist 483 (RSA)	82	39.4
<i>Ambrosia chenopodiifolia</i> (Benth.) Payne	Raven 17032 (RSA)	57	33.8
<i>Ambrosia dumosa</i> (Gray) Payne	Carlquist 425 (RSA)	94	29.9
<i>Ambrosia eriocentra</i> (Gray) Payne	Stork 1622 (RSA)	86	29.2
<i>Ambrosia hispida</i> Pursh	Stern 282 (RSA)	90	40.1
<i>Ambrosia psilostachya</i> DC.	Johnston s.n. (POM)	71	32.9
<i>Ambrosia trifida</i> L.	Anderson 2979 (KSC)	122	73.4
<i>Dicoria canescens</i> T. & G.	Wolf 11182 (RSA)	171	84.0
<i>Hymenoclea monogyra</i> T. & G.	Raven 16677 (RSA)	94	32.3
<i>Hymenoclea salsola</i> T. & G.	Carlquist 1704 (RSA)	90	30.1
<i>Iva axillaris</i> Pursh	Pollard VII-24-1951 (RSA)	114	29.9
<i>Oxytenia acerosa</i> Nutt.	Wolf 9702 (RSA)	110	66.1
<i>Xanthium strumarium</i> L.	Anderson 2983 (KSC)	122	59.2
CALENDULEAE			
<i>Chrysanthemoides monilifera</i> (L.) T. Norl.	Carlquist 1065 (RSA)	122	52.6
<i>Dimorphotheca cuneata</i> Less.	H. Gerber 26 (PRE)	37	?
<i>Osteospermum ecklonis</i> (DC.) T. Norl.	Carlquist 1812 (RSA)	82	36.4
<i>Osteospermum</i> sp.	Carlquist 1815 (RSA)	61	33.7
ARCTOTIDEAE			
<i>Arctotis cuprea</i> Jacq.	H. Gerber 19 (PRE)	106	68.1
<i>Arctotis stoechadifolia</i> Berg.	Carlquist 1816 (RSA)	90	43.0

be crowded and altered in outline so as to form a honeycomb-like pattern was noted and illustrated earlier for *Hymenoclea salsola* (Carlquist, 1958a). Such pits are also characteristic of *H. monogyra*, *Oxytenia acerosa*, and *Xanthium strumarium*. Wide gaping pit apertures and elliptical pits were observed in vessels of lower stems of *Oxytenia acerosa*.

Most Anthemideae and a scattering of Ambrosieae, Arctotideae, and Calenduleae have grooves which interconnect pit apertures. Each groove is usually accompanied by raised margins, which form a pair of fine bands along the groove. These are illustrated here for *Eriocephalus africanus* (fig. 28) and, less conspicuously, *Dimorphotheca cuneata* (fig. 33). In *Artemisia*, grooves

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
1.69	192	340	17.6	2	5				.37	131	2.5	—	+
1.70	188	415	23.0	2-3	5				.75		3.1	+	+
2.91	230	428	22.3	6-7	4	sg, cg	wv, mv, ap	v, ap	.65		2.7	0	+
2.46	169	581	13.9	4-5	5	sg			.45	126	2.1	+	+
1- ∞	167	318	22.0	6	5	cg, fb	wv	nv, vt, ap, ff	2.25		4.4	0	+
1- ∞	143	326	19.6	4	5	cg, fb		wv	1.11		4.6	+	+
1.33	217	530	20.2	5	5	cg			1.73		4.4	—	+
5.15	254	510	20.9	3-4	4-5	sg, cg		wv	.93		4.3	—	+
2.04	224	571	20.3	1-3	5				1.32		3.5	+	+
2.31	215	410	31.1	2-3	6			ff	.95		3.5	—	+
1- ∞	212	367	19.6	2-3	5	cg, fb	wv	nv	.93	73	4.8	+	—
1- ∞	141	318	19.4	4	5	cg, fb	wv	nv	1.44		?	+	+
1- ∞	139	294	21.3	3	5	cg	wv	nv, ap	.68		<10	+	+
2.90	169	510	22.5	3-4	8	sg		ff	.88		5.6	0	+
4.26	145	420	20.6	2-3	7				.99	105	4.2	+	+
2.47	215	416	21.3	4-5	5	cg	sc		.32	93	3.0	+	+
∞	162	253	13.5	4	4	cg, fb			.37	166	2.9	—	+
5.47	121	294	24.8	3	4				.25	89	3.6	+	+
2.22	133	339	28.0	3-4	5		mv, wv		.45	106	4.2	+	+
2.23	128	326	31.1	4-5	5	cg			.80	101	4.0	+	+
4.82	129	388	26.2	1-2	5	cg			.69		5.0	+	+

and accompanying bands are most conspicuous in late wood vessels. The fact that these vessels are formed during drier portions of the year suggests that this form of helical sculpture may be regarded as a type of xeromorphy. By increasing surface area of the vessel walls—and thereby surface tension in the water film which contacts vessel walls—conduction under conditions of water stress may be aided. *Artemisia rothrockii*, which occupies markedly xeric habitats, has the most prominent bands and grooves in Anthemideae. In the various species of *Artemisia* with well-marked growth rings, the narrow vessels formed during drier portions of the year have more pronounced grooves and bands than do wider vessels formed under relatively mesic conditions.

Vessel Grouping.—Interesting tendencies in vessel grouping occur in *Artemisia*, providing a series in this regard unparalleled in Compositae except perhaps for *Baccharis* and *Olearia* (Carlquist, 1960a). A relatively low degree of vessel aggregation characterizes *Artemisia arborescens* (fig. 1) and *A. kauaiensis* (fig. 3). Larger groupings occur in *A. pycnocephala*, which has radial chains (fig. 9). Many species of *Artemisia* have vessels grouped into large bands of almost indefinite extent. In part these bands form almost exclusively the axial portion of late wood xylem, as in *A. filifolia* (fig. 5) and *A. cana* subsp. *bolanderi* (fig. 7). Extensive groupings can occur in early wood also, as in *A. arbuscula* (fig. 23). Diagonal strips of vessels also characterize these species with well-marked growth rings, such as *A. cana* (fig. 7) and *A. filifolia* (fig. 5).

Among other genera of Anthemideae, radial chains may be seen in *Athanasia parviflora* (fig. 11); aggregations into tangential bands in early and late wood occur in *Santolina chamaecyparissus* (fig. 15); and diagonal bands may be found in both species of *Santolina*.

In Ambrosieae, radial chains occur in *Ambrosia chenopodiifolia* and *A. psilostachya*. Grouping into pore multiples characterizes most species; two desert species, *A. dumosa* and *A. eriocentra*, have large aggregations, as do the two species of *Hymenoclea* and *Iva axillaris* (fig. 17). Grouping is moderate in most Arctotideae and Calenduleae; the near-exclusive presence of vessels and vascular tracheids in fascicular xylem in *Dimorphotheca cuneata* represents maximal vessel aggregation.

LIBRIFORM FIBERS

Some species of *Artemisia* have narrow thick-walled fibers. This is suggested in fig. 2 and fig. 5, and shown clearly in fig. 23. *Artemisia pycnocephala* (fig. 9, 10) has fibers which vary from thin-walled to very thin-walled. The latter kind of libriform fibers intergrades in shape and morphology with erect ray cells. Because erect cells characterize ray areas, near-identity between ray cells and libriform fibers may be said to produce a near-rayless condition.

Notably thick-walled fibers characterize *Tanacetum canum* (fig. 24), *Eriocephalus africanus* (fig. 25), and *Arctotis cuprea* (fig. 21, 22). Fibers are thick-walled in early-formed secondary xylem of *Santolina chamaecyparissus* (fig. 13, 14), but thin-walled in later-formed portions (fig. 15, 16).

An interesting case of fiber dimorphism is found in the Hawaiian species of *Artemisia*: *A. kauaiensis* (fig. 3, 4), *A. australis*, and *A. muiensis*. Shorter fibers (as they are termed in table 1) might well be regarded as axial parenchyma cells; they occur in wide strips, mostly related to vessels and vessel groups, as shown in fig. 3. These shorter fibers are clearly storied (fig. 4). Their tendency to be distributed paratracheally is understandable in terms of the extent of bands; vessels would inevitably be incorporated within these bands. A theory of fiber dimorphism was originated earlier by the writer (1958a, 1960b) to account for conditions observed in *Dubautia* and other Compositae. It is notable that this phenomenon is well represented in insular Compositae. In addition to *Dubautia* and *Wilkesia*, *Psiadia rotundifolia* of St. Helena Island shows this type of structure (Carlquist, 1960a).

Fig. 1-4. Wood sections of *Artemisia*.—Fig. 1-2. *Artemisia arborescens*.—Fig. 1. Transection, showing tendency to form inconspicuous growth rings; vessels do not form large aggregations.—Fig. 2. Tangential section. Wood anatomy is relatively unspecialized.—Fig. 3-4. *Artemisia kauaiensis*.—Fig. 3. Transection. Light areas which tend to run diagonally are parenchyma-like shorter fibers.—Fig. 4. Tangential section. Short fibers are mostly storied; ordinary libriform fibers may be seen at left (dark). (All, $\times 65$.)

AXIAL PARENCHYMA

In all four tribes represented here, axial parenchyma can be described basically as scanty paratracheal. Such parenchyma cells are inconspicuous, but are easily seen in fig. 23 and 24 because they are outlined by dark-staining resin-like compounds. In no species was axial parenchyma not observed, although it is scarce in *Dimorphotheca cuneata* (fig. 32). Relatively abundant vasicentric parenchyma was observed in *Artemisia californica*. Bands of axial parenchyma alternated with bands of tracheary elements in *Iva axillaris* (fig. 17). This mode of construction is apparently related to a growth form in which a thick, semi-succulent caudex bears upright branches. The upright branches possess thick-walled fibers and no parenchyma bands, whereas the basal caudex is parenchymatized. This was also strikingly demonstrated in *Oxytenia acerosa*. Such a mode of structure was observed in basal stems of *Hemizonia minthornii* and *Argyroxiphium caliginii* (Carlquist, 1958a). This might be an expression of fiber dimorphism considered in the preceding section.

In axial parenchyma of the species studied, parenchyma initials are subdivided into strands of one to three cells. In *Artemisia*, the strands are generally two-celled.

VASCULAR RAYS

Considerable diversity in ray histology may be seen within Anthemideae. In the genus *Artemisia*, heterocellular rays are exemplified by *A. arborescens* (fig. 2). In desert species, rays are composed mostly or exclusively of procumbent cells, as in *A. filifolia* (fig. 5) or *A. cana* (fig. 7). Predominance of erect ray cells characterizes the Hawaiian species, such as *A. kauaiensis* (fig. 4), and is represented in an extreme form by *A. pycnocephala* (fig. 10).

Uniseriate rays are rare to absent in many Anthemideae (fig. 2, 4, 6, 8, 10, 14, 16). Uniseriates could be said to be abundant only in *Athanasia parviflora* (fig. 12). Multiseriate rays often have uniseriate wings in this species. Relative abundance of uniseriate rays also characterizes Arctotideae (fig. 22) and Calenduleae (fig. 20). Uniseriates are scarce in Ambrosieae, such as *Hymenoclea monogyra* (fig. 18).

Metcalf and Chalk (1950) report raylessness for *Santolina chamaecyparissus*. This is true for smaller stems, but as secondary growth proceeds, a few multiseriate rays are formed (compare fig. 13 and 14 with fig. 15 and 16). This is also true in *Santolina virens*. Such an ontogenetic change is characteristic of many rayless woods (Barghoorn, 1941).

Rays exceeding 1 mm in height, reported for *Artemisia* by Metcalfe and Chalk (1950), are not unusual in this genus. However, as shown in table 1, average ray height in the species of *Artemisia* studied here is less than 1 mm. Of the species of Ambrosieae studied, however, nine have multiseriate rays which average nearly 1 mm or more in height, a fact which may be related to the greater herbaceousness of Ambrosieae compared with other Compositae. With the exception of *Hymenoclea salsola*, erect cells predominate in rays of Ambrosieae; this may be another aspect of herbaceous structure, in accordance with ideas of juvenilism in woods (Carlquist, 1962).

Fig. 5—8. Wood sections of *Artemisia*.—Fig. 5–6. *Artemisia filifolia*.—Fig. 5. Transection, showing end of one growth ring, beginning of another; note extremely narrow vessels closing growth ring.—Fig. 6. Tangential section. Libriform fibers (dark) and very narrow storied vessel elements may be seen.—Fig. 7–8. *Artemisia cana* subsp. *bolanderi*.—Fig. 7. Transection, showing two growth rings; some large groupings of vessels form diagonal bands.—Fig. 8. Tangential section. Rays are all multiseriate, are few in number and relative large. (All, $\times 65$.)

Ray cells vary from very thin-walled to thick-walled in the four tribes studied here. This can occur within a single ray, as in *Hymenoclea salsola* (fig. 27) and *Tanacetum canum* (fig. 24). The significance of this is not readily apparent, but it may bear some relation to splitting of stems into segments as the stem grows old, a characteristic of many desert shrubs. Some species have thin-walled ray cells exclusively, such as *Iva axillaris* (fig. 17), *Oxytenia acerosa* (lower stem), *Ambrosia acanthicarpa*, *A. artemisiifolia*, *Hymenoclea monogyra*, *Artemisia absinthium* (thin-walled at margins of some rays), *A. ludoviciana*, *A. rothrockii*, and *A. tridentata*. Notably thick-walled ray cells occur in *Artemisia abrotanum*, *A. cana* subsp. *bolanderi* (fig. 7), *Tanacetum canum*, *Ambrosia camphorata*, *A. chenopodiifolia*, *A. eriocentra*, *Hymenoclea monogyra* (fig. 18), and *Dimorphotheca cuneata* (fig. 31, 33). Rays composed mainly of thin-walled parenchyma cells but also containing nests of brachysclereids were observed in lower stems of *Oxytenia acerosa*.

Perforated ray cells were observed in *Osteospermum* sp. and *Artemisia californica*. The significance of perforated ray cells has been explored earlier (Chalk and Chattaway, 1933; Carlquist, 1960a).

Secretory canals have not been reported from most tribes of Compositae. They do occur, however, in rays of certain Anthemideae and Ambrosieae. Ray secretory canals have been observed in *Artemisia tridentata* and *Hymenoclea salsola* (Webber, 1936) as well as in *Ambrosia hispida* (Carlquist, 1958b). *Oxytenia acerosa* can be added to this list on the basis of the present study.

GROWTH RINGS

Of chief interest among the species studied here are the growth rings which incorporate formation of interxylary cork in certain species of *Artemisia*. Such cork was noted by Diettert (1939) in *Artemisia tridentata*, and cork bands in *Artemisia* was the subject of a paper by Moss (1940). Moss reports "some cork" in *A. longifolia*, *A. herriotii*, and *A. bigelovii*, whereas species having "regular and extensive development of cork" include *A. dracunculoides*, *A. pedatifida*, *A. spinescens*, *A. tridentata*, *A. nova*, *A. cana*, *A. rigida*, and *A. pygmaea*. The present study confirms the occurrence of cork bands in *A. spinescens* and *A. tridentata*, and to the list of species with "regular and extensive development of cork," *A. arbuscula* and *A. rothrockii* can be added. The growth ring phenomena of species with interxylary cork is complicated, and deserves detailed comment. The sequence of elements discovered here may be demonstrated by *Artemisia arbuscula* (fig. 23). This species shows the following sequence: wide vessels with paratracheal parenchyma + libriform fibers; resin-filled narrow vessels and vascular tracheids; large thin-walled interxylary cork cells; narrow thick-walled cork cells; intermediate-diameter vessels with paratracheal parenchyma; wide vessels with paratracheal parenchyma + libriform fibers. This same sequence was observed in *A. rothrockii*, *A. spinescens*, and *A. tridentata*. This sequence can be seen across a tangential section in fig. 29 (late wood narrow vessels above, early wood wide vessels at bottom). The elements designated "narrow thick-walled cork cells" in the sequence above provide an interesting problem, for they are apparently not mentioned by Diettert (1939) or Moss (1940). The figures by neither author show appearance of interxylary cork cells in longitudinal section. As shown in fig. 29, inter-

Fig. 9—12. Wood sections of Anthemideae.—Fig. 9–10. *Artemisia pycnocephala*.—Fig. 9. Transection. Thin-walled fibers predominate.—Fig. 10. Tangential section. Thin-walled libriform fibers intergrade with ray cells, so that limits of rays are difficult to define and a near-rayless condition results.—Fig. 11–12. *Athanasia parviflora*.—Fig. 11. Transection, showing end of growth ring near top (older elements below).—Fig. 12. Tangential section. Uniseriate rays are relatively abundant. (All, $\times 65$.)

Fig. 13—18. Wood sections of Anthemideae and Ambrosieae.—Fig. 13–16. *Santolina chamaecyparissus*.—Fig. 13–14. Sections from near center of an old stem.—Fig. 13. Transverse section, showing the rayless condition.—Fig. 14. Tangential section. Droplets of resin-like compounds are visible.—Fig. 15–16. Sections from near periphery of old stem.—Fig. 15. Transverse section, showing aggregation of vessels into prominent tangential and diagonal bands.

xylary cork cells occur in strands of two. The two-strand condition characterizes the narrow thick-walled cells as well as the "typical" cork cells. The thicker walls of the narrow cork cells may contain lignin, but their staining and resistance to wetting (note air bubbles in fig. 29) are indicative of suberization. These may be cells derived directly from activity of the vascular cambium rather than secondarily from phellogen within the xylem, the mode of origin described by Moss (1940) for the "typical" cork cells.

Interxylary cork cells of the narrow thick-walled sort proved to be present in *Tanacetum canum* (fig. 24), a species which lacks the wide thin-walled cells. Suberization of ray cells was observed in *Tanacetum canum* (fig. 24, top center). Suberization of ray cells was mentioned in *Artemisia* by Diettert (1939) and Moss (1940). This suberization is radially wider than the fascicular cork bands, and where growth rings are close together, rays may be suberized without interruption across several such bands.

Artemisia filifolia, not observed to have interxylary cork, has the following growth-ring sequence: wide vessels with paratracheal parenchyma + libriform fibers; narrow vessels and vascular tracheids; medium-diameter vessels with paratracheal parenchyma; wide vessels and paratracheal parenchyma + libriform fibers. This sequence is like the sequence given for cork-containing species above except for absence of the interxylary cork bands. In most species of Anthemideae and the other tribes studied here, growth rings take the form of presence of wider vessels, more numerous vessels, or both in early wood, with narrower and fewer vessels in late wood (table 1).

STORIED WOOD STRUCTURE

As indicated in table 1, storying is common in *Artemisia*. Where present, this does not extend to all fibers, although in the Hawaiian *Artemisias* all of the shorter fibers, which may be termed parenchyma, are storied (fig. 4). The relatively great length of libriform fibers as compared with that of the cambial initials from which they are derived prevents expression of storying, so that the storied pattern of cambia is demonstrated by vessels and axial parenchyma. Abundance of vessel elements and vascular tracheids in some species of *Artemisia* makes storying conspicuous, however, as may be seen in *A. filifolia* (fig. 6) and *A. cana* subsp. *bolanderi* (fig. 9). A moderate degree of storying may be seen in *Santolina chamaecyparissus* (fig. 16).

Ambrosieae are not noteworthy for storying, although this condition is clearly expressed in *Ambrosia dumosa*. This specialization may be related to the desert habitat which this species occupies. Storying is notably absent in the Arctotideae and Calenduleae studied.

ANOMALOUS GROWTH

Anomalous secondary growth in *Osteospermum* (including the species now segregated as *Chrysanthemoides*) was described by Adamson (1937) and need

—Fig. 16. Tangential section, showing a few libriform fibers (right), many vessels, and two small and inconspicuous rays.—Fig. 17. *Iva axillaris*. Transection of wood, showing (across center) band in which thin-walled parenchyma is present instead of tracheary elements.—Fig. 18. *Hymenoclea monogyra*. Tangential section, showing the prominent multiseriate rays composed of procumbent cells. (All, $\times 65$.)

Fig. 19—22. Wood sections of Calenduleae and Arctotideae.—Fig. 19–20. *Chrysanthemoides monilifera*.—Fig. 19. Transection, showing (from top to bottom) secondary xylem; parenchyma between bands; secondary phloem; secondary xylem.—Fig. 20. Tangential section through a band of phloem; sieve tubes appear dark.—Fig. 21–22. *Arctotis cuprea*.—Fig. 21. Transection, showing prominent rays, thick-walled fibers.—Fig. 22. Tangential section. Both multiseriate and uniseriate rays are present. (All, $\times 65$.)

not be described again in detail here. The only species in the present study in which anomalous growth occurs is *Chrysanthemoides monilifera* (fig. 19, 20). Any given successive cambium may extend around the entire stem in this species, or only limited areas of it. In each ring produced by a cambium, phloem areas are somewhat wedge-shaped; phloem bands are wider nearest each cambium (cf. also fig. 20, right), narrower distal to the cambium (fig. 20, left). Fibers are mingled with sieve-tube elements.

TYLOSES

Tyloses were observed in vessels in *Xanthium strumarium*.

RESINOUS DEPOSITS

Accumulations of resin-like compounds are exceptionally abundant in Anthemideae and Ambrosieae. These are present in the form of massive accumulations which fill cells, or droplets scattered over the wall surface, or both. The following modes of occurrence were observed in species of the present study:

Massive accumulations in at least a few vessels; massive accumulations or droplets also present in vessels and in other cell types as well: *Artemisia abrotanum*, *A. absinthium*, *A. arborescens* (fig. 1-2), *A. arbuscula* (fig. 23), *A. australis*, *A. cana* subsp. *bolanderi* (fig. 7-8), *A. kauaiensis* (fig. 3-4), *A. mauriense*, *A. rothrockii*, *A. tridentata*, *Eriocephalus africanus*, *Santolina chamaecyparissus* (fig. 13-16), *S. virens*, *Tanacetum canum* (fig. 24), *Ambrosia camphorata*, *A. chenopodiifolia*, *A. dumosa*, *A. eriocentra*, *A. hispida*, *A. psilostachya*, *A. trifida*, *Dicoria canescens*, *Hymenoclea salsola*, and *Chrysanthemoides monilifera* (fig. 19-20).

Droplets in vessels, fibers, and other cells: *Artemisia ludoviciana*, *Xanthium strumarium*.

Droplets in fibers: *Artemisia californica*.

Droplets in ray cells: *Artemisia spinescens*.

Carbonized resins present in intercellular spaces among ray cells: *Hymenoclea salsola* (fig. 27), *Iva axillaris*, *Oxytenia acerosa*.

Little or no accumulation of resin-like materials: *Artemisia filifolia*, *A. pycnocephala*, *Ambrosia acanthicarpa*, *A. artemisiifolia*, *Dimorphotheca cuneata* (fig. 30-33), *Osteospermum ecklonis*, *O. sp.*, *Arctotis cuprea*, *A. stoechadifolia*.

Exceptions to the above listings might be expected to be found if other specimens were examined; accumulation of resin-like materials within a species is probably only relatively constant.

CRYSTALS

Crystals are not common in Compositae, although some notable examples were observed in Mutisieae (Carlquist, 1957) and Astereae (Carlquist, 1960a). In the present study, crystals were noted only in Anthemideae from Africa. Small cuboidal and short prismatic crystals occur in ray cells of *Athanasia parviflora* (fig. 26). Each ray cell has one or two such crystals. A curious mode of crystal occurrence was observed in *Eriocephalus africanus* (fig. 25).

Fig. 23—29. Portions of wood sections of Anthemideae and Ambrosieae.—Fig. 23. *Artemisia arbuscula*. Transection, showing a prominent interxylary cork band; below the cork band, narrow vessels filled with resin-like materials may be seen.—Fig. 24. *Tanacetum*

In this species, small prismatic crystals occur in libriform fibers, but not in other cells. These crystals tend to occur in groups of two to eight in tips of the libriform fibers.

DISCUSSION

Relation of Wood Anatomy to Habit and Ecology.—The genus *Artemisia* is an excellent example of shift of wood patterns to suit particular climatic conditions. Although a boreal genus, it ranges from tropical conditions (Hawaiian Islands) to Arctic-Alpine habitats. Patterns of wood structure can be closely correlated with these various climatic regions.

The uniformity of a maritime climate is revealed in the wood of the Mediterranean species *Artemisia arborescens* (fig. 1–2). In this species, only a modest amount of growth-ring formation is present. *Artemisia arborescens* has a low rate of vessel grouping, vessel elements of moderate length, presence of both multiseriate and uniseriate rays, heterocellular rays, and relatively modest storying and helical sculpture on vessels. These features suggest lack of adaptation to extreme ecological conditions.

The Hawaiian species of *Artemisia* (e.g., *A. kauaiensis*, fig. 3–4) show a low degree of vessel aggregation, relatively little evidence of growth rings, heterocellular rays, presence of uniseriate as well as multiseriate rays, and moderate sculpturing on vessels. However, vessel elements are relatively short, and storying is prominent; these two features suggest the possibility of derivation of the Hawaiian species from a relatively specialized ancestor—perhaps a North American one. The presence of marked fiber dimorphism leading to a high degree of parenchymatization seems clearly related to the moderate Hawaiian climate. Similar fiber dimorphism is very characteristic of other Hawaiian Compositae, and Hawaiian lobelioids have wood rich in parenchyma. The reasons why parenchymatization should be a response to the Hawaiian climate are not clear, although one may note that the area of vessels in transection is small in the Hawaiian species compared with the abundance of vessels in xeric species. Production of a large volume of vessels is probably unnecessary in the Hawaiian climate, and substitution of parenchyma for tracheary tissue may reflect water relations. The highest degree of vessel aggregation was noted in *A. mauiensis*, which grows in the most extreme of the Hawaiian environments, rocky alpine slopes in Haleakala caldera.

canum. Transection, showing growth-ring phenomena. Ray is composed of cork cells (above) and sclereids (below).—Fig. 25. *Eriocephalus africanus*. Tangential section, showing libriform fibers containing small prismatic crystals, some of which are indicated by white pointers.—Fig. 26. *Athanasia parviflora*. Radial section, showing cuboidal and short prismatic crystals in ray cells.—Fig. 27. *Hymenoclea salsola*. Transection, showing rays composed of thin-walled parenchyma (above) and sclereids (below). Carbonized resin deposits (black) occur in intercellular spaces at ray margins.—Fig. 28. *Eriocephalus africanus*. Portion of vessel element from tangential section of wood. Pits are not visible owing to plane of focus, but grooves interconnecting pit apertures and raised margins (bands) beside grooves may be seen.—Fig. 29. *Artemisia arbuscula*. Margin of growth ring as seen in a tangential section. Between late wood vessels (above) and early wood vessels (below) are cork cells, subdivided into strands of two. Some cork cells show black because of air bubbles trapped in section, an artifact produced because cork cells are non-wettable. (Fig. 23, 24, 29, $\times 160$; Fig. 25–28, $\times 310$.)

Fig. 30—33. Wood sections of *Dimorphotheca cuneata*.—Fig. 30. Transection. Small diameter of vessels is evident.—Fig. 31. Tangential section. Multiseriate rays are present, but inconspicuous because walls are thick and cells are mostly erect.—Fig. 32. Transection, at higher power. Although both vessels and libriform fibers appear to be present, all axial elements shown in this photograph are vessels or vascular tracheids.—Fig. 33. Tangential

Artemisia californica illustrates an intermediate degree of specialization. Features related to extreme xeromorphism such as cork bands are and rays are heterocellular, with uniseriataes present. Vessels occur in groupings of intermediate size, and vessel-element length is quite short. Similar conditions may be found in *A. ludoviciana*. *Artemisia pycnocephala* (fig. 9-10) is an interesting adaptation to the maritime California climate. Specializations (other than those characteristic throughout Compositae) are few in this species, but several unusual features are present, such as the markedly erect ray cells, creating a near-rayless condition. Also very noteworthy is the average vessel-element length—the greatest in the species of *Artemisia* studied—and the thin-walled fibers. Rays, vessel elements, libriform fibers suggest (as does the habit of the plant) a juvenilism in *A. pycnocephala*. These features accord with the concept of paedomorphosis (Carlquist, 1962).

The remainder of the *Artemisia* species studied are mostly from desert and alpine conditions, and show a high degree of specialization: vessels ranging from intermediate to extremely narrow diameter; short average vessel-element length; grouping of vessels into bands and strips indefinite in extent; prominent grooves and bands on vessels; wide homocellular rays composed of procumbent cells; absence of uniseriate rays; and marked growth ring phenomena (incorporating interxylary cork). Features such as these make *Artemisia* an almost unequalled example of sensitive adaptation in wood characteristics to particular ecological conditions. The genus deserves detailed study in this respect, and the present data should be regarded only as a contribution toward such analysis.

The species of *Santolina* seem definitive examples of plants characteristic of the Mediterranean *macchi*. The occurrence of raylessness, together with rays composed almost exclusively of erect cells in later-formed secondary xylem, suggests juvenilism. Grouping of vessels suggests a moderate degree of specialization.

Athanasia parviflora (fig. 11, 12) suggests minimal specialization, as does *Eriocephalus africanus* (except for its prominent vessel sculpture, fig. 28). *Tanacetum canum* (fig. 24) corresponds in its wood characteristics to xeric species of *Artemisia*.

In Ambrosieae, most species could be considered herbs, and this is expressed in terms of wood anatomy. The relatively long vessel elements in certain Ambrosieae suggest juvenilism, as do the predominance of erect cells in rays and the very tall multiseriate rays. The heteromorphism in wood anatomy between lower caudex and upper branches in *Iva*, *Dicoria*, and *Oxytenia* is clearly related to the growth habit in these genera.

In Calenduleae, the occurrence of a wood in which prominently grooved vessels and vascular tracheids have been increased in abundance to the virtual exclusion of libriform fibers (*Dimorphotheca cuneata*, fig. 30-33) is interesting. This would be best interpreted as an adaption to physiologically xeric conditions. It is only one of several possible adaptations for xeromorphism,

section, at higher power. All cells are either ray cells, narrow vessels, or vascular tracheids. Fine grooves and bands are visible on the pitted tracheary elements. (Fig. 30, 31, $\times 65$; Fig. 32, 33, $\times 160$.)

which may explain why different types of wood anatomy occur in Compositae of xeric situations. One is tempted to offer an explanation for occurrence of anomalous secondary growth in certain species of Calenduleae, such as *Chrysanthemoides monilifera*. Without further study, speculations would be premature. Only a relatively few species of Compositae have anomalous secondary growth (Adamson, 1934, 1937), and it is possible that more than one evolutionary curriculum may account for these instances.

Taxonomic and Phylogenetic Relationships.—The sensitivity with which woods are adapted to particular ecological conditions must be kept in mind when assessing the value of wood anatomy to the taxonomic system. The wood characteristics of a genus may be a sort of expression of the ecological conditions tolerated by a genus. Divergence between two species with respect to wood anatomy may be not so much a measure of oldness of the separation between the species as it is an indication of the distinctness of their ecological requirements. This does not, of course, prevent taxonomic use of such divergences. Ecological adaptation presumably always guides evolutionary change in wood structure, but in *Artemisia* and similar genera we may be witnessing a "lack of conservatism" in which most specializations represent recent (and perhaps reversible) specializations, leaving few "old" wood characteristics as criteria for genera, sections of genera, etc. For example, Moss (1940) has shown that interxylary cork bands occur not in one, but in several sections of the genus *Artemisia*, and none of these sections possesses only species with cork bands.

The above discussion is intended to suggest that wood anatomy of Compositae is not likely to reward one with tribal or subtribal characters very often. Compositae all share a basically specialized wood plan, and the gamut between specialized and highly specialized has seemingly been exploited in a sensitive and "opportunistic" way many times within the family. One would expect that woods of ancestral members of each tribe would look very similar to each other.

These considerations do not rule out the occurrence of certain characters of systematic value within Anthemideae, Ambrosieae, Calenduleae, and Arctotideae. The presence of carbonized resins in intercellular spaces of rays seems to ally *Iva*, *Oxytenia*, and *Dicoria*. Occurrence of secretory canals in rays of both *Oxytenia* and *Ambrosia* is noteworthy. Patterns of crystal occurrence in *Eriocephalus africanus* and *Athanasia parviflora* are characters which may be of specific or generic value.

The interesting gamut of wood characters within *Artemisia* is certainly susceptible to systematic use. Presence of cork bands, occurrence of large vessel aggregations, fiber dimorphism, etc., characterize certain species. However, one must not construe these characteristics too broadly (for example, as mentioned, occurrence of cork bands cannot be used to delimit natural groupings within the genus). Two species of *Artemisia* in xeric environments might have similar woods, but the species might otherwise be distantly related.

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